

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

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4 Jokimäki, J.¹ Selonen, V.² Lehtikoinen, A.³ & Kaisanlahti-Jokimäki, M.-L.¹

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6 ¹ Arctic Centre, University of Lapland, P.O.Box 122, 96010-FI Rovaniemi, Finland

7 ²University of Turku, Department of Biology, Section of Ecology; FI-20014 Turku, Finland

8 ³ The Helsinki Lab of Ornithology, Finnish Museum of Natural History, University of Helsinki,

9 P. O. Box 17, FI-00014 University of Helsinki, Finland.

10

11 **Highlights**

- 12 • The winter abundance of red squirrels is higher in urban than in forest habitats.
- 13 • Feeding sites affect squirrel abundance.
- 14 • Urban environments are an important alternative habitat for the declining red squirrel in
15 Europe.
- 16 • The urbanization of squirrels can be monitored using citizen science based, large-scale
17 winter surveys.

18

19 **Abstract**

20 Because the amount of urban areas has increased, it is important to investigate the abundance of
21 wildlife species in relation to urban environments. Analyzing the impact of urbanization on the
22 presence of forest-dwelling mammals is of interest due to the possible effects of urbanization on
23 human-wildlife relationships and urban biodiversity. The Eurasian red squirrel (*Sciurus vulgaris*)

24 is a declining forest species, and its occurrence in urban environments has been inadequately
25 studied. The loss and fragmentation of forests due to urbanization may be detrimental for
26 squirrels, whereas the abundant and predictable food resources and the low number of natural
27 predators in urban areas may encourage squirrels to invade towns. We used large-scale data
28 collected by volunteer bird watchers along a 950 km south-north gradient to study whether the
29 winter abundance of squirrels in Finland is dependent on urbanization, while controlling for
30 effects of habitat type, food abundance (spruce cone crop; number of winter feeding sites),
31 predator abundance (northern goshawk, *Accipiter gentilis*; feral cat *Felis catus*), season and
32 latitude. We found that squirrel abundance increased with human population density, number of
33 feeding sites and cone crop and decreased with latitude and season. Feral cats showed weak
34 negative connection with squirrel numbers, but there were no effect of goshawks. Relative
35 squirrel abundance was approximately twice as high in urban habitats than in forests. Artificial
36 feeding rather than a low number of predators may attract squirrels in urban environments.
37 Increasing spruce stands in urban environments will also benefit squirrels. Our results indicate
38 that urban areas are an important habitat for the red squirrel even along the northern edge of their
39 distribution range, where natural forest areas are still widespread. We conclude also that a citizen
40 science -based bird survey protocol associated with mammal surveys seems to be a good large-
41 scale monitoring method to study the urbanization of squirrels.

42

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

44

45 **1. Introduction**

46 Globally, more people now live in urban than in rural areas, and at the same time, urbanized
47 areas are increasing at an even higher rate than the urban population (UN, 2014). According to
48 Seto et al. (2011), global urban land cover will increase approximately 30-fold by 2030.
49 Therefore, understanding the impact of urban development on animal populations is important
50 due to the possible effects on biodiversity and human-wildlife relationships (Baker and Harris,
51 2007; Bateman and Fleming, 2012). Urbanization is one of the most extreme forms of land-use
52 alteration, and only remnants of the original habitats persist in towns. At the same time, urban
53 areas are characterized by high levels of predictable anthropogenic food resources and human-
54 caused disturbances (e.g., traffic), milder microclimates, and an altered abundance of predators
55 (e.g., Rebele, 1994; Shochat et al., 2006; Gilbert, 2012; Francis and Chadwick, 2013;
56 Tryjanowski et al., 2015).

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

67

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

76

77 Arboreal squirrels (*Sciurus* spp.) are strictly dependent on forests. Therefore, they might be
78 sensitive to the forest loss caused by urbanization. However, urban areas also contain different
79 types of green spaces, such as remnant habitat patches, cemeteries, public parks and the gardens
80 of residential areas, which may be suitable living environments for many forest species (Adams,
81 2016). For example, squirrels can also inhabit fragments of forests within the urban matrix
82 (Veerboom and Abeldorf, 1990; Baker and Harris, 2007; Babińska-Werka and Żółw, 2008;
83 Parker and Nilon, 2012; Mäkeläinen et al., 2015; Fey et al., 2016).

