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The role of urban habitats in the abundance of red squirrels (*Sciurus vulgaris*, L.) in Finland

Highlights

- The winter abundance of red squirrels is higher in urban than in forest habitats.
- Spruce crop size increase squirrel abundance.
- Feeding sites (+) and cats (-) affect squirrel abundance.
- Urban environments are an important alternative habitat for the declining red squirrel in Europe.
- The urbanization of squirrels can be monitored using citizen science based, large-scale winter surveys.

Abstract

Because the amount of urban areas has increased, it is important to investigate the abundance of wildlife species in relation to urban environments. Analyzing the impact of urbanization on the presence of forest-dwelling mammals is of interest due to the possible effects of urbanization on human-wildlife relationships and urban biodiversity. The Eurasian red squirrel (*Sciurus vulgaris*) is a declining forest species, and its occurrence in urban environments has been inadequately studied. The loss and fragmentation of forests due to urbanization may be detrimental for squirrels, whereas the abundant and predictable food resources and the low number of natural predators in urban areas may encourage squirrels to invade towns. We used large-scale data collected by volunteer bird watchers along a 950 km south-north gradient to study whether the winter abundance of squirrels in Finland is dependent on urbanization, while controlling for

effects of habitat type, food abundance (spruce cone crop; number of winter feeding sites), predator abundance (northern goshawk, *Accipiter gentilis*; feral cat *Felis catus*), season and latitude. We found that squirrel abundance increased with human population density, number of feeding sites and spruce cone crop and decreased with latitude and season. Feral cats showed weak negative connection with squirrel numbers, but there were no effect of goshawks. Relative squirrel abundance was approximately twice as high in urban habitats than in forests. Artificial feeding rather than a low number of predators may attract squirrels in urban environments. Planting spruce trees in urban environments will also benefit squirrels. Our results indicate that urban areas are an important habitat for the red squirrel even along the northern edge of their distribution range, where natural forest areas are still widespread. We conclude also that a citizen science -based bird survey protocol associated with mammal surveys seems to be a good large-scale monitoring method to study the urbanization of squirrels.

Keywords: winter feeding; mammals; monitoring; predation; urbanization, citizen science

1. Introduction

Globally, more people now live in urban than in rural areas, and at the same time, urbanized areas are increasing at an even higher rate than the urban population (UN, 2014). According to Seto et al. (2011), global urban land cover will increase approximately 30-fold by 2030. Therefore, understanding the impact of urban development on animal populations is important due to the possible effects on biodiversity and human-wildlife relationships (Baker and Harris, 2007; Bateman and Fleming, 2012). Urbanization is one of the most extreme forms of land-use alteration, and only remnants of the original habitats persist in towns. At the same time, urban

47 areas are characterized by high levels of predictable anthropogenic food resources and human-
48 caused disturbances (e.g., traffic), milder microclimates, and an altered abundance of predators
49 (e.g., Rebele, 1994; Shochat et al., 2006; Gilbert, 2012; Francis and Chadwick, 2013;
50 Tryjanowski et al., 2015).

51
52 Urbanization is globally recognized as one of the main threats to biodiversity (Wilcox and
53 Murphy, 1985). An important challenge for urban ecology is to conserve species that live in
54 urban environments. In addition, most of the contacts between people and nature occur in urban
55 environments, and citizen views related to conservation are formed in urban environments
56 (Lepczyk and Warren, 2012; Shanahan et al., 2014). Urban mammals have been used by urban
57 inhabitants for aesthetic, biological and recreational purposes (Adams, 2016). Unfortunately,
58 mammalian diversity generally decreases with urbanization (McCleery, 2010). However, the
59 behavioral flexibility of individuals and increased human tolerance might favor the urbanization
60 of some species (Baker and Harris, 2007; McCleery, 2010; Lowry et al., 2012).

61
62 Natural environments that are modified by human activities possess challenges to native animals.
63 During recent decades, many new mammalian species, such as the European red fox (*Vulpes*
64 *vulpes*, L.; Francis and Chadwick, 2012), raccoon (*Procyon lotor*, L.; Adams, 2016), and
65 Eurasian badger (*Meles meles*, L.; Harris, 1984) have colonized urban areas. Some of them (e.g.,
66 the red fox) currently have even higher densities in urban areas than in their natural habitats
67 (Bateman and Fleming, 2012). However, only a few mammal species, such as the brown rat
68 (*Rattus norvegicus*, Berkenhaut) and the house mouse (*Mus musculus*, L.), are abundant in town
69 centers (Gilbert, 2012).

Urban areas have some features, such as stable and abundant food resources and low numbers of natural predators that may attract wildlife and promote, for example, the urbanization of squirrels (Francis and Chadwick, 2013; Adams, 2016). Artificial feeding stations and waste offer easily available food resources, especially to species feeding on seeds or having a generalist diet (Adams, 2016). Although feeders in gardens are primarily designed to feed birds, they also attract squirrels in urban areas, especially during the winter when food resources may become scarce in forest habitats. In general, urban areas contain a lower number of larger natural predators than do rural areas (Bateman and Fleming, 2012), but the abundance of medium-sized carnivores might be even higher in urban environments than in more natural environments (Nilon and Pais, 1997; Baker and Harris, 2007; Bateman and Fleming, 2012). However, at the same time, urban squirrels may be more vulnerable to predation by domestic cats than are squirrels living in rural and forest areas (Wauter et al., 1997; Shuttleworth, 2001; Magris and Gurnell, 2002). It is likely that there is an optimal level of human influence at which the living requirements for a species are best met or limit the level of urbanization that a species can tolerate (Francis and Chadwick, 2013; Adams, 2016). However, the roles of artificial food and the number of predators promoting the urbanization of squirrels are still not well known.

