Contrast in daily activity patterns of red squirrels inhabiting urban park and urban forest

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Abstract:
The Eurasian red squirrel is one of the species that has well adapted to urban habitats and is habituated to human presence. Its urban populations differ from those in rural habitats in terms of e.g. abundance, spatial organisation and behaviour. Food availability affects the ecology of red squirrels, so in this study we hypothesise that in the urban park with supplemental food, red squirrels will alter their activity rhythms to benefit from human presence. We therefore compared seasonal changes in the daily activity patterns of two red squirrel populations, inhabiting two different areas in Warsaw: a busy urban park (with plentiful supplemental feeding) and an urban forest reserve (closed for public). Between September 2018 and July 2019 we used camera traps to monitor red squirrels activity round-the-clock. In the park (contrarily to the forest), the number of records of red squirrels per 100 trap days was lowest in summer and highest in winter. Probably squirrels in the urban park, were able to maintain high activity during winter thanks to all-year-round availability of supplementary food. Daily activity patterns differed seasonally and between the study sites. In the forest they resembled those recorded in natural habitats, i.e. two activity peaks, one after the sunrise and second before the sunset. In contrast, park squirrels showed mostly one activity peak, beginning some hours after the sunrise and lasting until noon/early afternoon (depending on the season). Park squirrels were almost exclusively day-active, while forest squirrels were also recorded before sunrise and after sunset. We suggest that park squirrels shifted their activity to times with higher visitor frequency, which, assumingly, increased chances to obtain supplemental food.

Keywords: supplementary feeding, Sciurus vulgaris, human disturbances, camera-traps.

Received: 2021-08-02
Revised: 2021-10-21
Accepted: 2021-10-25
Final review: 2021-10-21

Running title: Contrast in squirrels' activity in park and forest

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Introduction

Historically, urban habitats have been ignored as potentially suitable wildlife habitats (McCleery et al. 2014). However, many animal species may adapt to these specific conditions (Jackowiak et al. 2021, Jasińska et al. 2021, Lesiński et al. 2021, Gryz and Krauze-Gryz 2018, Francis and Chadwick 2012, Alvey 2006), by changing e.g. their diet preference, home range size, behaviour, including vigilance and activity budget (Ritzel and Gallo 2020). Wildlife species exhibit a variety of responses to human presence, ranging from attraction to habituation to avoidance (review in Patten, Burger 2018). In example, bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) clearly avoided humans by becoming more nocturnal (George and Crooks 2006), while striped-field mouse (*Apodemus agrarius*), which is strictly nocturnal in nonurban habitats, became diurnal in town parks, despite the constant presence and high levels of human activity (Gliwicz et al. 1994). Understanding impacts of increasing urbanisation on wildlife is crucial for conservation of animal species (McCleery et al. 2014).

Eurasian red squirrel *Sciurus vulgaris* is one of the species that has adjusted to urban habitats and is habituated to human presence (Krauze-Gryz et al. 2021a, b, Kostrzewa and Krauze-Gryz 2020, Uchida et al. 2019, Haigh et al. 2017b, Fey et al. 2016, Reher et al. 2016, Rézouki et al. 2014, Babińska-Werka and Żółw 2008). In the past few years, research interest in urban populations of red squirrel has increased (reviewed in Fingland et al. 2021), and they were shown to differ from rural habitats, e.g. abundance of this species increased with human population density (Jokimäki et al. 2017), individuals occupied smaller home ranges (Krauze-Gryz et al. 2021a, Hämäläinen et al. 2018), and utilized various urban structures (Hämäläinen et al. 2018). Animals spent more time on the ground and frequently interacted with humans (Krauze-Gryz et al. 2021a, b), and an increasing boldness was one of the most prevalent behavioural modifications (Uchida et al. 2016, 2019). Surprisingly, little is known about activity pattern of red squirrels inhabiting cities. Yet, in Hamburg it was noted that red squirrels inhibiting city centre were less active throughout the day than their conspecifics in semi-natural habitat (Thomas et al. 2018). Nevertheless, that study was based only on late-winter/early-spring data.

Readily available food in urban environments is believed to be one of the reasons why numerous animal species are thriving in cities around the world (review in Spelt et al. 2021). In urban conditions, red squirrels are offered various sources of supplementary foods including the gathering of food from bird feeders as well as the provision of nuts offered directly by park visitors (Krauze-Gryz et al. 2021a, Kostrzewa and Krauze-Gryz 2020, Krauze-Gryz and Gryz 2015, Bosch and Lurz 2012). It has been shown that supplemental food is a crucial factor that may attract squirrels in urban environments (Jokimäki et al. 2017), and this extra food is most important when natural food availability is low (Magris and Gurnell 2006). Because food availability (i.e. tree seeds) affects the ecology of red squirrels (Jokimäki et al. 2017, Selonen et al. 2016, Wauters et al. 2008, 2007), we can hypothesise that in the urban park with plentiful supplemental food, red squirrels will alter their activity rhythms to benefit from human presence. Indeed, food provided by humans to wildlife in urban areas may lead to changes in behaviour of animals that use this resource (Sal et al. 2013, Lowry et al. 2013). For example chipmunks (*Tamias striatus*), in urban environment altered their seasonal behaviour patterns, i.e. there was no reduced activity levels, normally observed in rural habitats, because of human-suppled food resources (Ryan and Larson 1976). Coypus (*Myocastor coypus*) in the urban habitat (differently that in non-urban areas) were active during the day and early evening and this reversal of activity patterns was attributable to deposition of human food in the city area during the daytime (Meyer et al. 2005). Finally, gulls adapted their foraging behaviour to human time schedules when beneficial (Spelt et al. 2021).