84

85 Urban areas have some features, such as stable and abundant food resources and low numbers of
86 natural predators that may attract wildlife and promote, for example, the urbanization of squirrels
87 (Francis and Chadwick, 2013; Adams, 2016). Artificial feeding stations and waste offer easily
88 available food resources, especially to species feeding on seeds or having a generalist diet
89 (Adams, 2016). Although feeders in gardens are primarily designed to feed birds, they also
90 attract squirrels in urban areas, especially during the winter when food resources may become

91 scarce in forest habitats. In general, urban areas contain a lower number of larger natural
92 predators than do rural areas (Bateman and Fleming, 2012), but the abundance of medium-sized
93 carnivores might be even higher in urban environments than in more natural environments
94 (Nilon and Pais, 1997; Baker and Harris, 2007; Bateman and Fleming, 2012). However, at the
95 same time, urban squirrels may be more vulnerable to predation by domestic cats than are
96 squirrels living in rural and forest areas (Wauter et al., 1997; Shuttleworth, 2001; Magris and
97 Gurnell, 2002). It is likely that there is an optimal level of human influence at which the living
98 requirements for a species are best met or limit the level of urbanization that a species can
99 tolerate (Francis and Chadwick, 2013; Adams, 2016). However, the roles of artificial food and
100 the number of predators promoting the urbanization of squirrels are still not well known.

101

102 The red squirrel (*Sciurus vulgaris*, L.) is a native forest specialist species in most European
103 countries, and although the species still is common throughout most of its range (Gurnell and
104 Wauters, 1999), its current population is declining in many parts of Europe (Gurnell and Pepper,
105 1993; O 'Teangana et al., 2000; Bertolino and Genovesi, 2003; Shar et al., 2008; Selonen et al.,
106 2010). Most previous red squirrel studies were conducted within forest or agricultural areas and
107 considered the effects of fragmentation on the red squirrel at a relatively small local scale. These
108 studies indicated that red squirrel occurrence and abundance increase with woodland size
109 (Celada et al., 1994; Verbeylen et al., 2003) and the area of woodland covered by coniferous
110 trees (Veerboom and Abeldorf, 1990) but decrease with the distance from the nearest source area
111 (Veerboom and Abeldorf, 1990; Celada et al., 1994; Verbeylen et al., 2003).

112

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

123

124 The main aim of this study was to analyze how human density affects the winter abundance of
125 red squirrels throughout Finland. The analysis included also habitat type, natural (size of the
126 Norway spruce cone crop) or artificial (number of feeding sites) food abundance, and natural
127 (northern goshawk, *Accipiter gentilis*, L.) or human-associated (feral cats, *Felis domesticus*, L.)
128 predator abundance. In addition, we also studied whether latitude and the time of the winter
129 season affect the squirrel abundance. We conducted our study during the winter season because
130 winter is a critical period for the survival of squirrels in the northern latitudes (Selonen et al.
131 2015), and because due to the lack of leaves in the broad-leaved trees, the detectability of
132 squirrels is high during winter (Hernández, 2014). We predicted that if squirrels somehow
133 benefit from humans, then their abundance should increase with human density and should be
134 higher within urban than other habitat types. If food resources, either artificial or natural, have an
135 effect then squirrel abundance should increase with the number of feeding sites or with the size

136 of the Norway spruce cone crop. If squirrel winter abundance is dependent on predators, then
137 their abundance should change with predator abundance. Because the severity of winter
138 increases toward the north, we predicted that red squirrel abundance would decrease from the
139 south to the north. Due to winter mortality, we predicted that squirrel abundance would decrease
140 during the winter. However, the squirrel abundance could also increase towards to the spring,
141 because the visibility of squirrels increases due their early-starting mating season.

142

143

144 **2. Methods**

145

146 *2.1. Study area*

147

148 The study was conducted in Finland along an approximately 950 km south-north gradient (Suppl.
149 1; between 59°50' and 68°40' N and 19°40' and 30°20' E). The human population of Finland was
150 5.5 million in 2014 with a mean population density of 18/km² (Statistics Finland, 2015). The
151 majority of the human population is concentrated in the southern part of the country
152 (approximately 170 inhabitants/km²), whereas the population density is the lowest in the north
153 (approximately 0.2 inhabitants/km²; Statistic Finland, 2015). Approximately 78% of the total
154 area of Finland (390,906 km²) is land covered (Statistics Finland, 2015), and approximately 77%
155 of this is forests, 9% is agricultural areas and only 4% is built-up areas. Almost the entire country
156 belongs to the boreal taiga forest terrestrial biome, where forests are dominated by coniferous
157 trees. The study area lies within the cool boreal climate zone.

