

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

2 **Finland**

3

4 **Highlights**

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

12

13 **Abstract**

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

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

36

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

38

## 39 **1. Introduction**

40 Globally, more people now live in urban than in rural areas, and at the same time, urbanized  
41 areas are increasing at an even higher rate than the urban population (UN, 2014). According to  
42 Seto et al. (2011), global urban land cover will increase approximately 30-fold by 2030.  
43 Therefore, understanding the impact of urban development on animal populations is important  
44 due to the possible effects on biodiversity and human-wildlife relationships (Baker and Harris,  
45 2007; Bateman and Fleming, 2012). Urbanization is one of the most extreme forms of land-use  
46 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).

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

86  
87 Arboreal squirrels (*Sciurus* spp.) are strictly dependent on forests. Therefore, they might be  
88 sensitive to the forest loss caused by urbanization. However, urban areas also contain different  
89 types of green spaces, such as remnant habitat patches, cemeteries, public parks and the gardens  
90 of residential areas, which may be suitable living environments for many forest species (Adams,  
91 2016). For example, squirrels can also inhabit fragments of forests within the urban matrix  
92 (Veerboom and Abeldorf, 1990; Baker and Harris, 2007; Babińska-Werka and Żółw, 2008;

93 Parker and Nilon, 2012; Mäkeläinen et al., 2015; Fey et al., 2016). The red squirrel (*Sciurus*  
94 *vulgaris*, L.) is a native forest specialist species in most European countries, and although the  
95 species still is common throughout most of its range (Gurnell and Wauters, 1999), its current  
96 population is declining in many parts of Europe (Gurnell and Pepper, 1993; O 'Teangana et al.,  
97 2000; Bertolino and Genovesi, 2003; Shar et al., 2008; Selonen et al., 2010). Most previous red  
98 squirrel studies were conducted within forest or agricultural areas and considered the effects of  
99 fragmentation on the red squirrel at a relatively small local scale. These studies indicated that red  
100 squirrel occurrence and abundance increase with woodland size (Celada et al., 1994; Verbeylen  
101 et al., 2003) and the area of woodland covered by coniferous trees (Veerboom and Abeldorf,  
102 1990) but decrease with the distance from the nearest source area (Veerboom and Abeldorf,  
103 1990; Celada et al., 1994; Verbeylen et al., 2003).

104

105 Only a few red squirrel studies have been conducted within urban areas despite the fact that the  
106 species is currently quite common in urban habitats in Europe (Luniak, 2004; Babińska-Werka  
107 and Żółw, 2008). One local study conducted in Brussels indicated that patch size and patch  
108 quality have positive effects and that isolation has a negative effect on red squirrel patch  
109 occurrence in urban areas (Verbylen et al., 2003). A study in Warsaw parks also indicated that  
110 park size positively affects red squirrel abundance (Babinska-Werka and Zolow, 2008).

111 However, large-scale studies with multiple study sites and covering different habitats are needed  
112 to better understand the urbanization process of red squirrel. In addition, as squirrels are  
113 important dispersal agents of seeds (Steele, 2008), they may also impact on distribution of urban  
114 trees. Therefore, it is important to know how urbanization influence squirrel abundance.

115

116 The main aim of this study was to analyze how human density affects the winter abundance of  
117 red squirrels throughout Finland. The analysis included also habitat type, natural (size of the  
118 Norway spruce cone crop) or artificial (number of feeding sites) food abundance, and natural  
119 (northern goshawk, *Accipiter gentilis*, L.) or human-associated (feral cats, *Felis domesticus*, L.)  
120 predator abundance. In addition, we also studied whether latitude and the time of the winter  
121 season affect the squirrel abundance. We conducted our study during the winter season because  
122 winter is a critical period for the survival of squirrels in the northern latitudes (Selonen et al.  
123 2015), and because due to the lack of leaves in the broad-leaved trees, the detectability of  
124 squirrels is high during winter (Hernández, 2014). We predicted that if squirrels somehow  
125 benefit from humans, then their abundance should increase with human density and should be  
126 higher within urban than other habitat types. If food resources, either artificial or natural, have an  
127 effect then squirrel abundance should increase with the number of feeding sites or with the size  
128 of the Norway spruce cone crop. If squirrel winter abundance is dependent on predators, then  
129 their abundance should change with predator abundance. Because the severity of winter  
130 increases toward the north, we predicted that red squirrel abundance would decrease from the  
131 south to the north. Due to winter mortality, we predicted that squirrel abundance would decrease  
132 during the winter. However, the squirrel abundance could also increase towards to the spring,  
133 because the visibility of squirrels increases due their early-starting mating season.