Arboreal squirrels (*Sciurus* spp.) are strictly dependent on forests. Therefore, they might be sensitive to the forest loss caused by urbanization. However, urban areas also contain different types of green spaces, such as remnant habitat patches, cemeteries, public parks and the gardens of residential areas, which may be suitable living environments for many forest species (Adams, 2016). For example, squirrels can also inhabit fragments of forests within the urban matrix (Veerboom and Abeldorf, 1990; Baker and Harris, 2007; Babińska-Werka and Żółw, 2008;

Parker and Nilon, 2012; Mäkeläinen et al., 2015; Fey et al., 2016). The red squirrel (*Sciurus vulgaris*, L.) is a native forest specialist species in most European countries, and although the species still is common throughout most of its range (Gurnell and Wauters, 1999), its current population is declining in many parts of Europe (Gurnell and Pepper, 1993; O 'Teangana et al., 2000; Bertolino and Genovesi, 2003; Shar et al., 2008; Selonen et al., 2010). Most previous red squirrel studies were conducted within forest or agricultural areas and considered the effects of fragmentation on the red squirrel at a relatively small local scale. These studies indicated that red squirrel occurrence and abundance increase with woodland size (Celada et al., 1994; Verbeylen et al., 2003) and the area of woodland covered by coniferous trees (Veerboom and Abeldorf, 1990) but decrease with the distance from the nearest source area (Veerboom and Abeldorf, 1990; Celada et al., 1994; Verbeylen et al., 2003).

Only a few red squirrel studies have been conducted within urban areas despite the fact that the species is currently quite common in urban habitats in Europe (Luniak, 2004; Babińska-Werka and Żółw, 2008). One local study conducted in Brussels indicated that patch size and patch quality have positive effects and that isolation has a negative effect on red squirrel patch occurrence in urban areas (Verbeylen et al., 2003). A study in Warsaw parks also indicated that park size positively affects red squirrel abundance (Babinska-Werka and Zolow, 2008). However, large-scale studies with multiple study sites and covering different habitats are needed to better understand the urbanization process of red squirrel. In addition, as squirrels are important dispersal agents of seeds (Steele, 2008), they may also impact on distribution of urban trees. Therefore, it is important to know how urbanization influence squirrel abundance.

The main aim of this study was to analyze how human density affects the winter abundance of red squirrels throughout Finland. The analysis included also habitat type, natural (size of the Norway spruce cone crop) or artificial (number of feeding sites) food abundance, and natural (northern goshawk, *Accipiter gentilis*, L.) or human-associated (feral cats, *Felis domesticus*, L.) predator abundance. In addition, we also studied whether latitude and the time of the winter season affect the squirrel abundance. We conducted our study during the winter season because winter is a critical period for the survival of squirrels in the northern latitudes (Selonen et al. 2015), and because due to the lack of leaves in the broad-leaved trees, the detectability of squirrels is high during winter (Hernández, 2014). We predicted that if squirrels somehow benefit from humans, then their abundance should increase with human density and should be higher within urban than other habitat types. If food resources, either artificial or natural, have an effect then squirrel abundance should increase with the number of feeding sites or with the size of the Norway spruce cone crop. If squirrel winter abundance is dependent on predators, then their abundance should change with predator abundance. Because the severity of winter increases toward the north, we predicted that red squirrel abundance would decrease from the south to the north. Due to winter mortality, we predicted that squirrel abundance would decrease during the winter. However, the squirrel abundance could also increase towards to the spring, because the visibility of squirrels increases due their early-starting mating season.

2. Methods

2.1. Study area

139

140 The study was conducted in Finland along an approximately 950 km south-north gradient
141 (Appendix 1; between 59°50' and 68°40' N and 19°40' and 30°20' E). The human population of
142 Finland was 5.5 million in 2014 with a mean population density of 18/km² (Statistics Finland,
143 2015). The majority of the human population is concentrated in the southern part of the country
144 (approximately 170 inhabitants/km²), whereas the population density is the lowest in the north
145 (approximately 0.2 inhabitants/km²; Statistic Finland, 2015). Approximately 78% of the total
146 area of Finland (390,906 km²) is land covered (Statistics Finland, 2015), and approximately 77%
147 of this is forests, 9% is agricultural areas and only 4% is built-up areas. Almost the entire country
148 belongs to the boreal taiga forest terrestrial biome, where forests are dominated by coniferous
149 trees. The study area lies within the cool boreal climate zone.

150

151 The study was conducted during the winter season. The average monthly temperature during
152 mid-winter in December 2014 (study year) was -1.3°C (1981–2010 long-term average -3.2°C) in
153 southern Finland (Helsinki) and -8.4°C (-11.7°C) in northern Finland (Sodankylä; Finnish
154 Meteorological Institute, 2014). The corresponding amounts of snow cover on the 15th of
155 December were 4 cm (1981–2010 long-term average 6 cm) in Helsinki and 32 cm (1981–2010
156 long-term average 36 cm) in Sodankylä. The coniferous tree cone crop, the primary food of the
157 squirrels, was moderate during the studied winter (Finnish Museum of Natural History, hereafter
158 FMNH).