158

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

167

168 *2.2. Study species*

169 The red squirrel occupies the boreal and temperate areas of Eurasia and is mainly a coniferous
170 forest specialist (Shar et al., 2008). Individuals live in the same home ranges throughout the year,
171 although they may move between habitats depending on the food situation (Wauters and Dhondt,
172 1992). In Finland, urban squirrels were first observed in the southern part of the country in the
173 cities of Helsinki and Turku in the early 1930s (Haapanen, 1999).

174

175 The main natural food of the red squirrel is seeds of coniferous trees; in Finland, these are mainly
176 Norway spruce seeds (*Picea abies*, Karst) (Helle, 1996; Selonen et al., 2015). The main predator
177 of the red squirrel in Finland is the northern goshawk (Selonen et al., 2010, Sulkava et al., 2014).
178 In some other countries, red foxes and feral cats are also important squirrel predators (Loss et al.,
179 2013).

180

181 *2.3. Field data and sampling*

182

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

191 The Finnish winter bird surveys consist of transect routes with an average length of
192 approximately 10 km (Koskimies and Väisänen, 1991). Birds and mammals are surveyed along
193 the same transect route three times per winter: early winter (1–15 November), mid-winter (25
194 December to 7 January) and late winter (21 February to 6 March). The yearly surveys are
195 organized by the FMNH and are conducted by volunteer birders (610 during the studied winter
196 of 2014/2015). The participants can identify all winter birds and their calls. Thus, the observers
197 are skilled in species identification, and since the red squirrel is very easy to identify, there
198 should not be any differences between observers in ability to identify the target species of this
199 study.

200

201 The location of a transect route is selected freely by the volunteers, but the coordinator of the
202 surveys, the FMNH, ensures that the transect routes do not overlap. In this study, 355 transect
203 routes (279 surveyed during the early winter, 279 surveyed during the mid-winter and 258
204 surveyed during the late winter) with a total of 7,789 transect route kilometers (2,651 early

205 winter km, 2,669 mid-winter km and 2,469 late winter km) were surveyed during the winter of
206 2014/2015. The spatial distribution of the mid-winter (25 December to 7 January) survey transect
207 routes is shown in Appendix 1. The transect route is counted by walking during midday under
208 good weather and light conditions. When counting, the counter walks slowly, stops and listens,
209 and records observation notes. The survey cannot last longer than the duration of daylight in
210 mid-winter, that is, for example, approximately 4 hours in northern Finland. At each route the
211 survey time is kept about the same in all three survey periods. Note that no vehicles are used in
212 the surveys. The proportion of each habitat type along the route is estimated in advance from the
213 maps and air photos, and ground-checked in the field during the surveys. When the route runs
214 along a border of two habitats, the length is halved between them. Habitats along the route are
215 classified into eight categories within an accuracy of 100 meters: (a) dumping ground or fur farm
216 (data in this study: 11 km of transect routes); b) urban settlement (construction zones, town
217 centers, private homes with gardens, urban parks, etc.; 2003 km); c) rural settlement (widely
218 dispersed buildings within agricultural landscapes; 1233 km); d) arable land (897 km); e) forest
219 (2812 km); f) clear-cut area or stand of saplings (262 km); g) reed bed or shore scrub (150 km);
220 and h) other (including also over-flying individuals; 421 km). Thus, the distribution of transect
221 routes is somewhat concentrated near human settlements, but the sample size outside these areas
222 is also substantial (e.g., >2800 km in forests). All observed squirrels, northern goshawks and
223 feral cats (either seen or heard at an unlimited distance; note that no snow tracks are included in
224 the data) are placed in one of the eight habitat categories in the field. For example, one route may
225 consist 8000 meters of urban and 2000 meters of forest habitat including four squirrels observed
226 in urban and one squirrel in forest habitat type. The observers also count the number of winter
227 feeding sites in each of the above-mentioned habitats and estimate the size of the Norway spruce

228 cone crop in trees along the transect routes during the each survey (six cone abundance
229 categories; from 1 = no cones to 6 = very abundant cone availability; note that only the fresh
230 cones are used to do this estimation). Because the methods do not allow density estimates, an
231 index of relative abundance (individuals/10 km transect route) is used in this study. A more
232 detailed description of the survey protocol is given elsewhere (see Koskimies and Väisänen,
233 1991, Lehtikoinen et al., 2013; Fraixedas et al., 2015).

