


## Article

# Target Species and Other Residents—An Experiment with Nest Boxes for Red Squirrels in Central Poland

Jakub Gryz <sup>1</sup>, Tomasz Jaworski <sup>2</sup> and Dagny Krauze-Gryz <sup>3,\*</sup> 

<sup>1</sup> Department of Forest Ecology, Forest Research Institute, Braci Leśnej 3, Sękocin Stary, 05-090 Raszyn, Poland; j.gryz@ibles.waw.pl

<sup>2</sup> Department of Forest Protection, Forest Research Institute, Braci Leśnej 3, Sękocin Stary, 05-090 Raszyn, Poland; t.jaworski@ibles.waw.pl

<sup>3</sup> Department of Forest Zoology and Wildlife Management, Institute of Forest Sciences, Warsaw University of Life Sciences WULS-SGGW, Nowoursynowska 159, 02-776 Warsaw, Poland

\* Correspondence: dagny\_krauze\_gryz@sggw.edu.pl

**Abstract:** The red squirrel typically nests in dreys and tree hollows, but also (when given an opportunity) in large nest boxes. We assessed the occupancy rate of nest boxes by red squirrel and non-target species (120 boxes in the continuous forest, habitat mosaic and urban park, checked annually for eight years). Habitat type explained the variability in the occupancy of nest boxes by different species/taxa. Red squirrels used nest boxes in all habitats but occupancy rates were highest in the urban park (>50% of the boxes at maximum) and lowest in the forest. This could be explained by high population density, competition for shelters and willingness to explore alternative sheltering opportunities by urban squirrels. The yellow-necked mouse inhabited nest boxes infrequently and mostly in habitat mosaic. Tits mostly occurred in the forest and least often in the park, which suggests limited availability of natural cavities in managed forest. Nest box occupancy by starlings increased with an anthropopression level, which reflects high densities of urban and rural populations of the species. Hymenoptera (mainly wasps) were present only in rural areas, which may be due to their persecution by humans or use of anti-mosquito pesticides in urban parks. Additionally, 24 insect species were found to inhabit squirrel dreys.

**Keywords:** *Sciurus vulgaris*; yellow-necked mouse; tits; common starling; Hymenoptera; nest-dwelling invertebrates; anthropogenic transformation



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## 1. Introduction

The red squirrel *Sciurus vulgaris* is the only *Sciurus* species in Poland, widely distributed in the whole country [1]. The species primarily inhabits forests [2] but can easily adapt to mild environmental changes. That is why the red squirrel can be found in natural areas [3], but also in small woods in agricultural lands [4], as well as in the city parks [5–8]. These last habitats are, according to some studies, potentially suitable refuges for red squirrels [9]. In the cities, red squirrel abundance is approximately twice as high in urban habitats than in forests [10]. However, both in rural and urban areas, red squirrels need well-connected patches of habitat, as the species is sensitive to fragmentation [11].

Red squirrels typically nest in dreys and tree hollows, but also in large nest boxes (review in [12]). In an urban park in Warsaw, the capital city of Poland, red squirrels were also found to have their resting sites in the buildings and in other anthropogenic structures (i.e., wooden animal figures, street lamps, etc.) [13].

Anthropogenic habitat changes negatively affect the availability of natural cavities, i.e., in managed forests tree cavities are usually less abundant than in less disturbed ones [14,15] or in urban and rural areas (e.g., [16]). This negatively influences many vertebrate species that use tree cavities for breeding, hibernation or food storage [17–19], but also numerous invertebrates that develop in decaying wood and other organic material that accumulates

in these microhabitats [20–22]. To compensate for the loss of cavity trees, man-made nest boxes are widely used in forests and non-forest areas [23].

In Poland, about 25 types of nest boxes for birds and small mammals are used, of which more than 400,000 are currently installed only in the wooded areas managed by the Polish State Forests [24]. Apart from state forests, nest boxes are widely used in other wooded areas (including protected ones), urban parks and private gardens, where they are provided by municipal authorities, NGOs, scientific institutions and private land owners. Most of these nest boxes are dedicated to small birds from the Paridae family and the starling (*Sturnus vulgaris*). Nest boxes for mammals are hung less often and are dedicated mainly to bats, less often to mammals from the Gliridae family or the red squirrel.

Nest boxes can be inhabited by invertebrates, e.g., social wasps (Hymenoptera) [25], who build their nests inside boxes. Additionally, organic debris (e.g., plant parts, feces, hair) that accumulate in vertebrate nests can be exploited by numerous arthropods, primarily insects [26–28].

In Great Britain and Italy, the red squirrel populations have been in a decline due to disease-mediated competition from the introduced grey squirrel (*Sciurus carolinensis*) [29]. Replacement of red by grey squirrels occurs primarily due to exploitation competition [30] (and references therein). In Great Britain and Ireland the replacement is indeed accelerated by SQPV, but the virus is absent in Italy and replacement still occurs, albeit more slowly [31,32]. The remaining populations (and squirrel shelters) are protected [33]. Therefore, the use of nest boxes is considered a conservation tool for the red squirrel [12] allowing also the mitigation of the impact of forest operations on this threatened species [33]. Nest boxes for the red squirrel were also found to be a valuable research tool for monitoring breeding performance [34], interactions between the red squirrel and birds inhabiting nest boxes [35] or the response to predation [36].