159 *2.2. Study species*

160 The red squirrel occupies the boreal and temperate areas of Eurasia and is mainly a coniferous
161 forest specialist (Shar et al., 2008). Individuals live in the same home ranges throughout the year,

although they may move between habitats depending on the food situation (Wauters and Dhondt, 1992). In Finland, urban squirrels were first observed in the southern part of the country in the cities of Helsinki and Turku in the early 1930s (Haapanen, 1999).

The main natural food of the red squirrel is seeds of coniferous trees; in Finland, these are mainly Norway spruce seeds (*Picea abies*, Karst) (Helle, 1996; Selonen et al., 2015). The main predator of the red squirrel in Finland is the northern goshawk (Selonen et al., 2010, Sulkava et al., 2014). In some other countries, red foxes and feral cats are also important squirrel predators (Loss et al., 2013).

2.3. Field data and sampling

Earlier mammal survey monitoring in Finland has been based on wildlife transect route and triangle surveys conducted outside urban environments and coordinated by the Finnish Game and Fisheries Institute (currently the Natural Resources Institute Finland; Lindén et al., 1996). Due to the restrictions of the triangle surveys (no data from urban areas), we used data collected by bird watchers during the Finnish winter bird surveys (Koskimies and Väisänen, 1991). A similar approach combining avian and mammal surveys has also been used in the UK (Battersby et al., 2004). Since the winter of 2014/2015, the number of mammals (individuals/10 km transect route) has also been counted during the Finnish winter bird surveys.

The Finnish winter bird surveys consist of transect routes with an average length of approximately 10 km (Koskimies and Väisänen, 1991). Birds and mammals are surveyed along the same transect route three times per winter: early winter (1–15 November), mid-winter (25

December to 7 January) and late winter (21 February to 6 March). The yearly surveys are organized by the FMNH and are conducted by volunteer birders (610 during the studied winter of 2014/2015). The participants can identify all winter birds and their calls. Thus, the observers are skilled in species identification, and since the red squirrel is very easy to identify, there should not be any differences between observers in ability to identify the target species of this study.

The location of a transect route is selected freely by the volunteers, but the coordinator of the surveys, the FMNH, ensures that the transect routes do not overlap. In this study, 355 transect routes (279 surveyed during the early winter, 279 surveyed during the mid-winter and 258 surveyed during the late winter) with a total of 7,789 transect route kilometers (2,651 early winter km, 2,669 mid-winter km and 2,469 late winter km) were surveyed during the winter of 2014/2015. The spatial distribution of the mid-winter (25 December to 7 January) survey transect routes is shown in Appendix 1. The transect route is counted by walking during midday under good weather and light conditions. When counting, the counter walks slowly, stops and listens, and records observation notes. The survey cannot last longer than the duration of daylight in mid-winter, that is, for example, approximately 4 hours in northern Finland. At each route the survey time is kept about the same in all three survey periods. Note that no vehicles are used in the surveys. The proportion of each habitat type along the route is estimated in advance from the maps and air photos, and ground-checked in the field during the surveys. When the route runs along a border of two habitats, the length is halved between them. Habitats along the route are classified into eight categories within an accuracy of 100 meters: (a) dumping ground or fur farm (data in this study: 11 km of transect routes); b) urban settlement (construction zones, town

centers, private homes with gardens, urban parks, etc.; 2003 km); c) rural settlement (widely dispersed buildings within agricultural landscapes; 1233 km); d) arable land (897 km); e) forest (2812 km); f) clear-cut area or stand of saplings (262 km); g) reed bed or shore scrub (150 km); and h) other (including also over-flying individuals; 421 km). Thus, the distribution of transect routes is somewhat concentrated near human settlements, but the sample size outside these areas is also substantial (e.g., >2800 km in forests). All observed squirrels, northern goshawks and feral cats (either seen or heard at an unlimited distance; note that no snow tracks are included in the data) are placed in one of the eight habitat categories in the field. For example, one route may consist 8000 meters of urban and 2000 meters of forest habitat including four squirrels observed in urban and one squirrel in forest habitat type. The observers also count the number of winter feeding sites in each of the above-mentioned habitats and estimate the size of the Norway spruce cone crop in trees along the transect routes during the each survey (six cone abundance categories; from 1 = no cones to 6 = very abundant cone availability; note that only the fresh cones are used to do this estimation). Because the methods do not allow density estimates, an index of relative abundance (individuals/10 km transect route) is used in this study. A more detailed description of the survey protocol is given elsewhere (see Koskimies and Väisänen, 1991, Lehtikoinen et al., 2013; Fraixedas et al., 2015).

2.4. Human densities

The human densities (inhabitants/km²) around the survey transect routes were estimated using the coordinates of the transect route and the human density register of Statistics Finland provided by the IT Center of Science ([https://sui.csc.fi/applications/paituli\(PalTuli/index-html\)](https://sui.csc.fi/applications/paituli(PalTuli/index-html))). We placed a rectangle around the survey transect route based on the southernmost, northernmost, easternmost and westernmost location of the transect route. Based on the human density register, we estimated how many people live inside this rectangle and used it as a proxy for the human density around the survey transect route. This work was conducted using the ArcMap 10.3.1 software (Redlands, California, USA).

2.5. Statistical analyses

We conducted analyses at two scales. In the first analysis, we investigated which factors influence transect route-specific squirrel numbers at the large landscape level using transect route-specific variable values. In the second analysis, we used more detailed data within the transect routes to investigate the habitat selection of squirrels using habitat-specific transect route sections. The first analysis was only possible using 285 routes where the exact location of the route was available and we were thus possible to calculate the human densities around the route. In the second analyses all 355 routes were included.