234

235

236

237 *2.4. Human densities*

238

239 The human densities (inhabitants/km²) around the survey transect routes were estimated using
240 the coordinates of the transect route and the human density register of Statistics Finland provided
241 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
242 a rectangle around the survey transect route based on the southernmost, northernmost,
243 easternmost and westernmost location of the transect route. Based on the human density register,
244 we estimated how many people live inside this rectangle and used it as a proxy for the human
245 density around the survey transect route. This work was conducted using the ArcMap 10.3.1
246 software (Redlands, California, USA).

247

248 *2.5. Statistical analyses*

249

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

257 First, we evaluated the transect route-specific values of squirrel number using generalized mixed
258 effect models, where the transect route-specific number of observed squirrels was explained
259 using the length of the transect route, the survey season (categorical variable), the latitude and
260 longitude of the transect route, the linear and quadratic effects of human density (log
261 transformed), and the abundance of winter feeding sites (log transformed) and predators
262 (goshawks and feral cats). The length of the transect route accounts for the fact that the lengths
263 of the transects vary between routes. The quadratic effect of human density accounts for the
264 possibility that squirrel numbers can experience, e.g., a peak or drop in areas of average human
265 density. We also included an interaction term between latitude and human density as well as
266 human density and abundance of feeding sites in the analyses. These can take into account that
267 impact of human density can depend on latitude and feeding may affect squirrel numbers
268 differently in areas of high and low human densities. The transect route ID was used as a random
269 factor because most of the transect routes were surveyed during all three winter sub-seasons.

270 Length of the route, coordinates and census season were included in all the models, but
271 otherwise we used all model combinations of used variables. Altogether, this produced 56
272 different model combinations (Table 2). The length of the transect route (continuous variable),

273 latitude (continuous variable), longitude (continuous variable) and survey season (categorical
274 factor variable) were included in all models and thus formed the base model. The numbers of
275 predators (goshawks and cats) and winter feeding sites were transformed into relative
276 abundances (number of animals or feeders per survey kilometer).

277 Second, we investigated the habitat-specific values of squirrel numbers using generalized mixed
278 effect models. For this analysis, we split the transect routes into sections based on eight different
279 habitat categories (see section 2.3. Field data). Habitat was used as eight categorical factor
280 variable and forest habitat was used as a reference category. In this analysis, the squirrel numbers
281 were explained by the length of the transect route section (continuous variable), habitat type of
282 this transect route section, survey season (categorical factor variable), latitude of the transect
283 route (continuous variable), abundance of winter feeding sites in the transect route section
284 (continuous variable) and relative abundance of spruce cones along the full transect route
285 (continuous variable). Like in the first analysis, the ID of the transect route was used as a random
286 factor in the analysis. The length of the transect route section, latitude and census season were
287 included in all models and thus formed the base model. In this analysis, the habitat-specific
288 squirrel abundance was compared to that in the forested areas. In addition, we tested whether
289 detection probability might be season dependent between natural and urban areas by adding an
290 interaction between season and habitat. Altogether, we built 9 different model combinations
291 (Table 4).

292

293 Both analyses were conducted using the stepwise procedure. First, using the full model, we
294 measured which distribution models, (i) Poisson, (ii) zero-inflated Poisson, (iii) negative
295 binomial or (iv) zero-inflated negative binomial distribution, best fit the data. Second, among

296 these four alternatives, we used the best of the top-ranked distributions in the full set of candidate
297 models (Tables 2 and 4). We used the Akaike information criterion (AIC hereafter) to perform
298 model selection (Burnham and Anderson, 2002).

299

300 All analyses were conducted in R version 3.2.2 (R Development Core Team, 2013) and models
301 were fitted using glmmadmb-package. When analyzing spatial data, it is possible that
302 autocorrelation of variables may bias the results. The potential spatial autocorrelation of
303 residuals of the best model was investigated by using the ncf-package in R. No spatial
304 autocorrelation was found from the residuals of the best models. Also multicollinearity among
305 explanatory variables may have confounding effects on results. In our case, there was no strong
306 correlation between the explanatory variables. The maximum Pearson's correlation coefficient
307 was always below 0.5 (Booth et al. 1994), except in the case of human densities and quadratic
308 effect of human densities. In this case only one of these two variables were used at time.