As the red squirrel population in Poland is stable and is not threatened by alien and invasive squirrel species, it is not targeted by conservation programs. Nevertheless, one of the first nest boxes for the red squirrel was exposed in 2007 in central Poland, and was quickly inhabited by this species with breeding success (four juveniles, Figure A1, [37]). Additionally, our experience from other studies showed that bird nest boxes were inhabited by the red squirrel. For example, in 15 nest boxes for stock pigeon *Columba oenas* checked yearly (2014–2020), four dreys of the red squirrel were found [38]. In turn, in 47 nest boxes dedicated to the tawny owl *Strix aluco* checked between 2012–2018 [39], we found four red squirrel dreys [38].

These observations were a trigger to start a scientific project in order to assess the occupancy rate of artificial shelters (i.e., nest boxes) by red squirrels in Poland as a potential conservation and research tool. We assumed that, especially in urban parks, red squirrels from an abundant population would inhabit nest boxes readily. The nest box design (i.e., entrance hole placement) was supposed to limit occupancy by non-target species (i.e., birds) so we also focused on birds building their nests in the boxes. As previous studies showed, faunistic exploration of nest boxes for the tawny owl led to new records of some moths [40,41]. This is why we also focused on invertebrates building their nests in the boxes, and other invertebrates inhabiting dreys built by the red squirrel, assuming that drey material may provide sheltering opportunities for nest-inhabiting insects.

## 2. Materials and Methods

### 2.1. Study Areas

The study was conducted in central Poland, a region that is under the influence of the mild oceanic climate of Western Europe and the harsh and dry continental climate of Eastern Europe and Asia. The duration of the growing season is 210 days; the total precipitation is 600 mm per year; and the mean ambient temperature ranges from  $-4$  °C in January to  $+18$  °C in July.

We conducted the research in study areas representing three habitat types of various levels of anthropogenic pressure, two of which were located in rural areas (1. continuous

forest, 2. habitat mosaic), and one in an urban area (3. urban park). The first two study areas were managed by the Experimental Forest Station of Warsaw University of Life Sciences in Rogów. Here, forests accounted for 25% of the area (approx. 2400 ha), formed seven complexes (70–1000 ha) and were surrounded by a mosaic of different crops, pastures, fallow land and forest stands. The remaining area included arable lands (59%), orchards (5%), grasslands (5%) and scattered buildings [42–44]. The first study area was Głuchów forest (51°45′11.8″ N, 20°06′24.1″ E), the biggest unfragmented forest complex of 1000 ha, surrounded by open fields, woodlots and the Rawka River valley (which is a nature reserve). The main forest-forming species was Scots pine (*Pinus sylvestris*), with an admixture of oaks (*Quercus* spp). Part of the area was covered by wet black alder (*Alnus glutinosa*) forest. The second study area (habitat mosaic) was located near Rogów village (51°49′17.98″ N, 19°53′54.15″ E) in smaller and much more fragmented forests covered by Scots pine and oaks with an admixture of larches (*Larix* spp.), with a busy, national road and railway cutting through the forested area. Part of the forest complex was also covered by a forest nursery. The study area also encompassed the neighboring Rogów arboretum and WULS campus. The arboretum was founded in 1925. Fragments of the forest which existed before the arboretum was organized included 150-year-old pines. The third study area was located in Łazienki Park, a 76 ha urban park located in the central district of Warsaw (the capital city of Poland, approximately 2 million inhabitants). It is a representative area with numerous old trees that provide a rich and natural food base [5]. In addition, as a result of being founded in the 17th century, it also contains historical buildings. The park has 92 species of trees and shrubs, comprising both native and exotic species. The tree cover in the park is approximately 70% and roughly one in every five trees is more than 140 years old [5]. The park is very popular among both tourists and the local inhabitants, and is visited by more than 2 million people every year [45]. Squirrels are often fed nuts by visitors [46,47], and their population here reaches very high density (i.e., more 2 ind./ha, [13]). Squirrels occupy small home ranges and human-delivered food plays an important role in the diet of some individuals [7,8].

## 2.2. Data Collection and Laboratory Analyses

In autumn 2012, 40 wooden boxes dedicated to the red squirrel were hung in the second (landscape mosaic) and the third (urban park) study area. Next, 40 nest boxes were hung in autumn 2013 in the first study area (continuous forest). These were modified nest boxes for dormice, i.e., they had an entrance hole at the back (facing the tree trunk); inner bottom measurements were 16 × 16 cm, maximum height was 49 cm and the board was 2 cm thick. The entrance hole diameter was 5.5 cm (Figures A1 and A2). The nest boxes were attached to a tree trunk with nails at 5 m height. They were set at least 100 m apart. All nest boxes were checked and cleaned every year in winter (usually December/January), old nests were removed and nest boxes were repaired if necessary. During control, the species (or higher taxa) were determined on the basis of the nest appearance built in the nest box. The nest boxes in the landscape mosaic and the urban park (study areas no. 2 and 3) were first checked in winter 2013/14 (which delivered data on their occupancy in 2013), and nest boxes in the forest (study area no. 1) were first checked in winter 2014/15 (data on their occupancy in 2014). The last nest box check was carried out in January 2021 in all three study areas (data on their occupancy in 2020).