The aim of a study was to compare seasonal changes in the daily activity patterns of the two red squirrel populations inhabiting the same city but two utterly different areas: a busy urban park and an urban forest. Both green spaces are within city districts. Nevertheless, one is expected to be highly influenced by the human presence and supplementary food from park visitors, whereas the effect of human disturbance on the other population should be negligible. Indeed, an earlier study showed that park squirrels significantly altered their behaviour in response to human presence by spending more time on the ground and tolerating close contact. Moreover human-delivered nuts made the bulk of a diet (Krauze-Gryz et al. 2021 a). We hypothesise that daily activity patterns of squirrels inhabiting urban park will also differ from those observed for forest squirrels as they may adjust their activity to benefit from supplemental feeding.

Materials and methods

Study area

We conducted our study in Warsaw (52°14'13.37" N, 21°1'3.11" E), Poland, a large city with approximately two million inhabitants. It is located in the central part of the country, a region that is affected by both 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 approximately 210 days, the total precipitation measures 600 mm per year, and the mean ambient temperature ranges from -4°C in January to 18°C in July. Nevertheless, the minimum temperature may drop below -30°C and the maximum temperature may rise above 35°C.

This research was conducted in two green areas. The first was an urban park (together with historical buildings) named Łazienki Royal Museum (52°12'27.60" N 21°01'34.80" E). The park was formed in the 17th century, is located in the city centre and is very popular among visitors and local inhabitants – every year the park is visited by more than 2 million people (Kruczek 2015). Squirrels are often fed nuts by visitors (Krauze-Gryz et al. 2021a, b, Kostrzewa and Krauze-Gryz 2020, Krauze-Gryz and Gryz 2015). The park covers 76 ha and it has 92 species of trees and shrubs. Tree cover is about 70% and about 20% of trees reach more than 140 years (Babińska-Werka and Żółw 2008). Tree species are mostly deciduous, e.g. hornbeam (*Carpinus betulus*), common oak (*Quercus robur*), beech (*Fagus sylvatica*), as well as hazel (*Corylus avellana*), walnut (*Juglans regia*) and North American walnut (*Juglans nigra*) (Babińska-Werka and Żółw 2008).

The second study site was Natolin Forest Reserve (52°8′20″ N, 21°4′25″ E), which is located about 10 km from the city centre (we assumed the Palace of Culture and Science to be the most central point of the city). An area of the reserve measuring 105 ha has been protected since 1991, the reserve is closed to the public and a permission is needed for entrance. Although this land was formerly parkland, spontaneous regenerations of woodland occurred during the post-war period, nowadays the whole area of the reserve is tree covered. The oldest stands are more than 250 years old, dead or fallen trees are left for natural decomposition, only natural regeneration occurs, in practice very little human intervention is allowed. Trees are mostly deciduous, e.g. hornbeam, common oak, ash (*Fraxinus excelsior*), elms (*Ulmus* spp.), hazel and black alder (*Alnus glutinosa*).

In both areas avian predators were present, this included tawny owl *Strix aluco* (Gryz et al. 2008), and sparrowhawk *Accipiter nissus* (Gryz J., pers. observ.). One pair of the Northern goshawk *Accipiter genitilis* nested in the Natolin reserve (Gryz J., pers. observ.), while corvids (mainly hooded crows *Corvus corone* and rooks *Corvus frugilegus*) were numerous in the Łazienki park (Beliniak and Krauze-Gryz, under rev.). As for mammals, red fox *Vulpes vulpes* (Jackowiak et al. 2021), stone marten *Martes foina* (Krauze-Gryz D., pers. obs.), and free-ranging domestic cat (*Felis catus*) were present in both areas, with the last species being recorded very often in the urban park (Krauze-Gryz D., pers. obs.).

In the Łazienki Park, squirrel density was estimated to be more than 2 ind./ha (Krauze-Gryz et al. 2021a, Babińska-Werka and Żółt 2008), whereas in the Natolin Reserve it was 0.29 ind./ha (Krauze-Gryz et al. 2021 a).