134

135

## 136 **2. Methods**

137

### 138 *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/km<sup>2</sup> (Statistics Finland,  
143 2015). The majority of the human population is concentrated in the southern part of the country  
144 (approximately 170 inhabitants/km<sup>2</sup>), whereas the population density is the lowest in the north  
145 (approximately 0.2 inhabitants/km<sup>2</sup>; Statistic Finland, 2015). Approximately 78% of the total  
146 area of Finland (390,906 km<sup>2</sup>) 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 15<sup>th</sup> 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,

162 although they may move between habitats depending on the food situation (Wauters and Dhondt,  
163 1992). In Finland, urban squirrels were first observed in the southern part of the country in the  
164 cities of Helsinki and Turku in the early 1930s (Haapanen, 1999).

165  
166 The main natural food of the red squirrel is seeds of coniferous trees; in Finland, these are mainly  
167 Norway spruce seeds (*Picea abies*, Karst) (Helle, 1996; Selonen et al., 2015). The main predator  
168 of the red squirrel in Finland is the northern goshawk (Selonen et al., 2010, Sulkava et al., 2014).  
169 In some other countries, red foxes and feral cats are also important squirrel predators (Loss et al.,  
170 2013).

171

### 172 2.3. *Field data and sampling*

173

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

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



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

191  
192 The location of a transect route is selected freely by the volunteers, but the coordinator of the  
193 surveys, the FMNH, ensures that the transect routes do not overlap. In this study, 355 transect  
194 routes (279 surveyed during the early winter, 279 surveyed during the mid-winter and 258  
195 surveyed during the late winter) with a total of 7,789 transect route kilometers (2,651 early  
196 winter km, 2,669 mid-winter km and 2,469 late winter km) were surveyed during the winter of  
197 2014/2015. The spatial distribution of the mid-winter (25 December to 7 January) survey transect  
198 routes is shown in Appendix 1. The transect route is counted by walking during midday under  
199 good weather and light conditions. When counting, the counter walks slowly, stops and listens,  
200 and records observation notes. The survey cannot last longer than the duration of daylight in  
201 mid-winter, that is, for example, approximately 4 hours in northern Finland. At each route the  
202 survey time is kept about the same in all three survey periods. Note that no vehicles are used in  
203 the surveys. The proportion of each habitat type along the route is estimated in advance from the  
204 maps and air photos, and ground-checked in the field during the surveys. When the route runs  
205 along a border of two habitats, the length is halved between them. Habitats along the route are  
206 classified into eight categories within an accuracy of 100 meters: (a) dumping ground or fur farm  
207 (data in this study: 11 km of transect routes); b) urban settlement (construction zones, town