In addition, to monitor vertebrate species visiting the nest boxes, six trail cameras were placed next to selected nest boxes (Figure A3) in the second study area (habitat mosaic) shortly after their installation (in November 2012). Trail cameras were exposed for one year (until 8 December 2013), they were checked every six weeks (to replace memory cards and batteries) and were then moved to another nest box. Altogether, 21 of 40 nest boxes were monitored by trail cameras. Three different camera trap models were used: one RECONYX PC900 HyperFire Professional IR, one RECONYX PC90 and four Ecotone SGN-5220. All cameras were set to make a series of three photos at 1 s intervals. Each registered animal was considered as a single observation if a minimum of 15 min elapsed

between subsequent photos or series of photos of the animal. The exception to this rule was only made in circumstances clearly indicating that the animal in the photo was different from the previously registered one (different gender, age, color pattern, etc.).

To study insects inhabiting nests of red squirrels, dreys found in the nest boxes were taken to a laboratory and placed separately in plastic containers with ventilated lids. The containers were left in a non-heated room for a few weeks to allow the insects to complete their winter diapause. They were then brought to the heated laboratory and checked every 2–3 days. Adult insects were then collected and preserved as dry specimens or in ethyl alcohol. The insects were identified on the basis of their morphology and in certain cases (moths) were also identified by the morphology of their genitalia. Species identification was done by: Radosław Plewa (Forest Research Institute, Sękocin Stary, Poland)—Coleoptera, Seweryn Grobelny (Poznań, Poland)—Dermaptera, Grzegorz Hebda (University of Opole, Opole, Poland)—Hemiptera, Waldemar Żyła (Upper Silesian Museum, Bytom, Poland)—Hymenoptera, Tomasz Jaworski (author)—Lepidoptera and Roland Dobosz (Upper Silesian Museum, Bytom, Poland)—Neuroptera and Raphidioptera. Insect larvae were not identified due to difficulties in their identification. Additionally, some insect groups (e.g., flies—Diptera) were left out due to lack of specialists being able to do the identification.

### 2.3. Statistical Analysis

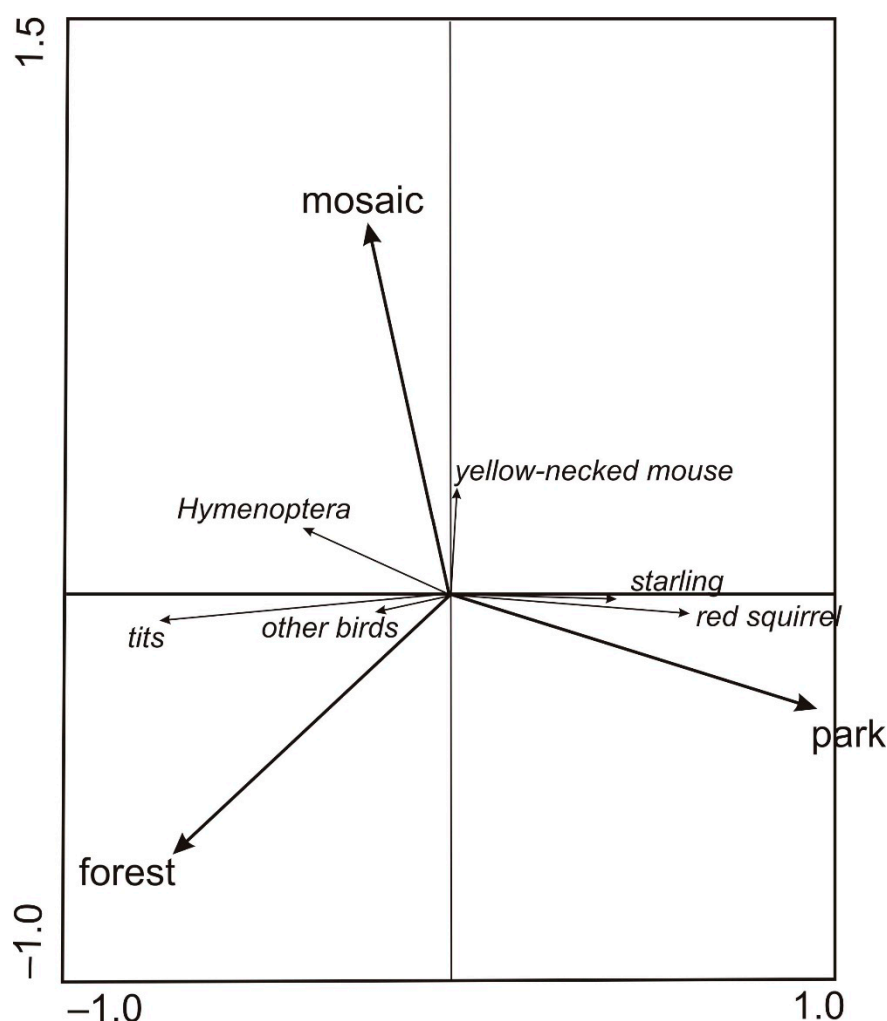
As nest boxes in the first study area (continuous forest) were hung one year later than in the second and third ones, to compare occupancy of nest boxes by various species/taxa between study areas, only data from the years 2014–2020 were taken for comparisons. Data on the recorded species were pooled for single nest boxes. To investigate differences in the occupancy of a nest box by main species/taxa (i.e., red squirrel, yellow-necked mouse (*Apodemus flavicollis*), tits, common starling, Hymenoptera) between the three studied areas, a redundancy analysis (RDA) was implemented in CANOCO software. The pooled number of records of a given species was calculated for each nest box, which gave 40 samples for each study area. The occupancy rates by each species for a given nest box were defined as the response variables, whereas the study area served as the explanatory variable. A Monte Carlo test (499 permutations) was used to test the statistical significance of the differences between the occupancy rates by different taxa in three habitats. To compare the occupancy rates separately of each species/taxa (red squirrel, yellow-necked mouse, tits, starling, Hymenoptera) between study areas we used the Kruskal–Wallis test (data did not follow a normal distribution—Shapiro–Wilk W test), with a Mann–Whitney pairwise test for post-hoc analysis (Bonferroni-corrected  $p$  values).