Camera-trap data collection

In this study, we used camera traps to monitor red squirrels activity, i.e. the number of squirrel observations per hour of a day (e.g. Andreoni et al. 2021, Jasińska et al. 2021, Cerbo and Biancardi 2013, please see below for more details), and round-the-clock. The study started in September 2018 and ended in July 2019. We used camera traps (LTL - Acorn 6210MC/MG, USA), which recorded date of the observation, time (24 h record) in Central European Time (CET). Each camera trap captured three still images, and a 5-sec video, shortly one after another (no interval was set). It also recorded date and hour. Cameras were located in front of the live-traps for squirrels (squirrels were live-trapped for another study, this data is not analysed here but the study design was similar to Krauze-Gryz et al. 2021 a, b), about 20-150 cm above ground (depending if a trap was located on a ground or in a tree on a wooden platform). Traps were pre-baited with unshelled hazelnuts and walnuts for seven days (mostly around 8-10 AM), and then baited and set for five to nine days. They were set at dawn and checked after approximately 2–4 h, depending on the temperature, and blocked open for the night (with nuts left inside). After every checking and securing traps, bait was provided, regular baiting ensured the presence of food at all times (including night). Five camera traps, located at least 100 meters apart, were placed in each study site. In the forest, the camera traps were set at one of trapping points (i.e. locations of live-traps) that were distributed on a regular grid. In the park, due to its representational character and high-visitor frequency, the traps were hidden and placed in three trapping areas distributed in different park zones and separated by 200-400 m (Krauze-Gryz et al. 2021 a). Camera traps were set in each of these locations. In total, data was collected in six months: September, November 2018 and January, March, May, July 2019in both study areas, for a total of 76 days in the forest and 104 days in the park (Table S1). Trap-days, an index of the trapping effort, were calculated as the number of devices multiplied by the number of operational days. Number of trap-days was 432 in the forest and 482 days in the park, the trapping effort depended on the number of trapping sessions (i.e. months in which trapping was done) in a given season (Tab. 1). Every photo was checked for presence of animals, the species and number or individuals were recoded (if present together on the same photo). We recorded each squirrel appearing in the images without distinguishing between individuals. A new observation was considered if a minimum of 15 minutes elapsed between subsequent photos or series of photos showing an animal/animals. This rule was abandoned only when an animal in the photo was different in plumage, age class or in other characteristics (i.e. had a radio-collar, ear-tag), indicating clearly that the animal in the photo was a different one than the previously registered. The intermission length ranged from 0 to 30 min in other studies (review in Cerdo and Biancardi 2013). In our case, there were mostly cumulated observations of one squirrel taking bait, which were treated as a single observation; new observations took place after a few/several hours or on the other day. Thus, we believe 15 minutes break allowed to avoid pseudo-replication. The year was divided into four astronomical seasons: spring (1 March–31 May), summer (1 June–31 August), autumn (1 September–30 November) and winter (1 December–28 February). Squirrel records were attributed to one of four parts of 24-hours day: dawn (one hour before sunrise), day (the time between sunrise and sunset), dusk (one hour after sunset) and night (the time between one hour after sunset and one hour before sunrise) (Jasińska et al. 2021). Time of sunrise and sunset was downloaded for Warsaw from https://www.timeanddate.com and converted to CET.

Access to the Natolin Forest Reserve was allowed with the permission issued by the Regional Directorates for Environmental Protection.

Statistical analysis

Differences between the frequencies of records of red squirrels in the two study sites and in subsequent seasons, subsequent hours and times of a day were compared with chi-square test. For observation of squirrels that took place before 12 PM, we calculated time that elapsed from the sunrise, for observations after 12 PM, we measured time between the observation and the sunset. Next, to compare the number of hours after the sunrise and before the sunset and the time when squirrels were recorded, Kruskal-Wallis test was used, with Mann-Whitney pairwise test for post hoc analysis (Bonferroni-corrected *P* values). Normality of data distribution was checked with Shapiro–Wilk W test ($P < 0.05$). The analyses were done in Past 4.05 (Hammer et al. 2001) software.

Results

Number of records of red squirrels per 100 trap days in a given season (Table 1) differed between study areas (Chi-square test: χ^2= 158.3, DF=3, P<0.0001). In the park, the number of records per 100 trap-days was lowest in summer and highest in winter. In the forest the number of records was lowest in winter and highest in summer (Table 1). Number of observations of squirrels recorded per hours of a day varied between the two study sites in all seasons: in spring (Chi-square test: χ2= 53.4, DF=15, P<0.0001), summer (χ^2= 28.8, DF=15, P<0.05), autumn (χ2= 66.8, DF=11, P<0.0001), and winter (χ^2= 160.3, DF=10, P<0.0001) (Fig. 1).

Table1. Number of trap-days, squirrel records in total and records per 100 trap days as recorded by camera traps by season in the two study sites in Warsaw: park and forest.