First, we evaluated the transect route-specific values of squirrel number using generalized mixed effect models, where the transect route-specific number of observed squirrels was explained using the length of the transect route, the survey season (categorical variable), the latitude and longitude of the transect route, the linear and quadratic effects of human density (log

transformed), and the abundance of winter feeding sites (log transformed) and predators (goshawks and feral cats). The length of the transect route accounts for the fact that the lengths of the transects vary between routes. The quadratic effect of human density accounts for the possibility that squirrel numbers can experience, e.g., a peak or drop in areas of average human density. We also included an interaction term between latitude and human density as well as human density and abundance of feeding sites in the analyses. These can take into account that impact of human density can depend on latitude and feeding may affect squirrel numbers differently in areas of high and low human densities. The transect route ID was used as a random factor because most of the transect routes were surveyed during all three winter sub-seasons. Length of the route, coordinates and census season were included in all the models, but otherwise we used all model combinations of used variables. Altogether, this produced 56 different model combinations. The length of the transect route (continuous variable), latitude (continuous variable), longitude (continuous variable) and survey season (categorical factor variable) were included in all models and thus formed the base model. The numbers of predators (goshawks and cats) and winter feeding sites were transformed into relative abundances (number of animals or feeders per 10 survey kilometer).

Second, we investigated the habitat-specific values of squirrel numbers using generalized mixed effect models. For this analysis, we split the transect routes into sections based on eight different habitat categories (see section 2.3. Field data). Habitat was used as eight categorical factor variable and forest habitat was used as a reference category. In this analysis, the squirrel numbers were explained by the length of the transect route section (continuous variable), habitat type of this transect route section, survey season (categorical factor variable), latitude of the transect

route (continuous variable), abundance of winter feeding sites in the transect route section (continuous variable) and relative abundance of spruce cones along the full transect route (continuous variable). Like in the first analysis, the ID of the transect route was used as a random factor in the analysis. The length of the transect route section, latitude and census season were included in all models and thus formed the base model. In this analysis, the habitat-specific squirrel abundance was compared to that in the forested areas. In addition, we tested whether detection probability might be season dependent between natural and urban areas by adding an interaction between season and habitat. Altogether, we built 9 different model combinations.

Both analyses were conducted using the stepwise procedure. First, using the full model, we measured which distribution models, (i) Poisson, (ii) zero-inflated Poisson, (iii) negative binomial or (iv) zero-inflated negative binomial distribution, best fit the data. Second, among these four alternatives, we used the best of the top-ranked distributions in the full set of candidate models. We used the Akaike information criterion (AIC hereafter) to perform model selection (Burnham and Anderson, 2002).

All analyses were conducted in R version 3.2.2 (R Development Core Team, 2013) and models were fitted using glmmadmb-package. When analyzing spatial data, it is possible that autocorrelation of variables may bias the results. The potential spatial autocorrelation of residuals of the best model was investigated by using the ncf-package in R. No spatial autocorrelation was found from the residuals of the best models. Also multicollinearity among explanatory variables may have confounding effects on results. In our case, there was no strong correlation between the explanatory variables. The maximum Pearson's correlation coefficient

was always below 0.5 (Booth et al. 1994), except in the case of human densities and quadratic effect of human densities. In this case only one of these two variables were used at time.

3. Results

Altogether, 1781 squirrels were observed along the transect routes across all seasons (early winter 785, mid-winter 448, late winter 548). The relative squirrel abundance, feeding sites, goshawks and cats in the different habitats are shown in Table 1. In general, the relative squirrel abundance was lower in forest (1.43 individuals/10 km transect route) than in rural (4.00 individuals/10 km transect route) or urban (4.24 individuals/10 km transect route) habitats. In addition, the number of feeding sites per 10 km transect route was lower in forest (0.72) than in rural (19.46) or urban (18.26) habitats. The relative abundance of northern goshawks in urban areas (0.57 individuals/10 km transect route) was approximately twice as high as in forest (0.27) or rural (0.22) habitats. Approximately twice the number of feral cats was observed in rural (0.66 individuals/10 km transect route) than in urban habitats (0.30), whereas only one cat was observed in the forest habitats (Table 1).

In the transect route analyses, the zero-inflated negative binomial models were top-ranked in the first model selection step (results not shown). In the second step of the transect route-specific analysis, the top-ranked model included the length of the transect route, latitude, longitude, season, abundance of feral cats, quadratic effect of human density and abundance of feeding places and their interaction. The other model within 2 Δ AIC of the best model included these

same variables, but also interaction between quadratic human density and latitude (Table 2). However, since this interaction was not significant this variable can be considered as uninformative parameter (*sensu* Arnold 2010) and only the top ranked model was investigated later on. The number of squirrels increased with the increasing length of a transect route, quadratic effect of human density (Fig. 1a) and abundance of feeding sites (Fig 1b) and decreased with increasing latitude (Table 3). The significant negative interaction between quadratic human population and abundance of feeding sites suggest that feeding increased squirrel numbers more in areas where there was lower human densities (Table 3). There was also tendency that abundance of feral cats decreased squirrel numbers (Table 3). The relative squirrel abundance was significantly lower during the mid-winter and late winter counts than the early winter counts. The abundances of goshawks was not significantly associated with squirrel numbers (Table 2).