To compare the proportion of nest boxes used by vertebrates/all animals each year between study areas we used the Kruskal–Wallis test.

The analyses were done in Canoco 4.5 [48] and Past 4.05 [49] software.

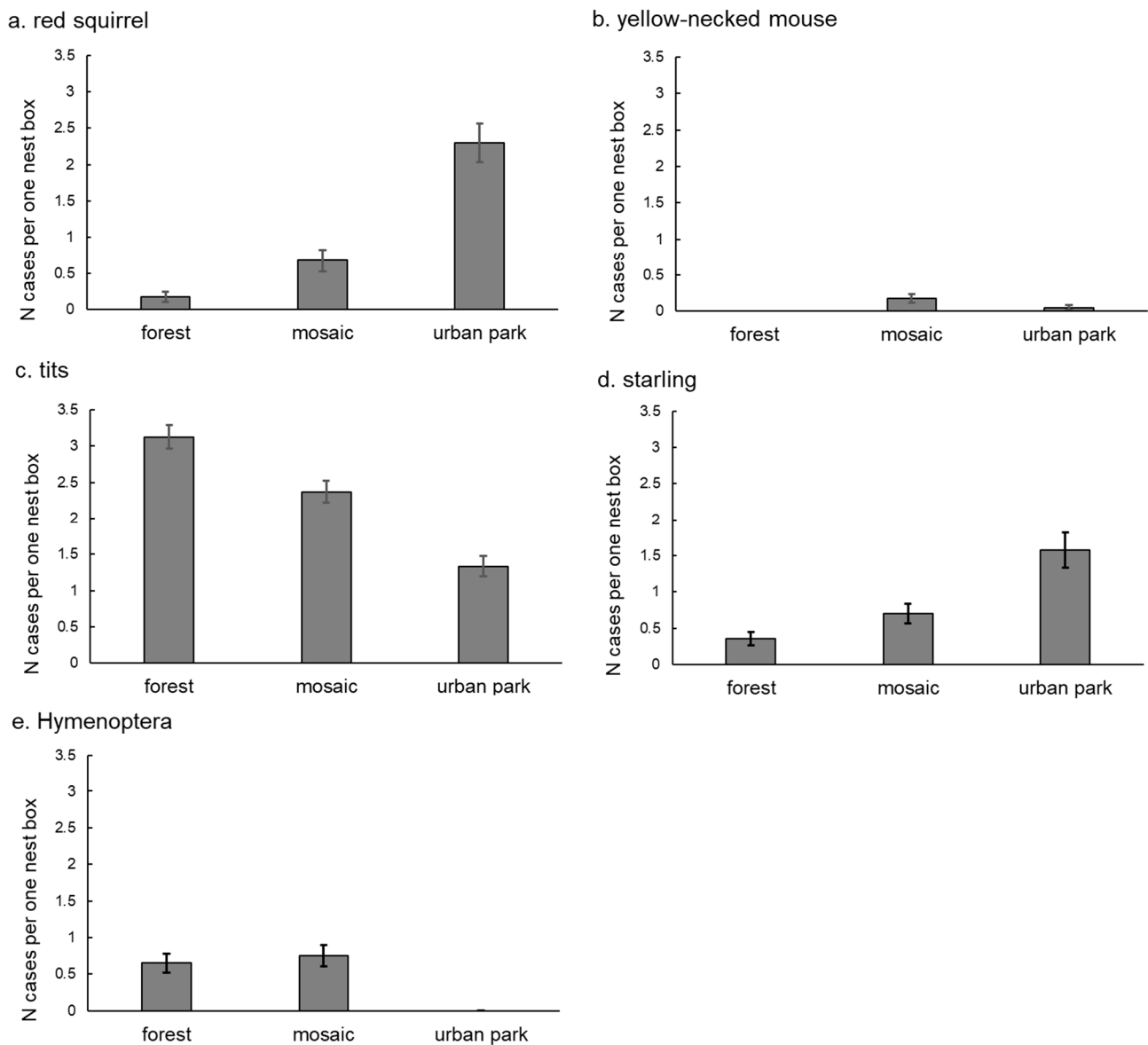
## 3. Results

RDA revealed that the landscape type (continuous forest, habitat mosaic, urban park) significantly explained the variability (the amount of variation explained by landscape type was 38.5%) in occupancy of nest boxes by different species/taxa (pseudo- $F = 71.272$ ,  $p < 0.005$ ) (Figure 1). Red squirrel and starling were mostly connected to the urban park, yellow-necked mouse and Hymenoptera to the habitat mosaic and tits to the forest.



**Figure 1.** Biplot from redundancy analysis (RDA) showing the influence of the habitat (continuous forest, habitat mosaic, urban park) on the variability in species of animals building their nests in the boxes dedicated to the red squirrel in central Poland in the years 2014–2020.