Season	Park			Forest		
	number of					
	trap days	squirrel records	records per 100 trap days	trap days	squirrel records	records per 100 trap days
Spring	102	108	105.9	176	139	79.0
Summer	51	19	37.3	72	98	136.1
Autumn	135	153	113.3	100	61	61.0
Winter	194	324	167.0	84	25	29.8
Total	482	604	-	432	323	-

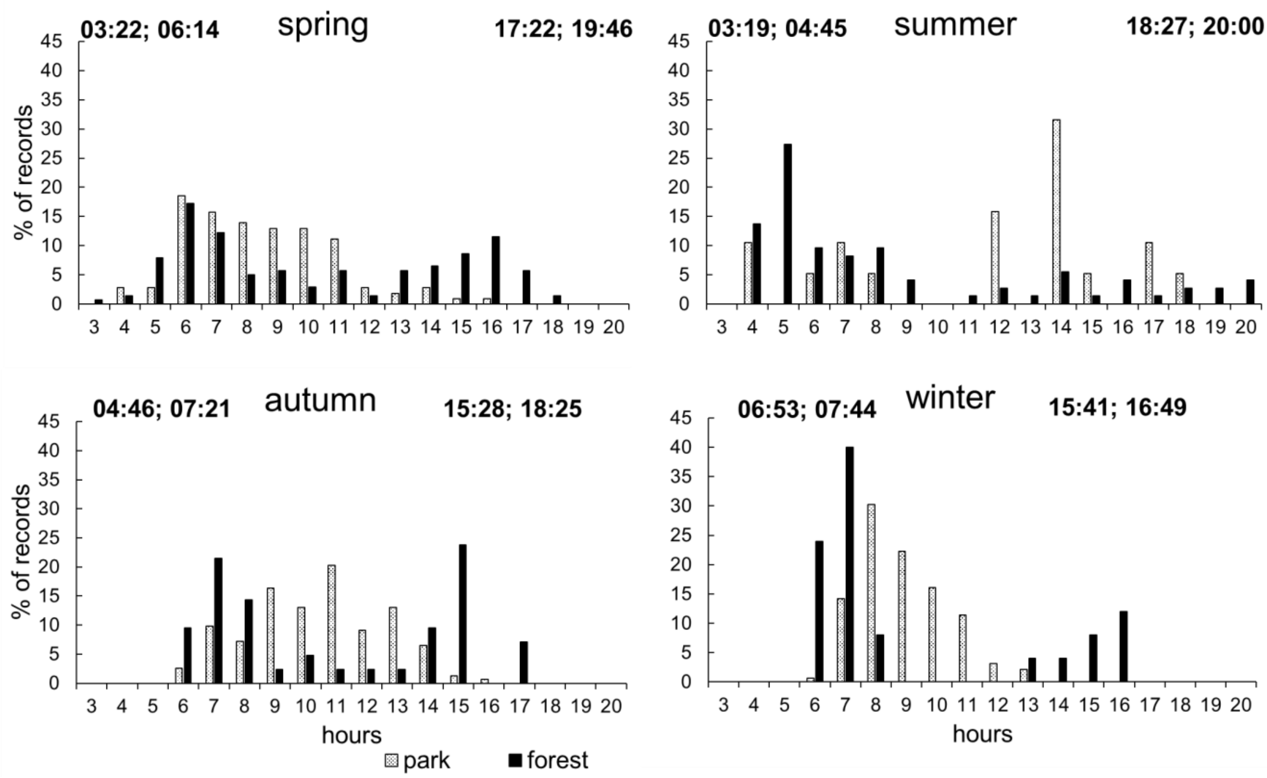

Fig.1. Percentage of records of red squirrels in hours of a day in subsequent seasons in the two study sites in Warsaw: park and forest, as recorded by camera traps. Hours of the earliest and latest times of sunrise or sunset (converted to CET) are given above the graphs. The total number of records of squirrels in each season was in the park: spring – 108, summer – 19, autumn – 153, winter – 324; and in the forest: spring – 139, summer – 73, autumn – 42, winter – 25.

Activity patterns of squirrels in the two study areas seemed to be different (Fig. 1). In spring, forest squirrels were mostly recorded in the early morning (6-7 AM), after sunrise, and then in the afternoon (3-5 PM), two peaks of activity were visible (Fig. 1). On the other hand, park squirrels were mostly recorded between 6 and 11 AM, with no afternoon activity peak. In summer, most records of forest squirrels were taken between 4 and 8 AM, with some observations recorded also in other day hours (till 8 PM). Park squirrels were also recorded in high proportion in the morning (4-8 AM), but bigger share of observations were from noon and some afternoon hours (i.e. 2 and 5 PM). In autumn, activity of park squirrels was clearly unimodal, with biggest share of observations between 9 AM to 1 PM and very few observations afterwards. In contrast, forest squirrels showed bimodal activity pattern, i.e. first between 6-8 AM, and later 2-3 PM, clearly connected to the sunrise and the sunset. This difference was even clearer in winter. Park squirrels were recorded almost exclusively between 7 and 11 AM, while forest squirrels had two activity peaks, i.e. between 6-8 AM and 1-4 PM (Fig. 1).