In the habitat-specific analyses, the negative binomial models were top-ranked in the first model selection step (results not shown). In the second step of the habitat-specific analysis, the full model was clearly the best model (Table 4). This top-ranked model included the length of the transect route, latitude, season, habitat, number of feeding sites and spruce cone crop. Based on the top-ranked model coefficients, transect route length, most habitat types, abundances of feeders and the size of the Norway spruce cone crop and seasons differed significantly from zero (Table 5). The highest abundances were observed in urban and rural settlements, where the relative squirrel abundances (approximately 4 squirrels per 10 km transect route) were significantly higher than those in forests (approximately 2 squirrels per 10 km transect route) or other habitats (0-1 squirrels per 10 km transect route; Fig. 2a). In contrast, the relative abundance

of red squirrels in arable land and reed beds was significantly lower than that in forests (Fig. 2a, Table 5). In addition, the relative squirrel abundance increased with increasing transect length, number of feeders and number of spruce cones (Table 5; Fig. 2b). As in the transect route-specific analysis, the relative squirrel abundance decreased from early winter to the mid-winter and late winter (Table 5).

4. Discussion

Our analysis indicated that red squirrel abundance increased with human density. The relationship between squirrel abundance and human density was nonlinear, as squirrel abundance increased more rapidly in areas with the highest human densities. Our habitat-specific analysis further showed that the squirrel abundance was significantly higher in urban and rural settlements than in other habitats, such as forests. These results suggest that the wintering red squirrels benefits from urbanization.

We found a higher red squirrel abundance in urban and rural settlements than in forest habitats. Red squirrels inhabited urban habitats similarly in different parts of Finland, as indicated by the non-significant interaction term between latitude and human density. Therefore, the urbanization of the red squirrel in Finland appears to be in a phase in which no geographical difference in the level of urbanization can be seen. It has been concluded that the spread of urbanization in different geographical regions depends on whether urbanization in different cities occurs independently or through the migration of urbanized individuals from one city to another (Evans et al., 2009, 2010, Fey et al., 2015). In the case of the red squirrel in Finland, the process of how

different cities have become urbanized remains unknown, but it is known that the arrival of squirrels to urban areas began in the southwestern cities of Finland approximately 90 years ago (Haapanen, 1999). The population dynamics of urbanized squirrels remain unclear in our study. However, the squirrels abundances observed in this study should reflect the local population size, because dispersal distances of red squirrels are short, usually 1-2 km, although occasionally even 10-20 km moved distances can be observed (Selonen and Hanski, 2015). In other words, squirrels in our study areas likely do not make migrations between urban and rural areas (Selonen & Hanski 2015, Fey et al. 2016) but the abundances observed here reflect the local population size. In Warsaw, Poland, it is observed that red squirrel abundance has increased threefold from 1956 to 2000 in the urban areas (Babinska-Werka and Zolow, 2008). In our study, squirrel abundance decreased toward the north (both in rural and urban habitats), a trend that could be expected because the productivity of forests declines and winter harshness increases toward the north.

Squirrel abundance was greatest in areas with the highest human population density. Because we evaluated human density at a relatively coarse scale, we cannot compare squirrel abundance, for example, between town centers and suburban areas. In general, the amount of woodlands decreases with increasing human density, but parks with trees are common in Finland, even in town centers. Red squirrels may survive quite well within these urban areas (Fey et al., 2016). However, it is fair to suppose that squirrel abundance is higher in suburban areas than in more urbanized areas because winter feeding is more common in these residential private-house areas than in urban core areas (Väisänen, 1999).

One factor related to the high squirrel abundance observed in urban areas could be winter feeding. Our study indicated that squirrel abundance increased with the number of winter feeding sites. Many mammal species living in urban areas use feeding sites. According to the results of the Finnish winter feeding site study program 1988/89-1998/99, almost all (about 40) Finnish winter-active mammal species are detected in the feeding sites ($n = 455$ sites), and the red squirrel is the most common mammalian species occurring at 71% of these sites (Väisänen, 1999). Our results indirectly indicated that squirrels are more able to utilize feeding sites in areas with a lower human density. Therefore, putting artificial feeders in natural areas may be a good management option. Supplemental food provided by humans is one possible reason why squirrels have urbanized. Likely because of artificial feeding, escape distances of squirrels have declined, and they have become tame (Luniak, 2004; Parker, and Nilon, 2012; Uchida et al., 2015). In addition, behavioral flexibility may be one reason for the success of some mammal species, such as squirrels, in urban environments (Bateman and Fleming, 2014).

Previous studies have indicated that winter feeding may be beneficial, e.g., for the grey squirrel (e.g., Bonnington et al., 2014). Winter feeding and anthropogenic waste offer great and predictable food resources for animals, especially during the winter period and years when the main food sources of squirrels, i.e., the seeds of conifers, are scarce. For example, Verbeylen et al. (2003) found that patches with supplementary feeding had a higher probability of being occupied by the red squirrel. Winter feeding has apparently helped squirrels adjust to urban and suburban habitats. Feeding wildlife is widespread and have a many impacts on the wildlife (Orams, 2002). While many previous studies have suggested artificial feeding have positive effects especially on birds (Siriwardena et al., 2007; Harrison et al., 2009), some other papers

have also indicated its risk (Jones et al., 2008). Currently, negative aspects of supplemental feeding have been actively discussed in urban areas (Galbraith et al., 2015), for instance, animals aggregated by artificial feeding could be more vulnerable to pathogen transmission (Bradley, and Altizer 2006). Also, the possibility of ecological traps may be worth to consider (Robertson et al., 2013; Hanmer et al., 2017). However, there are also psychological benefits of the wildlife for the humans, enhanced by artificial feeding (Orams, 2002).