The red squirrel most often inhabited nest boxes in the urban park (i.e., 2.3 records per one nest box in the years 2014–2020), and the lowest value was recorded for the continuous forest (0.18) (Figure 2a). The occupancy rate differed between habitats (Kruskal–Wallis test,  $H = 42.96$ ,  $p < 0.001$ ) and in post-hoc analysis differences were found between all pairs of habitats. In total (data from all seasons, 2013–2020), in the urban park red squirrels were recorded 95 times, in the habitat mosaic 27 times and just 7 times in the forest (Table A1). In the urban park, the highest number of red squirrel dreys were recorded in the second year of exposition (2014) when they were found in more than half ( $n = 21$ ) of the boxes, and the lowest was in the last but one year, 2019 ( $n = 9$ ). In the habitat mosaic, 7 boxes were occupied by the red squirrels at maximum (in 2017), while in the forest only 0–2 boxes were inhabited each year.



**Figure 2.** The occupancy of the nest boxes dedicated to the red squirrel (mean  $\pm$  SE occupancy per one nest box in the 2014–2020 research period) by a target (i.e. red squirrel—figure (a)) and non-target species/taxa ((b). yellow-necked mouse, (c). tits, (d). European starling, (e). Hymenoptera) in the three habitats of various anthropoppression in central Poland. Each nest box was checked once a year (in winter), and data on records (presence of the nest inside a box) of species/taxa for each nest box from the whole research period were pooled together.

The other mammal species present in the nest boxes was the yellow-necked mouse. Yet, its occupancy rate was much lower: mice were never found in the forest, in the mosaic the occupancy rate was 0.18 records per one nest box and in the urban park it was 0.05 (Figure 2b) and the occupancy rate did not differ between the two habitats ( $H = 0.92$ ,  $p > 0.05$ ).

Among birds, tits inhabited the nest boxes most often (they were recorded 240 times in total and were the most frequently recorded from all species, Table A1). Additionally, in this case a clear difference between study areas was found ( $H = 25.9$ ,  $p < 0.001$ , post-hoc differences between all pairs). The highest occupancy rate was recorded for the forest complex (3.13 records/nest box), where nests were found 125 times (Table A1), while the lowest was for the urban park (1.33) (Figure 2c). The other bird whose nests were often recorded in the boxes was the starling (Figure 2d). In contrast to tits, starlings were most

often recorded in the urban park (1.58 records per one nest box), and least often in the forest (0.35); this difference was statistically significant ( $H = 15.03$ ,  $p < 0.001$ , post-hoc differences found to be significant for all pairs). Other birds that nested occasionally in the boxes were flycatchers (Muscicapidae) and the Eurasian nuthatch (*Sitta europea*).

Among invertebrates, nests of Hymenoptera (mainly wasps, Vespidae) were often found (68 records) in the boxes dedicated to red squirrels, but only in rural areas ( $H = 19.09$ ,  $p < 0.001$ , Figure 2e).

On average, signs of animals' presence in the nest boxes were found during 62.7 (min = 35.0, max = 92.5) and 54.2% (min = 27.5, max = 32.5) of nest box checks ( $n = 920$ ) for all species and vertebrates, respectively (data from years 2013–2020). These values did not differ between study areas in the subsequent years, neither for all species (Kruskal–Wallis test,  $H = 1.25$ ,  $p > 0.05$ ), nor for vertebrates ( $H = 1.03$ ,  $p > 0.05$ ). Out of 40 nest boxes installed in each study area, 7 were used by the red squirrel in the forest, 18 in the habitat mosaic and 34 in the urban park. All nest boxes were used by tits in the forest (min number of records per one nest box = 1, max = 5), 36 in the habitat mosaic and 14 in the urban park. Overall, all nest boxes were used at least once by a vertebrate inhabitant. Wasps were recorded in 18 nest boxes in the forest and 26 nest boxes in the habitat mosaic.

On the basis of data collected from trail cameras installed next to nest boxes in the habitat mosaic, the red squirrel was the most often recorded species (43.2% of all records). Additionally, the great spotted woodpecker (*Dendrocopos major*) and great tit (*Parus major*) were observed frequently (17.3 and 15.5% of records, respectively). The other species were birds: Eurasian nuthatch, tawny owl, common chaffinch (*Fringilla coelebs*), Eurasian jay (*Garrulus glandarius*), European robin (*Erithacus rubecula*), European green woodpecker (*Picus viridis*) and common buzzard (*Buteo buteo*); and mammals: yellow-necked mouse, stone marten (*Martes foina*) and domestic cat (*Felis catus*). The animals were seen to enter the nest box, examine the entrance hole or perch on the nest box.

Our study revealed 24 insect species inhabiting dreys of red squirrels built in nest boxes. Beetles (Coleoptera) were the most diverse, with 16 species, followed by moths (Lepidoptera; 5 species), earwigs (Dermaptera; 1 species), true bugs (Hemiptera; 1 species) and net-winged insects (Neuroptera; 1 species) (Table A2).

#### 4. Discussion

Nest-site availability limits cavity-using populations in many managed forests (review in [50]) and numerous birds (review in [23]) and mammals (review in [12]) are known to use nest boxes as natural cavity replacements.