309

310 **3. Results**

311

312 Altogether, 1781 squirrels were observed along the transect routes across all seasons (early
313 winter 785, mid-winter 448, late winter 548). The relative squirrel abundance, feeding sites,
314 goshawks and cats in the different habitats are shown in Table 1. In general, the relative squirrel
315 abundance was lower in forest (1.43 individuals/10 km transect route) than in rural (4.00
316 individuals/10 km transect route) or urban (4.24 individuals/10 km transect route) habitats. In
317 addition, the number of feeding sites per 10 km transect route was lower in forest (0.72) than in

318 rural (19.46) or urban (18.26) habitats. The relative abundance of northern goshawks in urban
319 areas (0.57 individuals/10 km transect route) was approximately twice as high as in forest (0.27)
320 or rural (0.22) habitats. Approximately twice the number of feral cats was observed in rural (0.66
321 individuals/10 km transect route) than in urban habitats (0.30), whereas only one cat was
322 observed in the forest habitats (Table 1).

323

324 In the transect route analyses, the zero-inflated negative binomial models were top-ranked in the
325 first model selection step (results not shown). In the second step of the transect route-specific
326 analysis, the top-ranked model included the length of the transect route, latitude, longitude,
327 season, abundance of feral cats, quadratic effect of human density and abundance of feeding
328 places and their interaction. The other model within 2 Δ AIC of the best model included these
329 same variables, but also interaction between quadratic human density and latitude (Table 2).
330 However, since this interaction was not significant this variable can be considered as
331 uninformative parameter (sensu Arnold 2010) and only the top ranked model was investigated
332 later on. The number of squirrels increased with the increasing length of a transect route,
333 quadratic effect of human density (Fig. 1a) and abundance of feeding sites (Fig 1b) and
334 decreased with increasing latitude (Table 3). The significant negative interaction between
335 quadratic human population and abundance of feeding sites suggest that feeding increased
336 squirrel numbers more in areas where there was lower human densities (Table 3). There was also
337 tendency that abundance of feral cats decreased squirrel numbers (Table 3). The relative squirrel
338 abundance was significantly lower during the mid-winter and late winter counts than the early
339 winter counts. The abundances of goshawks was not significantly associated with squirrel
340 numbers (Table 2).

341

342 In the habitat-specific analyses, the negative binomial models were top-ranked in the first model
343 selection step (results not shown). In the second step of the habitat-specific analysis, the full
344 model was clearly the best model (Table 4). This top-ranked model included the length of the
345 transect route, latitude, season, habitat, number of feeding sites and spruce cone crop. Based on
346 the top-ranked model coefficients, transect route length, most habitat types, abundances of
347 feeders and the size of the Norway spruce cone crop and seasons differed significantly from zero
348 (Table 5). The highest abundances were observed in urban and rural settlements, where the
349 relative squirrel abundances (approximately 4 squirrels per 10 km transect route) were
350 significantly higher than those in forests (approximately 2 squirrels per 10 km transect route) or
351 other habitats (0-1 squirrels per 10 km transect route; Fig. 2a). In contrast, the relative abundance
352 of red squirrels in arable land and reed beds was significantly lower than that in forests (Fig. 2a,
353 Table 5). In addition, the relative squirrel abundance increased with increasing transect length,
354 number of feeders and number of spruce cones (Table 5; Fig. 2b). As in the transect route-
355 specific analysis, the relative squirrel abundance decreased from early winter to the mid-winter
356 and late winter (Table 5).

357

358 **4. Discussion**

359

360 Our analysis indicated that red squirrel abundance increased with human density. The
361 relationship between squirrel abundance and human density was nonlinear, as squirrel abundance
362 increased more rapidly in areas with the highest human densities. Our habitat-specific analysis
363 further showed that the squirrel abundance was significantly higher in urban and rural

364 settlements than in other habitats, such as forests. These results suggest that the wintering red
365 squirrels benefits from urbanization.

366

367 Red squirrels inhabited urban habitats similarly in different parts of Finland, as indicated by the
368 non-significant interaction term between latitude and human density. Therefore, the urbanization
369 of the red squirrel in Finland appears to be in a phase in which no geographical difference in the
370 level of urbanization can be seen. It has been concluded that the spread of urbanization in
371 different geographical regions depends on whether urbanization in different cities occurs
372 independently or through the migration of urbanized individuals from one city to another (Evans
373 et al., 2009, 2010, Fey et al., 2015). In the case of the red squirrel in Finland, the process of how
374 different cities have become urbanized remains unknown, but it is known that the arrival of
375 squirrels to urban areas began in the southwestern cities of Finland approximately 90 years ago
376 (Haapanen, 1999). The population dynamics of urbanized squirrels remain unclear in our study.