Observations of forest squirrels were distributed across all defined times of a day, while park squirrels were almost exclusively active during day (Chi-square test: χ^2=333.6, DF=21, P<0.0001) (Fig. 2). No more than 1% of observations of park squirrels came from dawn (one record in spring and autumn, four records in winter), with 100% of diurnal observations in summer. In all seasons, there were no observations of park squirrels at dusk or at night. Forest squirrels were also recorded mostly during day in most seasons, but dawn and dusk observations were always recorded. Only in winter, half of records came from dawn, around one third came from day while 12 and 8% of observations came from dusk and night, respectively.

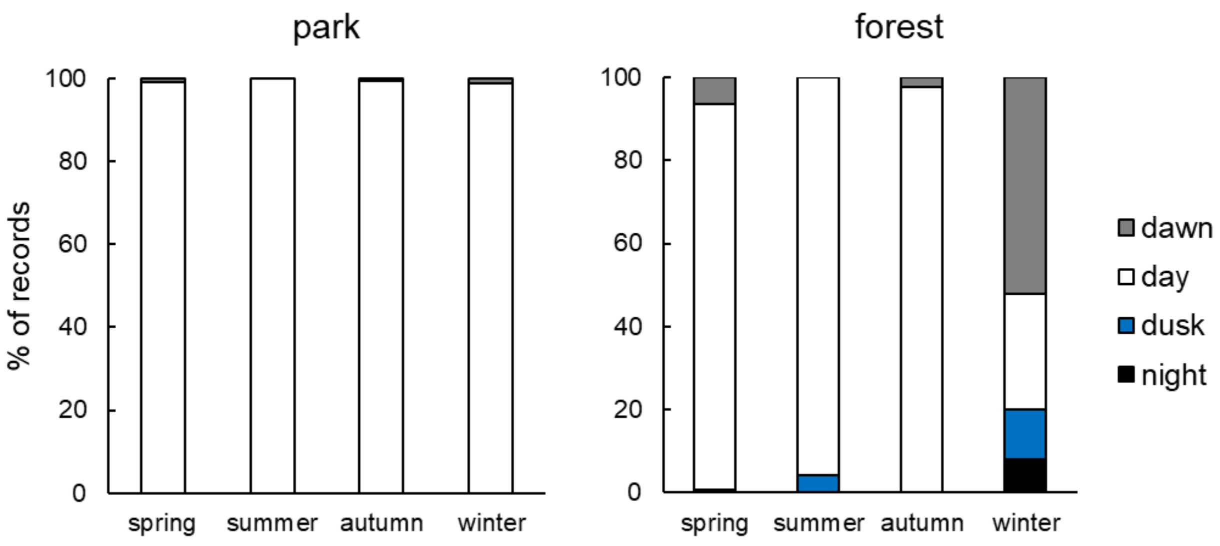

Fig. 2. Seasonal changes in the share of records of red squirrels in four parts of 24-hour day: dawn (one hour before sunrise), day, dusk (one hour after sunset) and night as recorded by

camera traps, in the two study sites in Warsaw: forest and park. The total number of records of squirrels in each season was in the park: spring – 108, summer – 19, autumn – 153, winter – 324; and in the forest: spring – 139, summer – 73, autumn – 42, winter – 25.

For all observations of squirrels recorded before noon we calculated time (n of hours) that elapsed from the sunrise, these values (2.4 and 2.5 for park and forest, respectively) did not differ between the two study sites (Kruskal-Wallis test, $H=0.055$, $P>0.05$). Nevertheless, in both study sites (Fig. 3), differences were found between seasons (Kruskal-Wallis test, park: $H=45.22$, $P<0.001$, forest: $H=50.61$, $P<0.001$). In the park, in winter, squirrels were recorded earlier than in spring or autumn, as shown by Mann-Whitney post hoc test ($P<0.05$), i.e. in winter squirrels were recorded on average two hours after the sunrise, while in other seasons approximately three hours after the sunrise. In the forest, red squirrels were recorded approximately three hours after the sunrise in spring and autumn, less than two hours in autumn while in winter they were observed mostly before the sunrise (mean=-0.48) (Fig. 3). In this case, Mann-Whitney post hoc test showed differences ($P<0.05$) between autumn and winter and the remaining seasons.