In our study, red squirrels used nest boxes in all habitats but occupancy rates were highest in the urban park. This can be explained by the very high density of the red squirrel population in this area, driven by supplementary feeding [7]. The occupancy rates recorded in the urban park in our study (from a few to around 50% of the nest boxes available) were very similar to what was found in Great Britain (2 to maximum 53%) in a very abundant red squirrel population [12]. Local density may inversely affect the number of nests used by individual squirrels [51] and high density of population may result in competition for shelters and willingness to explore new resting possibilities. Squirrels in the urban park were also observed to build their dreys inside various anthropogenic shelters, such as buildings, street lamps or wooden ornamental figures of animals [13], which may be because of the high behavioral plasticity of urban populations of this species. In most cases the nest boxes in the urban park did not seem to be used by red squirrels for breeding. Nevertheless, squirrels can use several nests in sequence, and for various purposes (such as daytime or nighttime rest, breeding, etc.) [51]. On one hand, nest boxes offer a more permanent sheltered nest site than bolus nests, which are more vulnerable to unfavorable weather conditions (such as strong wind, rain, heavy snowfall). On the other hand, they are more permanent, which may place occupants at a greater risk of predation from mammalian predators [34]. In the urban park under study (as in other green spaces of Warsaw) the stone marten was abundant and this species was also often recorded to visit

and look into the squirrel nest boxes. Both marten species (*M. martes* and *M. foina*) were also present in our rural study areas [39,52]. Martens are also known to use nest (or den) boxes readily for breeding [53]. In the case of our earlier studies, both pine and stone martens were recorded in nest boxes dedicated to the tawny owl [52]. Yet, nest boxes provided for the red squirrels in our study were much smaller than the tawny owl boxes and (as assumed at the construction stage) entrance holes were not large enough for martens to enter their heads. Other mammalian predators that were recorded by camera traps to look into nest boxes were domestic cats. Domestic cats are abundant in our rural study areas [52,54] and both in rural and urban sites are one of the most important mammalian predators [55,56]. Additionally, in rural areas, the northern goshawk (*Accipiter gentilis*), who is known to be an important red squirrel predator [36], was present [43], and the predation risk might have affected nest box use by the red squirrel [36].

In this study, nest box occupancy by the red squirrel was dependent on the habitat, i.e., boxes placed in rural areas were occupied less often than in urban areas. Especially in the first study area (continuous forest), nest box occupancy was low. Additionally, in Finland, red squirrel occurrence in nest boxes was positively associated with the amount of farmland in the landscape surrounding the nest box (which may be explained by the fact that farmland is usually established on rich soils and forest edges are dominated by deciduous trees, a source of high-quality seeds), and also with built-up areas (which may be related to availability of supplemental food in bird feeders). In turn, mature birch–spruce forest had a negative impact on the red squirrel occurrence [36]. This is in contrast to British studies where, in a coniferous habitat, nest boxes were used by adults, subadults, lactating females and their young. It was concluded that the box occupancy may partly depend upon the density of squirrels (and the density of boxes). Indeed, in the British study site, population density was very high (3.5–4 ind./ha) thanks to supplemental feeding [34]. We may expect that densities in rural areas in our study were far lower [52,57]. Nest boxes for red squirrels may be especially important in heavily managed forests or younger stands. In another study performed in Great Britain, thinning in a commercial forest led to squirrels occupying more nest boxes, which were assessed as useful to mitigate the impacts of forest operations. However, no evidence of breeding in nest boxes was found in that case; the boxes could be important as shelters during forest operations and potentially for juveniles during natal dispersal [33]. In the case of another squirrel species, the grey squirrel, a population living in a young forest reacted with an abundance increase after artificial dens were erected. This was attributed to better survival of both young and adult individuals, thanks to providing structures that could afford secure nest sites [58]. Yet, when assessing the significance of nest boxes for the red squirrel, it must be taken into account that squirrels use various shelters (review in [59]) so they may switch from bolus nests to nest boxes and vice versa. Indeed, in the mature mixed forests of British Columbia, the American red squirrel and northern flying squirrel (*Glaucomys sabrinus*) used many exposed nest boxes (and this nest box addition presumably led to an increase in squirrel abundance) but this could have been attributed to squirrels moving from bolus nests to nest boxes, not solely to population increase [50]. Overall, our results suggest that nest box use by red squirrels can (at least to some extent) depend on the density of the population. It may also be assumed that urban red squirrels, being accustomed to various anthropogenic changes, will more readily accept alternative shelters in the form of nest boxes. In our case, no significant differences were found between nest box occupancy in the subsequent years. Yet, in the case of the urban park, the most ( $n = 21$ ) nest boxes were used by red squirrels in the second year of their deployment. This resembles what was shown in the other study in the forest in Great Britain [33], and suggests that squirrels habituate to nest boxes over time. In our case, as in Finland, nest box occupancy decreased over time [36], which may be explained by the nest box natural deterioration over time.

The other rodents whose nests were found in the nest boxes were yellow-necked mice. This species is known to use nest boxes, e.g., dedicated to a dormouse (*Muscardinus*



*avellanarius*) [60]. Yet, the occupancy rates were rather low and mice were present mostly in rural areas.

Squirrels and birds may interact when using the same cavities. First of all, squirrels will compete for cavities with birds. In a forest in Great Britain, the presence of great tit clutches and broods did not prevent red squirrels from occupying boxes (only 28% of all recorded clutches were found to have produced fledglings, squirrels were found to eat some of the chicks and eggs) [35]. There was a strong negative interaction between spring great tit box occupancy and the use of boxes by red squirrels [12]. On the other hand, when the jackdaw *Corvus monedula* occupied nest boxes, the red squirrel started to avoid this shelter [35]. On the other hand, the dry material of abandoned squirrel nests can be explored and used by songbirds [61]. In this study, nest boxes in the forest were mostly occupied by tits. This may suggest that natural cavities are limited in this area (but might have also been driven by differences in the population density; this could not be tested as no density estimates were available). Indeed, in the urban park there are numerous deciduous trees which provide tree holes. In the habitat mosaic there were old trees (in the arboretum, in the form of experimental stands and in a nature reserve) which were absent in the first study area (continuous forest). It was shown that there was a high difference in the cavity resources between a Białowieża national park (12.5/ha) and managed stands (3.0/ha), as most cavities were in dead (mostly pine) trees (over 74%) [14]. Similar results were obtained in northern Swedish boreal forests, i.e., unmanaged forests had a significantly higher density of cavities (2.4/ha) than managed old forests (1.1/ha) [15].