Our results indicated that squirrel abundance increased with the spruce cone crop. This is not a surprising result since spruce seeds are main food for the red squirrel (Gurnell and Wauters, 1999; Selonen et al., 2015). Favoring spruce trees will likely increase the living possibilities of squirrels in urban environments. We note that our study year had a moderate spruce cone crop; thus, crop failure did not push animals to feeders in urban areas. Bowers and Breland (1996) and Petty et al. (2003) also indicated that food availability (either artificial food or conifer seeds) is the main factor limiting the number of tree squirrels. However, because previous studies have indicated that the squirrel numbers in winter follow spruce cone production in Finland (Selonen et al., 2015), multi-year surveys are needed to study the role of artificial feeding for squirrels in a more detailed way. For example, it may be that feeding sites are even more important for squirrels during poor cone years than during those years with average cone production, as in our case. However, Reher et al. (2016) found that food provision in semi-urban habitat had positive effect on red squirrels also in years when natural food sources were available. One factor that might promote the urbanization of squirrels is the so- called “urban heat island” phenomenon (Adams, 2016). Animals living in warmer conditions may survive with less energy than

individuals occupying in colder environments. Unfortunately, we had no data to analyze this topic, but it might be a relevant topic for further study.

Earlier studies have suggested that predator presence, but not food supplementation, affects red squirrel abundances in forest habitats during winter (Selonen et al., 2016). Some studies have indicated that urban areas have few predators, which may support the urbanization of some species (Bateman and Fleming, 2012). However, in our case, the main squirrel predator in our areas, the goshawk, was more abundant in human-dominated areas than in forest habitats. This result is affected by the fact that many goshawks (especially juveniles) migrate to cities in winter in Finland. In any case, urban environments can no longer be considered predator-free areas for red squirrels. Similar to our study, other studies have also indicated that predators, either natural or human-associated, have no role in relative squirrel abundance (Bateman and Breland, 1996; Petty et al. 2003). Our results indicate that amount of feral cats can limit squirrel numbers. Also many earlier studies have indicated the harmful impact of the non-native cat predation on native animal fauna in general (Moseby et al., 2015; Adams, 2016) and also on squirrels (Baker et al., 2005). Limiting cat numbers could help squirrel populations in urban and rural areas.

We must stress that we were not able to control for the detectability of squirrels in different seasons (Hernández, 2014) and habitats (see e.g. Amori et al., 2011), and this may have partly affected our results. For example, detectability of squirrels has been reported to be higher in late autumn and winter than summer or spring because dense foliage decreased the detectability of squirrels during summer (Hernández, 2014). We detected the lowest relative squirrel abundance during the mid-winter, indicating an increase towards the end of winter. Towards to early-spring

(i.e. late winter season in our case) day length becomes longer and the activity of squirrels would also increase partly due to mating activities. The detectability of the red squirrel may be either higher in human-dominated habitats than in more natural habitats due to the attraction to artificial feeders, less hiding places (e.g. tree cavities, dense woods) or changing individual personalities (bolder in urban habitat; Lowry et al., 2013), or the detectability of squirrels may also be low in urban environments because buildings decrease detectability of squirrels (our personal observations). However, the detectability of squirrels may be higher in open rural areas than in more closed forest and urban habitats, which may partly explain the high squirrel abundance in the rural landscape. In any case, supporting our results, previous studies have indicated that squirrel densities are lower in rural than in urban environments (Babińska-Werka and Żółw, 2008; Dozières et al., 2012). In addition, we tested whether detection probability might be season dependent in urban areas compared to more natural areas, by testing the effect of interaction between season and human population size. This interaction was not significant.

We used mammalian data collected by the volunteer bird watchers during their winter bird surveys. This citizen science-based survey and monitoring method has several benefits. First, the winter bird transect routes also cover urban environments, which are lacking in Finnish wildlife monitoring efforts. Second, a large number of bird watchers can collect mammalian data from large areas. The use of volunteer-based annual monitoring enables the production of long-term datasets of the distribution and population trends of many mammalian species (Battersby and Greenwood, 2004). In addition, winter surveys are a good method for monitoring squirrel abundance because squirrels are easiest to detect in winter (Babińska-Werka and Żółw, 2008).

5. Conclusions

Our results indicate that the level of urbanization is high among European red squirrel populations (Verbeylen et al., 2003, Babińska-Werka and Żółw, 2008; Dozières et al., 2012; Rézouki et al., 2014). Based on our data, red squirrels use urban areas even along the northern edge of their distribution range, where natural forest areas are still widespread. During winter, more red squirrels were detected in urban than in forest habitats. In the light of observations that red squirrels in forests and rural areas are declining in many European countries (Shar, 2008; Selonon et al., 2010), urbanized areas may provide an important alternative habitat for the red squirrel. Consequences of urban development are not always disadvantages for native species. Our study indicated that human presence may have positive effect on red squirrels, for example winter feeding sites attract squirrels within urban environments and thereafter offer more wildlife contact for urbanites and suburbanites. Increasing amount of spruce trees in urban environments will increase food resources and offer hiding places for the squirrels. Citizen science has become more and more popular for ecological and evolutionary studies (e.g. Newman et al., 2003; Silvertown, 2009), unfortunately very few studies have been conducted in mammals. Our study show how citizen science data can be used for monitoring mammal species in urban areas.

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Appendix 1. Relative abundances of red squirrels at Finnish survey sites (black circles; larger circles indicate higher abundances). X markings show sites where the species was not observed in counts. The red circles show the locations of the 20 largest cities in Finland.