208 centers, private homes with gardens, urban parks, etc.; 2003 km); c) rural settlement (widely  
209 dispersed buildings within agricultural landscapes; 1233 km); d) arable land (897 km); e) forest  
210 (2812 km); f) clear-cut area or stand of saplings (262 km); g) reed bed or shore scrub (150 km);  
211 and h) other (including also over-flying individuals; 421 km). Thus, the distribution of transect  
212 routes is somewhat concentrated near human settlements, but the sample size outside these areas  
213 is also substantial (e.g., >2800 km in forests). All observed squirrels, northern goshawks and  
214 feral cats (either seen or heard at an unlimited distance; note that no snow tracks are included in  
215 the data) are placed in one of the eight habitat categories in the field. For example, one route may  
216 consist 8000 meters of urban and 2000 meters of forest habitat including four squirrels observed  
217 in urban and one squirrel in forest habitat type. The observers also count the number of winter  
218 feeding sites in each of the above-mentioned habitats and estimate the size of the Norway spruce  
219 cone crop in trees along the transect routes during the each survey (six cone abundance  
220 categories; from 1 = no cones to 6 = very abundant cone availability; note that only the fresh  
221 cones are used to do this estimation). Because the methods do not allow density estimates, an  
222 index of relative abundance (individuals/10 km transect route) is used in this study. A more  
223 detailed description of the survey protocol is given elsewhere (see Koskimies and Väisänen,  
224 1991, Lehtikoinen et al., 2013; Fraixedas et al., 2015).

225

226

227

228 *2.4. Human densities*

229

230 The human densities (inhabitants/km<sup>2</sup>) around the survey transect routes were estimated using  
231 the coordinates of the transect route and the human density register of Statistics Finland provided  
232 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  
233 a rectangle around the survey transect route based on the southernmost, northernmost,  
234 easternmost and westernmost location of the transect route. Based on the human density register,  
235 we estimated how many people live inside this rectangle and used it as a proxy for the human  
236 density around the survey transect route. This work was conducted using the ArcMap 10.3.1  
237 software (Redlands, California, USA).

238

## 239 *2.5. Statistical analyses*

240

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

248

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

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

269

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

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

284

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

291

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

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

301

### 302 **3. Results**

303

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

315

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

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

333

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

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

349

#### 350 **4. Discussion**

351

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

358

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



367 different cities have become urbanized remains unknown, but it is known that the arrival of  
368 squirrels to urban areas began in the southwestern cities of Finland approximately 90 years ago  
369 (Haapanen, 1999). The population dynamics of urbanized squirrels remain unclear in our study.  
370 However, the squirrels abundances observed in this study should reflect the local population size,  
371 because dispersal distances of red squirrels are short, usually 1-2 km, although occasionally even  
372 10-20 km moved distances can be observed (Selonen and Hanski, 2015). In other words,  
373 squirrels in our study areas likely do not make migrations between urban and rural areas  
374 (Selonen & Hanski 2015, Fey et al. 2016) but the abundances observed here reflect the local  
375 population size. In Warsaw, Poland, it is observed that red squirrel abundance has increased  
376 threefold from 1956 to 2000 in the urban areas (Babinska-Werka and Zolow, 2008). In our study,  
377 squirrel abundance decreased toward the north (both in rural and urban habitats), a trend that  
378 could be expected because the productivity of forests declines and winter harshness increases  
379 toward the north.

380

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

389 One factor related to the high squirrel abundance observed in urban areas could be winter  
390 feeding. Our study indicated that squirrel abundance increased with the number of winter feeding  
391 sites. Many mammal species living in urban areas use feeding sites. According to the results of  
392 the Finnish winter feeding site study program 1988/89-1998/99, almost all (about 40) Finnish  
393 winter-active mammal species are detected in the feeding sites (n = 455 sites), and the red  
394 squirrel is the most common mammalian species occurring at 71% of these sites (Väisänen,  
395 1999). Our results indirectly indicated that squirrels are more able to utilize feeding sites in areas  
396 with a lower human density. Therefore, putting artificial feeders in natural areas may be a good  
397 management option. Supplemental food provided by humans is one possible reason why  
398 squirrels have urbanized. Likely because of artificial feeding, escape distances of squirrels have  
399 declined, and they have become tame (Luniak, 2004; Parker, and Nilon, 2012; Uchida et al.,  
400 2015). In addition, behavioral flexibility may be one reason for the success of some mammal  
401 species, such as squirrels, in urban environments (Bateman and Fleming, 2014).