In Great Britain, the occupancy of nest boxes for red squirrels by great tits varied between 10 and 43%, and the occupancy rate of great tits increased over the years [12]. Similarly, in our case nest box occupancy by tits seemed to rise in the first few years but then dropped, probably due to natural wood deterioration and unfavorable conditions inside the box. It was shown that massive nest box supplementation boosted fecundity, survival and immigration in a recovering hoopoe (*Upupa epops*) population [62]. Additionally, density of mountain chickadee (*Poecile gambeli*, Paridae) increased after nest box addition and declined following box removal in mature mixed conifer forest in British Columbia, suggesting that populations were limited by cavity availability [50]. On the other hand, hole-nesting birds seem to be very flexible and often locate their nests in anthropogenic breeding sites (in the suburbs of Warsaw this included even vertical metal pipes), and in the case of great tits this type of shelter was dominant [63].

The other bird species that occupied nest boxes was the common starling, which in our case was mostly connected to the urban park but also to the habitat mosaic. In Poland, this species is most common in rural and urban areas, nesting also in the ecotone but avoiding continuous forests [64]. This species is known to breed in various habitats, although urbanization can negatively affect the reproductive parameters of starlings [65]. Starlings often occupy nest boxes, but they prefer deeper ones and those without old nests [66], which may be explained by the cost of old nest material removal [67]. Starlings are able to compete for nesting holes with many primary and secondary cavity nesters. In an experiment conducted in Poland, in an urban forest, starlings took some of the holes chosen by nuthatches for breeding. Yet, it is claimed that where starling is a native species, it is not able to influence the cavity-nesting community to a great extent [68]. The boxes exposed in our study were very similar in dimensions to nest boxes dedicated to starlings, so it was not surprising these birds occupied a high proportion of the boxes. Yet, we may expect that the red squirrel, being heavier, would be able to successfully compete with starlings for these shelters.

The last group of animals that built their nests in the nest boxes in our study were Hymenoptera (mainly wasps, *Vespa* sp., and less often hornets, *Vespa crabro*). Wasps are known to build their nests in various spaces, including nest boxes for birds (e.g., [69,70]). Other species from this group (bumblebees, *Bombus* spp., and honey bees, *Apis* spp.) were found in the nest boxes in Great Britain [12,35]. Yet, it was shown that occupation of nest boxes by these insects was generally low (and, interestingly, these insects were never found

in tree cavities) [25]. It is hard to explain absence of Hymenoptera in the urban park in our study as this insect group is widespread and common. We can only hypothesize than in the cities, wasps and hornets are persecuted due to their harmfulness for humans. Additionally, some insecticides are used in the park to limit the number of mosquitoes (or other pests), which may also affect Hymenoptera negatively (e.g., [71], and the literature cited therein). Moreover, urban habitats are characterized by a relatively low abundance of insects [72], so the food base for predatory insects, including wasps and hornets, may be limited.

Not only nest boxes themselves provided animals with sheltering opportunities, but the nests of red squirrels built in nest boxes were also inhabited by numerous species of nidicolous, i.e., nest-associated, insects. Most of them were saprophagous, i.e., feeding on plant or animal detritus. In the first group, there were representatives of a few families of beetles (Histeridae, Ptinidae, Latridiidae, Tenebrionidae), which, both as larvae and adults, feed on the various remains building the nest lining. The second group included beetles, whose larvae feed on keratin and animal fat (fur, animals carcasses) accumulating in the nests. This mainly included beetles from the Dermestidae family [73] and moths from the Tineidae [74–77] and Oecophoridae [78] families.

Seasonally unfavorable conditions, mainly low winter temperatures, force most insects to stop their activity and search for refuges (e.g., [79]). Usually, natural cavities are used, e.g., tree holes, spaces under tree bark. Yet, some species have adapted to inhabiting shelters of an anthropogenic origin, which includes nest boxes for birds [40,41,80]. As we have shown in this study, nest boxes for the red squirrel can also be used by numerous insects as overwintering sites. Insects that inhabited dreys in nest boxes were some beetles (e.g., *Harmonia axyridis* in this study), Hemiptera, including Lygaeidae recorded in this study, Neuroptera, including green lacewings (*Chrysoperla* spp.), and also some moths (Bucculatricidae, Elachistidae) [41,81]. Further, wasp nests inside nest boxes for vertebrates can serve as habitats for other insects, i.e., the bee moth *Aphomia sociella*, whose caterpillars feed on wax and honey and are even predators of wasp larvae (e.g., [81]). The group of nidicolous insects include predatory species, such as earwigs (Dermaptera) (e.g., [82]).

Nest boxes can be a valuable conservation and research tool, yet variables such as their dimensions, placement height and the way they are constructed and maintained may affect their use, thus producing potential bias [23]. As shown by other studies, both positive and negative influences of nest box provision on the reproductive output of target species have been documented and this may depend on the habitat. It may be strongly positive in one habitat and smaller or even negative in another habitat within the same study area. Furthermore, nest boxes may create an ecological trap by causing a supra-optimal breeding density (review in [83]).