Similarly, for all observations of squirrels recorded after noon we calculated time (n of hours) before the sunset. On average, observations of squirrels in the forest were recorded closer to the sunset (on average 2.4 hours before the sunset) than those in the park (3.5 hours before the sunset) (Kruskal-Wallis test, $H=18.04$, $P<0.001$). Again, for both study sites (Fig. 4), seasonal differences were found (Kruskal-Wallis test, park: $H=36.00$, $P<0.001$, forest: $H=17.12$, $P<0.001$). In the park, red squirrels were recorded shortest before the sunset in autumn (2.7 hours before sunset) as compared to other seasons (i.e. in spring and summer this was approximately 5 hours before the sunset). Differences were also found between winter and spring (Mann-Whitney test for post hoc-comparisons, $P<0.05$). In the forest, in winter, red squirrels were on average recorded almost at the sunset, i.e. 0.4 hours before the sunset, while in spring and summer this was approximately three hours before the sunset (Mann-Whitney test for post-hoc comparisons showed differences between spring and autumn and winter, $P<0.05$).

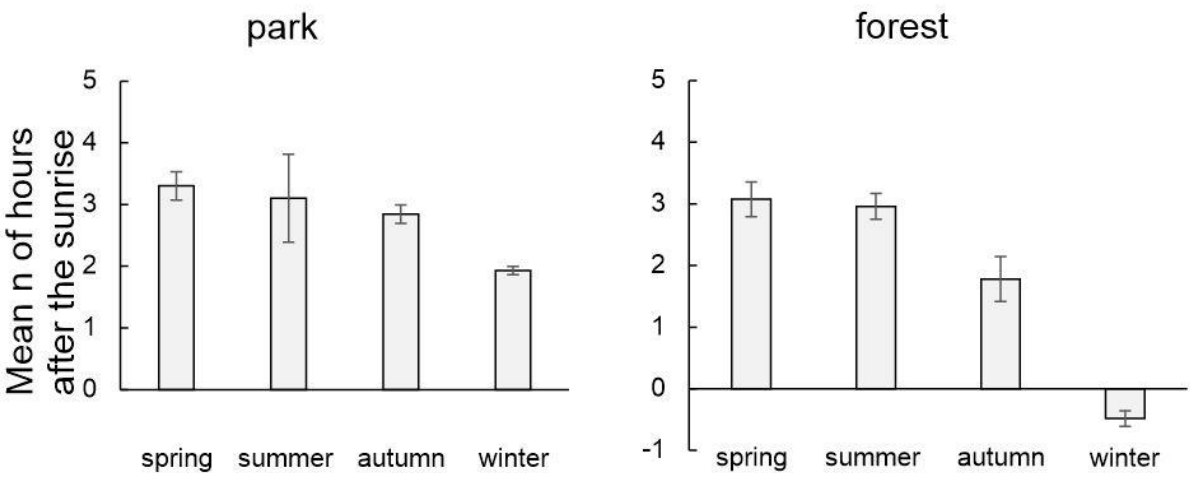

Fig. 3. Seasonal changes in the mean (±SE) number of hours than passed from the sunrise to time of observations of red squirrels as recorded by camera traps in the two study sites in Warsaw: park and forest. Only observations that were recoded before noon (CET) were taken into analysis. The number of records of squirrels in each season was in the park: spring – 95, summer – 6, autumn – 106, winter – 303; and in the forest: spring – 82, summer – 54, autumn – 23, winter – 18.

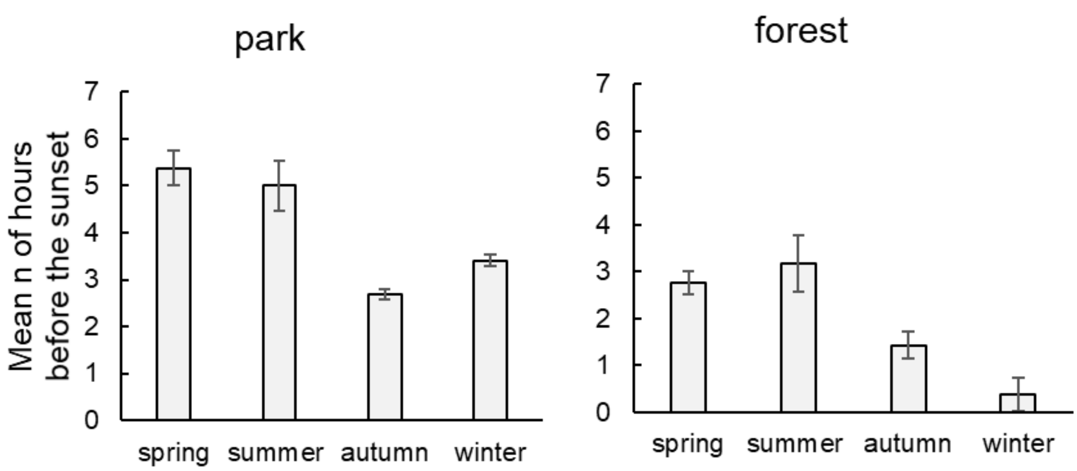

Fig. 4. Seasonal changes in the mean (±SE) number of hours before the sunset to time of observations of red squirrels as recorded by camera traps in the two study sites in Warsaw: park and forest. Only observations that were recoded after noon were taken into analysis. The number of records of squirrels in each season was in the park: spring – 10, summer – 13, autumn – 47, winter – 17; and in the forest: spring – 57, summer – 19, autumn – 19, winter – 7.