377 However, the squirrels abundances observed in this study should reflect the local population size,
378 because dispersal distances of red squirrels are short, usually 1-2 km, although occasionally even
379 10-20 km moved distances can be observed (Selonen and Hanski, 2015). In other words,
380 squirrels in our study areas likely do not make migrations between urban and rural areas
381 (Selonen & Hanski 2015, Fey et al. 2016) but the abundances observed here reflect the local
382 population size. In Warsaw, Poland, it is observed that red squirrel abundance have increased
383 threefold from 1956 to 2000 in the urban areas (Babinska-Werka and Zolow, 2008). In our study,
384 squirrel abundance decreased toward the north (both in rural and urban habitats), a trend that
385 could be expected because the productivity of forests declines and winter harshness increases
386 toward the north.

387

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

396

397 One factor related to the high squirrel abundance observed in urban areas could be winter
398 feeding. Our study indicated that squirrel abundance increased with the number of winter feeding
399 sites. Many mammal species living in urban areas use feeding sites. According to the results of
400 the Finnish winter feeding site study program 1988/89-1998/99, almost all (about 40) Finnish
401 winter-active mammal species are detected in the feeding sites (n = 455 sites), and the red
402 squirrel is the most common mammalian species occurring at 71% of these sites (Väisänen,
403 1999). Our results indirectly indicated that squirrels are more able to utilize feeding sites in areas
404 with a lower human density. Therefore putting artificial feeders in natural areas may be a good
405 management option. Supplemental food provided by humans is one possible reason why
406 squirrels have urbanized. In addition, behavioral flexibility may be one reason for the success of
407 some mammal species, such as squirrels, in urban environments (Bateman and Fleming, 2014).

408

409 Previous studies have indicated that winter feeding may be beneficial, e.g., for the grey squirrel
410 (e.g., Bonnington et al., 2014). Winter feeding and anthropogenic waste offer great and
411 predictable food resources for animals, especially during the winter period and years when the
412 main food sources of squirrels, i.e., the seeds of conifers, are scarce. For example, Verbeylen et
413 al. (2003) found that patches with supplementary feeding had a higher probability of being
414 occupied by the red squirrel. Winter feeding has apparently helped squirrels adjust to urban and
415 suburban habitats. Feeding wildlife is widespread and have a many impacts on the wildlife
416 (Orams, 2002). While many previous studies have suggested artificial feeding have positive
417 effects especially on birds (Siriwardena et al., 2007; Harrison et al., 2009), some other papers
418 have also indicated its risk (Jones et al., 2008). Currently, negative aspects of supplemental
419 feeding have been actively discussed in urban areas (Galbraith et al., 2015), for instance, animals
420 aggregated by artificial feeding could be more vulnerable to pathogen transmission (Bradley, and
421 Altizer 2006). Also, the possibility of ecological traps may be worth to consider (Robertson et
422 al., 2013). However, there are also psychological benefits of the wildlife for the humans,
423 enhanced by artificial feeding (Orams, 2002).

424

425 Our results indicated that squirrel abundance increased with the spruce cone crop. This is not a
426 surprising result since spruce seeds are main food for the red squirrel (Gurnell and Wauters 1999,
427 Selonen et al. 2015). Favoring spruce trees will likely increase the living possibilities of squirrels
428 in urban environments. We note that our study year had a moderate spruce cone crop; thus, crop
429 failure did not push animals to feeders in urban areas. Bowers and Breland (1996) and Petty et al.
430 (2003) also indicated that food availability (either artificial food or conifer seeds) is the main
431 factor limiting the number of tree squirrels. However, because previous studies have indicated

432 that the squirrel numbers in winter follow spruce cone production in Finland (Selonen et al.,
433 2015), multi-year surveys are needed to study the role of artificial feeding for squirrels in a more
434 detailed way. For example, it may be that feeding sites are even more important for squirrels
435 during poor cone years than during those years with average cone production, as in our case.
436 However, Reher et al. (2016) found that food provision in semi-urban habitat had positive effect
437 on red squirrels also in years when natural food sources were available. One factor that might
438 promote the urbanization of squirrels is the so-called “urban heat island” phenomenon (Adams,
439 2016). Animals living in warmer conditions may survive with less energy than individuals
440 occupying in colder environments. Unfortunately, we had no data to analyze this topic, but it
441 might be a relevant topic for further study.