To conclude, as we have shown in our study, the occupancy of nest boxes by the red squirrel depended on the habitat type and was presumably driven by the red squirrel population density, higher competition for shelters in urban habitats and willingness to explore alternative sheltering opportunities by urban populations. This shows that nest boxes can help limit the competition for shelters. Nest boxes dedicated to and designed for red squirrels were readily occupied by two bird species/groups (tits and starlings) and Hymenoptera. Additionally, in this case, habitat type (and the anthropopression level) affected occupancy rate. Nevertheless, none of these taxa are supposed to effectively limit the occupancy of nest boxes by the red squirrel. High occupancy of nest boxes by tits in the forest suggests limited availability of natural cavities, while high occupancy of nest boxes by starlings in the urban park may result from the high densities of urban populations of the species.

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## Appendix A



**Figure A1.** Young squirrel *Sciurus vulgaris* in one of the first nest boxes dedicated to the red squirrels in Poland. The nest box was placed in 2007 in central Poland and the next year a reproductive success was recorded in it. The box has an entrance hole at the back, i.e., facing the tree trunk. Such nest boxes were used in this study in the years 2013–2020.



**Figure A2.** A check of the nest box dedicated to the red squirrel; the front panel is removed. The box was occupied by the target species (photo by Adam Tarłowski).



**Figure A3.** A red squirrel on nest box dedicated to this species (a camera-trap-taken photo). The nest box was placed autumn 2013 in a habitat mosaic of central Poland (study area no. 2) and monitored by photo traps.

## Appendix B

The nest boxes (40 nest boxes in each study area) were checked once a year (in winter). The total number of records of a given species/group of animals in all nest boxes was given for each year

**Table A1.** The number of records of presence of a species/higher taxa (red squirrel, yellow-necked mouse, tits, European starling, Hymenoptera) in the nest boxes dedicated to the red squirrels in the three habitats of different level of anthropopression in central Poland.

Years/Study Area	Squirrel	Mouse	Tits	Starling	Hymenoptera
n of records					
1. Continous forest					
2014	1		23		6
2015			29	5	
2016	1		24	4	2
2017	2		13	3	3
2018	1		12		5
2019	1		16	1	7
2020	1		8	1	3
Total	7		125	14	26
2. Habitat mosaic					
2013		1	14	3	12
2014	4	2	16	4	5
2015	5	2	14	5	1
2016	1	2	15	6	2
2017	7		11	3	6
2018	4		10	1	5
2019	3		9	5	9
2020	3	1	8	4	2
Total	27	8	97	31	42
3. Urban park					
2013	3		2	10	
2014	21		2	13	
2015	13		4	10	
2016	15		1	10	
2017	13		1	10	
2018	10		5	4	
2019	9	2	1	7	
2020	11		2	9	
Total	95	2	18	73	
All study areas	129	10	240	118	68

## Appendix C

**Table A2.** Species of insects found in nesting material accumulated in the nest boxes occupied by the red squirrel in central Poland in the three habitats (continuous forest, habitat mosaic and urban park) in the years 2013–2020.

Order	Family	Family/Species	Total Abundance	
Coleoptera	Coccinellidae	<i>Harmonia axyridis</i> (Pallas, 1773)	1	
	Cryptophagidae	<i>Cryptophagus</i> sp.	1	
	Curculionidae	<i>Phyllobius arborator</i> (Herbst, 1797)	1	
	Dermestidae	<i>Anthrenus museorum</i> (Linnaeus, 1761)	2	
		<i>Anthrenus pimpinellae</i> Fabricius, 1775	3	
		<i>Attagenus pellio</i> (Linnaeus, 1758)	1	
		<i>Ctesias serra</i> (Fabricius, 1792)	1	
		<i>Dermestes lardarius</i> Linnaeus, 1758	2	
		<i>Globicornis corticalis</i> (Eichhoff, 1863)	1	
		<i>Megatoma undata</i> (Linnaeus, 1758)	12	
		Latridiidae	<i>Latridius minutus</i> (Linnaeus, 1767)	1
		Malachiidae	<i>Malachius bipustulatus</i> (Linnaeus, 1758)	3
		Ptinidae	<i>Ptinus fur</i> (Linnaeus, 1758)	1
	<i>Ptinus raptor</i> Sturm, 1837		1	
	Tenebrionidae	<i>Stegobium paniceum</i> (Linnaeus, 1758)	1	
<i>Tenebrio molitor</i> Linnaeus, 1758		2		
Dermaptera	Forficulidae	<i>Forficula auricularia</i> Linnaeus, 1758	9	
Hemiptera	Lygaeidae	<i>Arocatus melanocephalus</i> (Fabricius, 1798)	1	
Lepidoptera	Bucculatricidae	<i>Bucculatrix thoracella</i> (Thunberg, 1794)	1	
	Elachistidae	<i>Agonopterix</i> sp.	1	
	Oecophoriadae	<i>Borkhausenia minutella</i> (Linnaeus, 1758)	1	
	Pyalidae	<i>Aphomia sociella</i> (Linnaeus, 1758)	4	
	Tineidae	<i>Tinea pellionella</i> Linnaeus, 1758	1	
Neuroptera	Chrysopidae	<i>Chrysopa</i> sp.	1	

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