Discussion

In this study we compared seasonal changes in the activity patterns of red squirrels based on camera traps observations in two study areas: a busy urban park (with plentiful supplemental feeding) and an urban forest reserve (closed for public). These two habitats were located within city districts of Warsaw, and the study was conducted in the same months in both areas, which was supposed to minimise an influence of abiotic cues such as photoperiod and temperature. Daily activity patterns differed seasonally and between the study sites. In the forest, they resembled those recorded in natural habitats, i.e. two activity peaks, one around the sunrise and second around the sunset, while park squirrels were almost exclusively day-active. We suggest that park squirrels shifted their activity to times with higher visitor frequency, which, assumingly, increased chances of obtaining supplementary food and may allow for limiting time devoted to food search. This is the first paper that shows changes in the activity patterns of red squirrels in relation to urbanization round-the-year.

In the park, the number of records per 100 trap days was lowest in summer and highest in winter. This high activity level in winter seems counterintuitive because at low temperatures, resting in the nest is an important behavioural response, which decreases the energy costs of thermoregulation (Wauters and Dhondt 1987). Moreover, the effect of temperature is more distinct in deciduous habitats, which do not provide much shelter for squirrels in winter (Wauters et al. 1992) and deciduous trees dominated in this areas. In contrast, in the forest the number of records was lowest in winter and highest in summer, which reflects typical decrease in the activity level of red squirrels with low ambient temperatures (Bosch and Lurz 2012, Wauters et al. 1992) because of the high thermoregulatory cost of foraging at low ambient temperature and shorter day-length (Bosch and Lurz 2012, Wauters et al. 1992, Pulliainen 1973). Abundant and predictable food sources in urban habitats can result in minimal physiological responses to the seasons through small changes in metabolism and conductance. In one study in Germany, squirrels were able to maintain a high body mass and positive energy balance year-round despite living in a climate with large seasonal changes in temperature. This was because of the presence of diverse food trees, and artificial food supplemented by cemetery visitors, as well as the modification of activity patterns (Turner et al. 2017). Probably also in our case, red squirrels in the urban park were able to maintain high activity during winter thanks to all-year-round availability of supplemental food. Also, higher temperature in the city centre (Kim 1992) might have allowed for high activity in winter. The lowest number of observations in summer may result from high availability of natural food combined with a very high frequency of park visitors (including tourists) during holidays. Squirrels are offered so much food they assumingly search for alternate food sources less often.