442

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

454

455 We must stress that we were not able to control for the detectability of squirrels in different
456 seasons (Hernández, 2014) and habitats (see e.g. Amori et al., 2011), and this may have partly
457 affected our results. For example, detectability of squirrels has been reported to be higher in late
458 autumn and winter than summer or spring because dense foliage decreased the detectability of
459 squirrels during summer (Hernández, 2014). We detected the lowest relative squirrel abundance
460 during the mid-winter, indicating an increase towards the end of winter. Towards to early-spring
461 (i.e. late winter season in our case) day length becomes longer and the activity of squirrels would
462 also increase partly due to mating activities. The detectability of the red squirrel may be either
463 higher in human-dominated habitats than in more natural habitats due to the attraction to
464 artificial feeders, less hiding places (e.g. tree cavities, dense woods) or changing individual
465 personalities (bolder in urban habitat; Lowry et al., 2013), or the detectability of squirrels may
466 also be low in urban environments because buildings decrease detectability of squirrels (our
467 personal observations). However, the detectability of squirrels may be higher in open rural areas
468 than in more closed forest and urban habitats, which may partly explain the high squirrel
469 abundance in the rural landscape. In any case, supporting our results, previous studies have
470 indicated that squirrel densities are lower in rural than in urban environments (Babińska-Werka
471 and Żółw, 2008; Dozières et al., 2012). In addition, we tested whether detection probability
472 might be season dependent in urban areas compared to more natural areas, by testing the effect
473 of interaction between season and human population size. This interaction was not significant.

474

475 We used mammalian data collected by the volunteer bird watchers during their winter bird
476 surveys. This citizen science-based survey and monitoring method has several benefits. First, the
477 winter bird transect routes also cover urban environments, which are lacking in Finnish wildlife

478 monitoring efforts. Second, a large number of bird watchers can collect mammalian data from
479 large areas. The use of volunteer-based annual monitoring enables the production of long-term
480 datasets of the distribution and population trends of many mammalian species (Battersby and
481 Greenwood, 2004). In addition, winter surveys are a good method for monitoring squirrel
482 abundance because squirrels are easiest to detect in winter (Babińska-Werka and Żółw, 2008).

483

484 **5. Conclusions**

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

500

501

502

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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.