Figure legends:

Fig. 1. Relative squirrel abundance per transect route in relation to (A) human density (humans/km²) and (B) abundance of feeding sites (feeding sites/transect route km). Note the log scale of the x-axis.

Fig 2. Relative abundances of red squirrels (individuals per 10 km survey transect route) in relation to (A) different habitat types (dumping grounds, urban and rural areas, arable land, forest (trees > 5 m), clear-cut areas and stands of saplings (trees < 5 m), reed beds, shore scrub, and others), and (B) different spruce cone crop levels (1 = none, 2 = very few, 3 = few, 4 = moderate, 5 = abundant, 6 = very abundant (only three transect routes of these)).

Jokimäki et al. Fig. 1.

Fig. 1. Relative squirrel abundance per transect route in relation to (A) human density (humans/km²) and (B) abundance of feeding sites (feeding sites/transect route km). Note the log scale of the x-axis.

Jokimäki et al. Fig 2.

Fig 2. Relative abundances of red squirrels (individuals per 10 km survey transect route) in relation to (A) different habitat types (dumping grounds, urban and rural areas, arable land, forest (trees > 5 m), clear-cut areas and stands of saplings (trees < 5 m), reed beds, shore scrub, and others), and (B) different spruce cone crop levels (1 = none, 2 = very few, 3 = few, 4 = moderate, 5 = abundant, 6 = very abundant (only three transect routes of these)).

Table 1. Relative squirrel abundance and number feeding sites in different habitats (and their lengths) surveyed during winter bird counts.

	Squirrels	Feeders	Goshawks	Cats	Kilometers
Forest	403	203	75	1	2812
Dump-land	1	4	2	0	11
Urban	850	3657	115	69	2003
Rural	493	2399	28	81	1233
Arable land	2	23	26	2	897
Clear-cut	26	54	1	0	421
Reed-bed	0	4	7	0	262
Other	6	9	67	29	150

Table 2. Models explaining the transect route-specific abundance of squirrels in Finnish winter surveys, ranked based on the AIC. The AIC difference (ΔAIC), AIC weight (w) and evidence ratio (E-rat) are shown. Transect route ID was used as a random factor in all models. Length is the length of the transect route. Lat and Lon are the latitude and longitude of the transect route, respectively. Season is the survey season. H and H2 are the log-transformed human density and its quadratic effect along the transect route, respectively. Hawk, Cat and Feed are the abundances of goshawks, cats and feeding sites, respectively.

Model	ΔAIC	w	E-ratio
Length+Lat+Lon+Season+H2*F+Cat	0.00	0.27	1.00
Length+Lat+Lon+Season+H2*Lat+Cat+H2*F	1.82	0.11	2.48
Length+Lat+Lon+Season+H2*F+Hawk+Cat	2.00	0.10	2.72
Length+Lat+Lon+Season+H2*F	2.12	0.09	2.89
Length+Lat+Lon+Season+Cat+H2+F	2.98	0.06	4.44
Length+Lat+Lon+Season+Cat+H2	3.82	0.04	6.75
Length+Lat+Lon+Season+H2*Lat+Hawk+Cat+H2*F	3.82	0.04	6.75
Length+Lat+Lon+Season+H2*Lat+H2*F	3.94	0.04	7.17
Length+Lat+Lon+Season+H2*F+Hawk	4.12	0.03	7.85
Length+Lat+Lon+Season+H2*Lat+Cat+F	4.60	0.03	9.97
Length+Lat+Lon+Season+H*F+Cat	4.68	0.03	10.38
Length+Lat+Lon+Season+H2+F	4.86	0.02	11.36
Length+Lat+Lon+Season+Hawk+Cat+H2+F	4.96	0.02	11.94
Length+Lat+Lon+Season+H+Cat+F	5.80	0.01	18.17
Length+Lat+Lon+Season+H2*Lat+Hawk+H2*F	5.94	0.01	19.49

Length+Lat+Lon+Season+H2*Lat+F	6.50	0.01	25.79
Length+Lat+Lon+Season+H*Lat+Cat+H*F	6.56	0.01	26.58
Length+Lat+Lon+Season+H2*Lat+Hawk+Cat+F	6.58	0.01	26.84
Length+Lat+Lon+Season+H*F	6.62	0.01	27.39
Length+Lat+Lon+Season+H*F+Hawk+Cat	6.64	0.01	27.66
Length+Lat+Lon+Season+Hawk+H2+F	6.84	0.01	30.57
Length+Lat+Lon+Season+H*Lat+Cat+F	7.50	0.01	42.52
Length+Lat+Lon+Season+H+F	7.56	0.01	43.82
Length+Lat+Lon+Season+H+Hawk+Cat+F	7.80	0.01	49.40
Length+Lat+Lon+Season+H2*Lat+Hawk+F	8.48	0.00	69.41
Length+Lat+Lon+Season+H*Lat+H*F	8.50	0.00	70.11
Length+Lat+Lon+Season+H*Lat+Hawk+Cat+H*F	8.52	0.00	70.81
Length+Lat+Lon+Season+H*F+Hawk	8.56	0.00	72.24
Length+Lat+Lon+Season+H*Lat+F	9.28	0.00	103.54
Length+Lat+Lon+Season+H+Hawk+F	9.54	0.00	117.92
Length+Lat+Lon+Season+H*Lat+Hawk+H*F	10.46	0.00	186.79