402

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

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

418

419 Our results indicated that squirrel abundance increased with the spruce cone crop. This is not a  
420 surprising result since spruce seeds are main food for the red squirrel (Gurnell and Wauters,  
421 1999; Selonen et al., 2015). Favoring spruce trees will likely increase the living possibilities of  
422 squirrels in urban environments. We note that our study year had a moderate spruce cone crop;  
423 thus, crop failure did not push animals to feeders in urban areas. Bowers and Breland (1996) and  
424 Petty et al. (2003) also indicated that food availability (either artificial food or conifer seeds) is  
425 the main factor limiting the number of tree squirrels. However, because previous studies have  
426 indicated that the squirrel numbers in winter follow spruce cone production in Finland (Selonen  
427 et al., 2015), multi-year surveys are needed to study the role of artificial feeding for squirrels in a  
428 more detailed way. For example, it may be that feeding sites are even more important for  
429 squirrels during poor cone years than during those years with average cone production, as in our  
430 case. However, Reher et al. (2016) found that food provision in semi-urban habitat had positive  
431 effect on red squirrels also in years when natural food sources were available. One factor that  
432 might promote the urbanization of squirrels is the so- called “urban heat island” phenomenon  
433 (Adams, 2016). Animals living in warmer conditions may survive with less energy than

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

436

437 Earlier studies have suggested that predator presence, but not food supplementation, affects red  
438 squirrel abundances in forest habitats during winter (Selonen et al., 2016). Some studies have  
439 indicated that urban areas have few predators, which may support the urbanization of some  
440 species (Bateman and Fleming, 2012). However, in our case, the main squirrel predator in our  
441 areas, the goshawk, was more abundant in human-dominated areas than in forest habitats. This  
442 result is affected by the fact that many goshawks (especially juveniles) migrate to cities in winter in  
443 Finland. In any case, urban environments can no longer be considered predator-free areas for red  
444 squirrels. Similar to our study, other studies have also indicated that predators, either natural or  
445 human-associated, have no role in relative squirrel abundance (Bateman and Breland, 1996;  
446 Petty et al. 2003). Our results indicate that amount of feral cats can limit squirrel numbers. Also  
447 many earlier studies have indicated the harmful impact of the non-native cat predation on native  
448 animal fauna in general (Moseby et al., 2015; Adams, 2016) and also on squirrels (Baker et al.,  
449 2005). Limiting cat numbers could help squirrel populations in urban and rural areas.

450

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

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

470

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

479

480 **5. Conclusions**

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

496

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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.