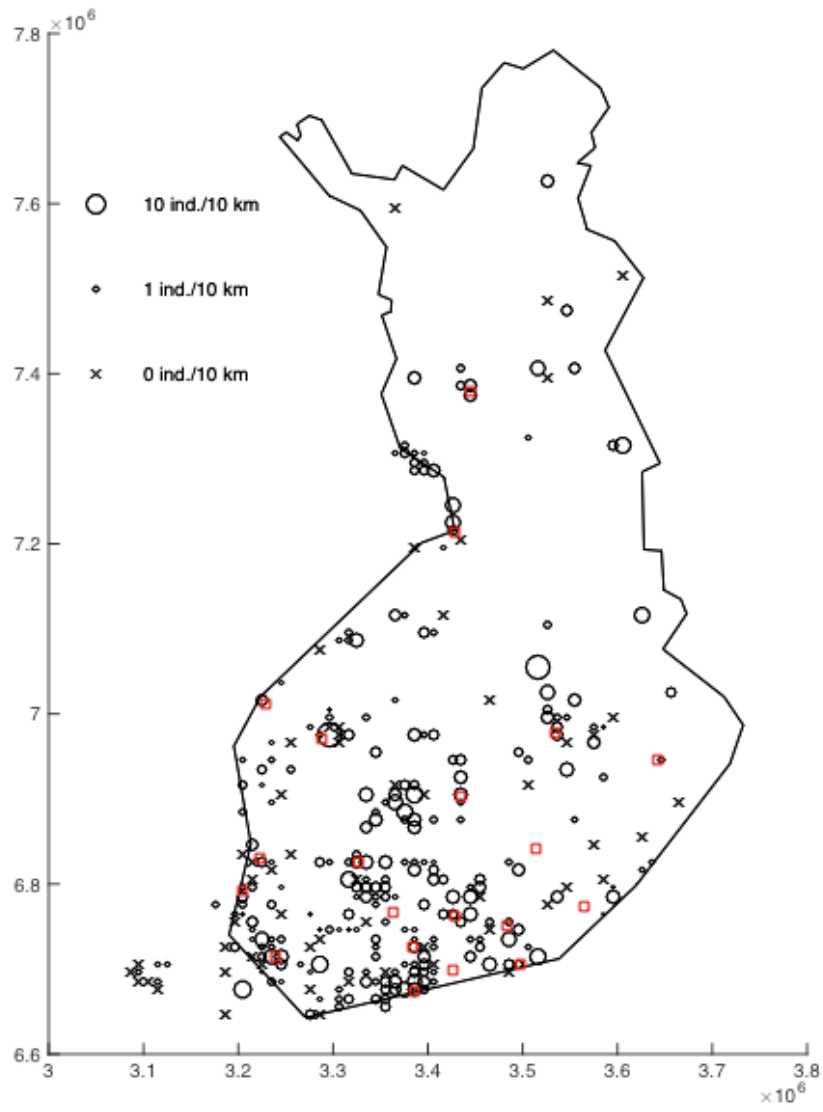
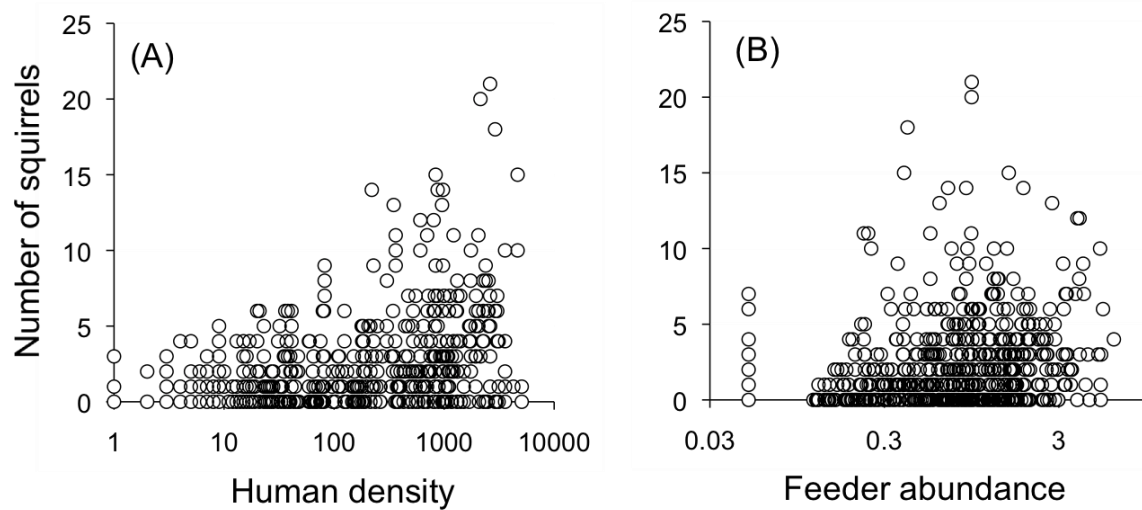


Figure legends:

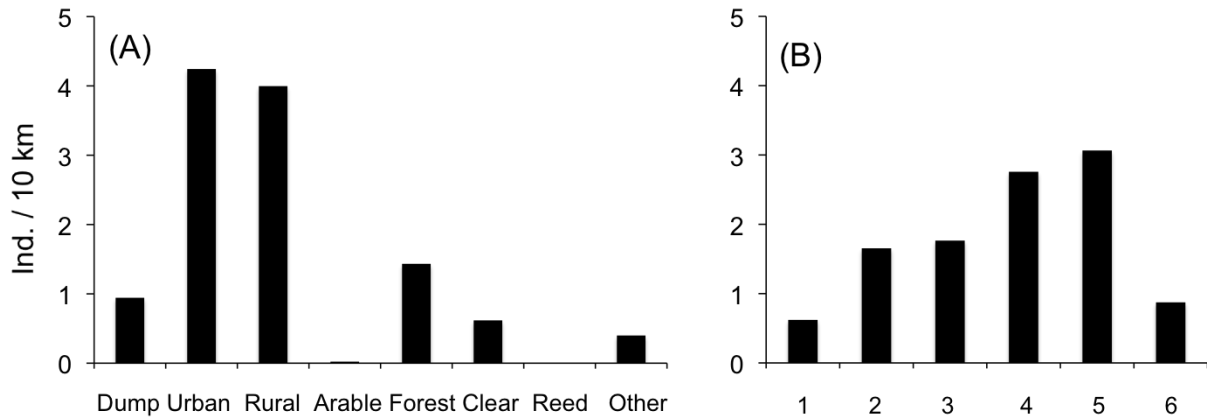
Fig. 1. Relative squirrel abundance per transect route in relation to (A) human density (humans/km²) and (B) abundance of feeding sites (feeding sites/transect route km). Note the log scale of the x-axis.

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