Length+Lat+Lon+Season+H	49.08	0.00	>10000
Length+Lat+Lon+Season+H+Cat	49.42	0.00	>10000
Length+Lat+Lon+Season+H*Lat	50.84	0.00	>10000
Length+Lat+Lon+Season+H+Hawk	51.08	0.00	>10000
Length+Lat+Lon+Season+H*Lat+Cat	51.16	0.00	>10000
Length+Lat+Lon+Season+H+Hawk+Cat	51.42	0.00	>10000
Length+Lat+Lon+Season+H*Lat+Hawk	52.84	0.00	>10000
Length+Lat+Lon+Season+H*Lat+Hawk	52.84	0.00	>10000
Length+Lat+Lon+Season+H*Lat+Hawk+Cat	53.16	0.00	>10000
Length+Lat+Lon+Season+H*Lat+Hawk+Cat	53.16	0.00	>10000
Length+Lat+Lon+Season+H2	53.80	0.00	>10000
Length+Lat+Lon+Season+H2*Lat	55.44	0.00	>10000
Length+Lat+Lon+Season+Hawk+H2	55.80	0.00	>10000
Length+Lat+Lon+Season+H2*Lat+Cat	55.86	0.00	>10000
Length+Lat+Lon+Season+Hawk+Cat+H2	56.24	0.00	>10000
Length+Lat+Lon+Season+H2*Lat+Hawk	57.42	0.00	>10000

Length+Lat+Lon+Season+H2*Lat+Hawk+Cat	57.84	0.00	>10000
Length+Lat+Lon+Season+Cat+F	70.62	0.00	>10000
Length+Lat+Lon+Season+F	71.14	0.00	>10000
Length+Lat+Lon+Season+Hawk+Cat+F	71.68	0.00	>10000
Length+Lat+Lon+Season+Hawk+F	72.14	0.00	>10000
Length+Lat+Lon+Season	142.04	0.00	>10000
Length+Lat+Lon+Season+Cat	143.18	0.00	>10000
Length+Lat+Lon+Season+Hawk	143.20	0.00	>10000
Length+Lat+Lon+Season+Hawk+Cat	144.36	0.00	>10000

Table 3. Parameter estimates and test values for variables explaining the transect route-specific abundances of red squirrels in Finland in winter surveys based on the top-ranked model.

Coefficients that differ significantly from zero are bolded and nearly significant values ($P < 0.1$) are show in *italic*.

Variable	B $\pm$ SE	z	P
Intercept	4.884 $\pm$ 2.215	2.21	0.0274
Length	0.043 $\pm$ 0.016	2.66	0.0078
Latitude	-0.008 $\pm$ 0.003	-3.01	0.0026
Longitude	0.002 $\pm$ 0.005	0.39	0.6986
Season, mid-winter	-0.931 $\pm$ 0.089	-10.48	< 0.0001
Season, late-winter	-0.637 $\pm$ 0.003	-7.48	< 0.0001
Human density ²	0.023 $\pm$ 0.003	7.36	< 0.0001
Feeding places	0.662 $\pm$ 0.111	5.97	< 0.0001
<i>Cat</i>	<i>-2.253 $\pm$ 1.161</i>	<i>-1.94</i>	<i>0.0522</i>
Human density ² *Feeding places	-0.006 $\pm$ 0.003	-2.18	0.0290

Table 4. Models explaining habitat-specific abundances of squirrels in Finnish winter surveys, ranked based on the AIC. AIC difference (ΔAIC), AIC weight (w) and evidence ratio (E-rat) are shown. Transect route was used as a random factor in all models. Length is the length of the transect route section. Lat is the latitude of the transect route. Season is the survey season. Hab is the habitat category of the transect route section. Feed is the abundance of feeders in the transect route section. Spruce is the transect route-specific spruce cone crop abundance.

Model	ΔAIC	w	E-rat
Length+Lat+Season+Hab+Feed+Spruce	0	0.997	1
Length+Lat+Season+Hab+Feed	11.90	0.003	363.8
Length+Lat+Season*Hab+Feed+Spruce	17.98	0	8022.5
Length+Lat+Season+Hab+Spruce	35.96	0	>10000
Length+Lat+Season+Hab	49.06	0	>10000
Length+Lat+Season+Feed+Spruce	612.52	0	>10000
Length+Lat+Season+Feed	621.50	0	>10000
Length+Lat+Season+Spruce	827.24	0	>10000
Length+Lat+Season	840.38	0	>10000

Table 5. Parameter estimates and test values for variables explaining the section-specific squirrel abundances in Finland based on the top-ranked model. Coefficients that differ significantly from zero are bolded.

Variable	B	SE	Z-value	P
Intercept	-0.56	1.65	-0.34	0.735
Length (per 100m)	0.01	0.00	6.70	< 0.001
Dumpland	-0.71	1.02	-0.69	0.489
Urban settlements	0.81	0.11	7.31	< 0.001
Rural settlements	0.50	0.10	4.95	< 0.001
Arable land	-4.37	0.71	-6.14	< 0.001
Clear-cut	-18.30	11.40	-0.02	0.987
Reedbeds	-3.37	0.71	-4.72	< 0.001
Other	-2.70	0.39	-6.98	< 0.001
Feeders	0.04	0.01	6.25	< 0.001
Spruce cones	0.17	0.04	3.75	< 0.001
Season, mid-winter	-0.65	0.08	-7.79	< 0.001
Season, late-winter	-0.41	0.08	-4.97	< 0.001

Latitude	-0.00	0.00	-0.58	0.562
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