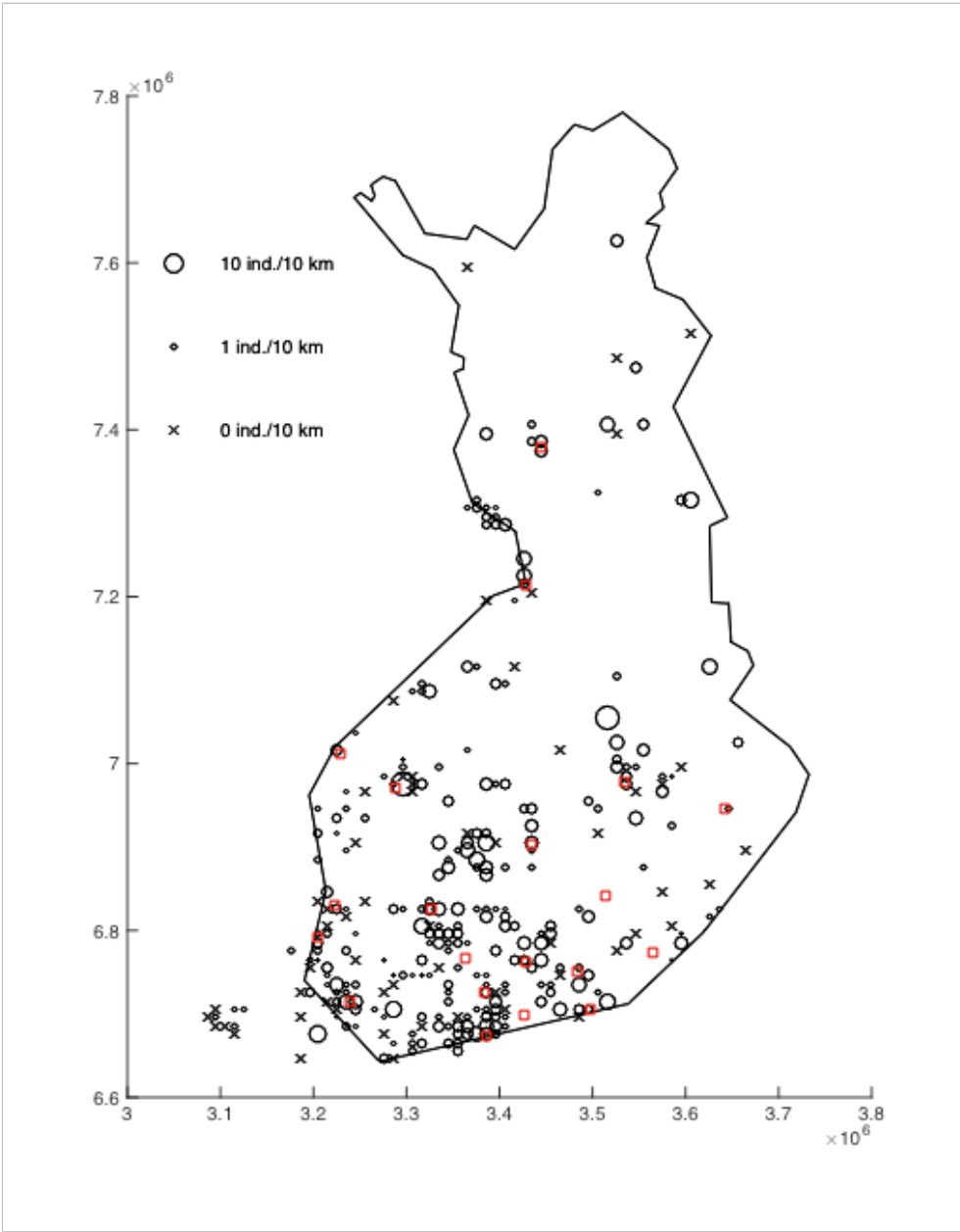
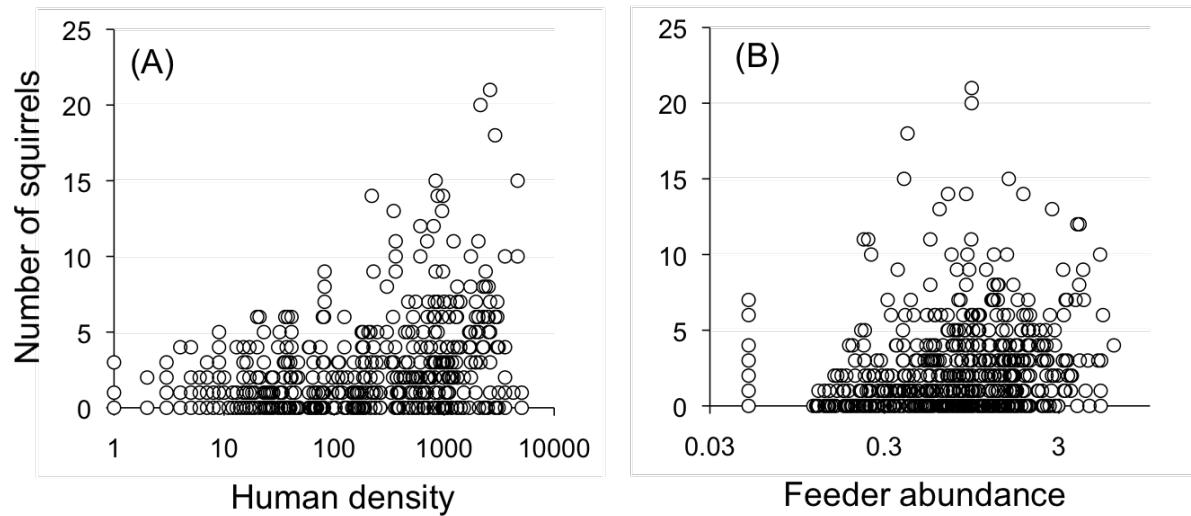