In spring and autumn, forest squirrels presented crepuscular activity, similarly to what was recorded in other rural habitats, both in coniferous and deciduous habitats (Wauters et al. 1992). In turn, park squirrels were mostly recorded in the morning, between the sunrise and till noon, with no afternoon activity peak. In warm months, red squirrels in rural habitats show bimodal activity pattern, with a rest period in the warmest hours of the day (Wauters et al. 1992, Wauters and Dhondt 1987, Tonkin 1983). In our study, no clear rest period was visible, possibly also due to small sample collected in the summer. In winter, we noticed the clearest difference between the two populations: activity of park squirrels was unimodal, i.e. they were recorded almost exclusively after the sunrise and till noon. In turn, forest squirrels showed crepuscular activity. As shown by earlier studies, winter activity of squirrels was unimodal in coniferous forest (Steen and Barmoen 2017, Wauters et al. 1992, Wauters and Dhondt 1987), and bimodal in deciduous forest (Wauters et al. 1992). In our case, both study sides were deciduous, so other factors should have affected this result. Consequently, forest squirrels were observed across all defined times of a 24-hour day (e.g. night, dusk, day and dawn), while in the park squirrels were almost only active during a day. In general, red squirrels are exclusively day-active, and the start of activity is closely related to sunrise (Wauters et al. 1992). Yet, when length of day is shortest, squirrels can be active soon after the first light, thus somewhat before sunrise and after sunset (Wauters et al. 1992, Wauters and Dhondt 1987). Indeed, in a study conducted in South Korea, which also involved camera traps, about 11% of photos were captured in night time photo rate (Lee et al. 2019). In the urban park we did not record any images of active squirrels before the sunrise and after the sunset and very few observations came from dawn (with none from dusk or night). It seems that squirrels in urban forest behaved more like their conspecifics in natural habitats and park squirrels changed their activity rhythm, i.e. their activity concentrated shortly after sunrise (as in natural habitats) and in the subsequent hours. We may assume that one of the possible factors driving this difference was the presence of park visitors and supplementary food supplies provided by people (Krauze-Gryz et al. 2021a, Kostrzewa and Krauze-Gryz 2020). Red squirrels can reduce activity and foraging time if food items are energy-rich and easy to handle (Wauters et al. 1992) and food availability affects duration of activity during a day (Wauters and Dhondt 1987, Tonkin 1983). Availability of anthropogenic food increases the habitat quality, especially in urban habitats (Fingland et al. 2021). Consequently, activity of red squirrels may be altered by food provisioning in urban parks (Thomas et al. 2018), which may also help animals to maintain a positive energy balance (Turner et al. 2017). It was previously suggested that food provided by people may be more important than abiotic factors in urban habitats (Thomas et al. 2018). The primary abiotic environmental cues influencing red squirrel activity timing appear to be temperature (Wauters et al. 1992), photoperiod (i.e., day length, Wauters and Dhondt 1987, Tonkin 1983) or a combination of both (Holm 1990). In our study, in both study sites, we compared data collected during the same month, with similar weather conditions (recordings were conducted at the same time or maximum seven days apart). We may thus assume that differences in activity patterns between urban and forest squirrels were not driven by those abiotic factors. We suggest that park squirrels shifted their activity to times with higher visitor frequency. Indeed, they also changed their behaviour in a way that made receiving food from people more likely, i.e. squirrel spent much time on the ground and often approached people and begged for food (Krauze-Gryz et al. 2021). This was different from population of squirrels inhabiting wildlife park in Ireland, which altered their activity to avoid human encounters, were observed to concentrate their activity in non-public areas and moved into public areas when the human disturbance was lower (Haigh et al. 2017a). What is more, squirrels inhibiting city centre were less active throughout the day than their conspecifics in semi-natural habitat in urban areas of Hamburg (Thomas et al. 2018). This shows that, in our case, urban park squirrels adjusted to human presence. Indeed, humans are important source of disturbance for animals (Sol et al. 2013), yet, the flight initiation distance (FIDs), is often shortened in urban habitats (Uchida et al. 2019, 2019, Sol et al. 2013). Nevertheless, other abiotic factors that may differ between the two study sites need to be considered, i.e. both artificial light at night and anthropogenic noise can drive changes in activity patterns of animals (Dominoni et al. 2020). In example, urban birds sing earlier during the day, have similar singing effort in the dawn chorus, but sing less than rural birds during the rest of the day (Bermúdez-Cuamatzin et al. 2020). Indeed, anthropogenic noise in the urban park, located in the city centre, was surely higher than in the urban forest. However, being a big park, this was rather a quiet zone, which was not close (at least our study plot) to any busy road, no vehicles were allowed there and gardeners used only electric cars. Also, times with highest noise (i.e. rush hours) did not seem to affect activity of squirrels, i.e. animals were mostly active in the morning but had a rest in the afternoon.

Although in this study we did not test directly an influence of supplemental feeding on shifts in the activity patterns in the population of urban squirrels, we suggest this factor played the crucial role. Squirrels in this park were shown to differ in their behaviour, i.e. some squirrels spent most of their time on the ground and reacted positively to people (approached them and/or begged for food), while others were mainly arboreal and reacted to humans with alert or escape behaviours (Krauze-Gryz et al. 2021b). Assumingly, activity patterns of certain individuals could also differ, which should be investigated in future studies.

To sum up, this study showed differences in daily activity patterns of the two urban populations, inhabiting the same city but different green areas with various levels of human disturbance. Urban forest squirrels showed mostly typical crepuscular activity, while park squirrels were active from the morning and until midday. We suggest a reason for these differences could have been a year-round access to supplementary food in the urban park, i.e. squirrels stayed active at times when park visitors were present and often provided food. This difference complete our earlier findings on how far urban park squirrels differed from their forest counterparts in other aspects of ecology (i.e. space use, food choice and interactions with people) and points to very high plasticity of this species, inhabiting human-dominated landscapes. Nevertheless, as we compared only two study sites located in one city, and we did not have independent replicates for the two populations, we cannot exclude other factors that could have played a role. Thus, more studies are needed to confirm that red squirrels changed their activity rhythms to benefit from human presence.

Acknowledgements

We would like to thank the students of the Warsaw University of Life Sciences who helped with fieldwork: Magdalena Naber, Aleksandra Boreczek, Mateusz Cieślik, Natalia Kozłowiec, Martyna Wirowska, Monika Marguż and Jadwiga Kaczyńska. We would also like to express gratitude to the Royal Łazienki Museum in Warsaw for site access and help whilst fieldwork in the park was being conducted.

We would also like to thank two anonymous reviewers, whose comments helped us to improve the manuscript.

The manuscript was financed by the Polish Ministry of Science and Higher Education with funds from the Institute of Forest Sciences, Warsaw University of Life Sciences (WULS), for the purpose of scientific research.

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Supplementary Material

Table S1. Number of days of trapping squirrels in seasons and months in two study sites: urban park and urban forest.

Season	Month	Number of days of trapping squirrels	
		Park	Forest
Spring			
	March	12	15
	May	16	12
Summer			
	July	12	12
Autumn			
	September	12	12
	November	16	13
Winter			
	January	36	12
Total		104	76