Figure legends:

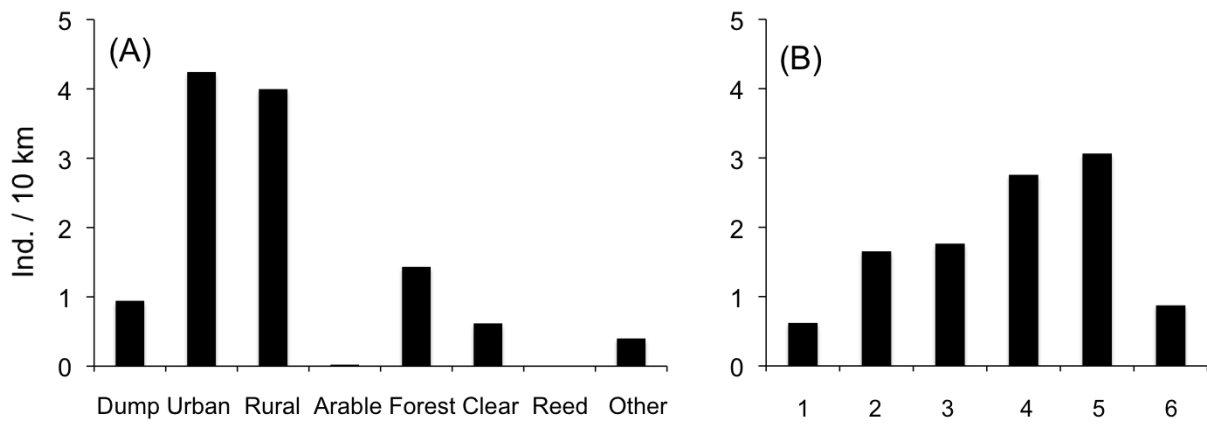
Fig. 1. Relative squirrel abundance per transect route in relation to (A) human density (humans/km<sup>2</sup>) and (B) abundance of feeding sites (feeding sites/transect route km). Note the log scale of the x-axis.

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/km<sup>2</sup>) 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 ( $\Delta AIC$ ), 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	$\Delta AIC$	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

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

Table 4. Models explaining habitat-specific abundances of squirrels in Finnish winter surveys, ranked based on the AIC. AIC difference ( $\Delta$ AIC), 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	$\Delta$ AIC	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)	<b>0.01</b>	<b>0.00</b>	<b>6.70</b>	<b>&lt; 0.001</b>
Dumpland	-0.71	1.02	-0.69	0.489
Urban settlements	<b>0.81</b>	<b>0.11</b>	<b>7.31</b>	<b>&lt; 0.001</b>
Rural settlements	<b>0.50</b>	<b>0.10</b>	<b>4.95</b>	<b>&lt; 0.001</b>
Arable land	<b>-4.37</b>	<b>0.71</b>	<b>-6.14</b>	<b>&lt; 0.001</b>
Clear-cut	-18.30	11.40	-0.02	0.987
Reedbeds	<b>-3.37</b>	<b>0.71</b>	<b>-4.72</b>	<b>&lt; 0.001</b>
Other	<b>-2.70</b>	<b>0.39</b>	<b>-6.98</b>	<b>&lt; 0.001</b>
Feeders	<b>0.04</b>	<b>0.01</b>	<b>6.25</b>	<b>&lt; 0.001</b>
Spruce cones	<b>0.17</b>	<b>0.04</b>	<b>3.75</b>	<b>&lt; 0.001</b>
Season, mid-winter	<b>-0.65</b>	<b>0.08</b>	<b>-7.79</b>	<b>&lt; 0.001</b>
Season, late-winter	<b>-0.41</b>	<b>0.08</b>	<b>-4.97</b>	<b>&lt; 0.001</b>

Latitude	-0.00	0.00	-0.58	0.562
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