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Research Article

Same yet different — individual red squirrels (*Sciurus vulgaris*) react differently to human presence in an urban park

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Abstract

Urbanisation influences animal populations. The European red squirrel is a highly adaptive species and its urban populations differ in terms of spatial use, behaviour, diet, and decreased vigilance levels. In this study, we focused on behavioural differences in individual squirrels to compare their reaction to human presence in a very busy, urban park, where squirrels were supplementarily fed by park visitors. Squirrels were radio-tagged and followed for 2–9 months (5.5 months on average). When a squirrel was located, its activity (active/in a drey), position (ground/tree) and behaviour were recorded. In general, behavioural differences between individuals were found. 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. This did not differ between sexes, but squirrels who spent more time in the trees occupied smaller core areas and with fewer nuclei. Chances of a positive reaction to humans were lower for squirrels that stayed in the trees, but higher for squirrels with larger core areas. It may be assumed that staying on the ground and approaching people is beneficial, as such squirrels are more likely to be offered food. However, to obtain food from park visitors, squirrels potentially needed to travel to park areas with the biggest visitor frequency (larger core areas). The observed behavioural changes were probably driven by different personality traits and/or intraspecific competition. To the best of our knowledge, this is the first study that focuses on the behaviour and feeding strategies of individual squirrels in urban conditions. If and how these behavioural differences affect squirrels' personal attributes (such as their body condition or reproduction performance), as well as if these effects are consistent over time, should be investigated further.

Introduction

Urbanisation processes in environments inhabited by vertebrates inevitably influence their populations (Gryz et al., 2008; McKinney, 2008; McCleery, 2010; Lesiński et al., 2021). In the case of sciurids, this includes modifying certain aspects of their ecology: population density (McCleery, 2010); spatial organisation and habitat use (McCleery et al., 2007); dietary composition (Bosch and Lurz, 2012; Krauze-Gryz and Gryz, 2015; Reher et al., 2016); causes of mortality and variables related to breeding (McCleery et al., 2008; McCleery, 2009b); activity patterns (Thomas et al., 2018); and/or behaviour (McCleery, 2009a; Uchida et al., 2016, 2019).

The red squirrel, *Sciurus vulgaris*, is a species that successfully inhabits cities (Babińska-Werka and Żółw, 2008; Bosch and Lurz, 2012; Reher et al., 2016; Jokimäki et al., 2017). Its abundance increases with human population density, being approximately twice as high in urban habitats than in forests (Jokimäki et al., 2017). In cities, squirrels are able to utilise urban structures (Hämäläinen et al., 2018) and, according to some studies, urban parks can be potentially suitable refuges for red squirrels (Rézouki et al., 2014).

In urban conditions, red squirrels are offered various supplemental feeding opportunities, from being able to use bird feeders to receiving nuts given to them directly by park visitors (Bosch and Lurz, 2012; Krauze-Gryz and Gryz, 2015; Kostrzewa and Krauze-Gryz, 2020). It was shown that artificial food is an important factor that may attract squirrels in urban environments (Jokimäki et al., 2017). Stable food sources in urban habitats are crucial as the body condition of females, depending on food abundance, strongly affects reproduction in the species (Wauters and Dhondt 1995, Wauters et al. 2008). Supplemental food may be used when natural food resources are limited (Shuttleworth, 2000) and provides a buffer against variations in natural food availability (Magris and Gurnell, 2006).

It is known that individual squirrels within a population can behave in different ways (Boon et al., 2007, 2008; Haigho et al., 2017; Santicchia et al., 2018). Differences in personality can affect squirrels' fitness via individual survival or reproductive success (Santicchia et al., 2018) and may be reflected in many aspects of an animal's behaviour and ecology, including its habitat use, interactions with conspecifics, and willingness to take risks (Boon et al., 2008). Individuals that can adjust their behaviours to changing urban conditions should have greater success in urban habitats (Lowry et al., 2013). On the other hand, fitness benefits related to various personality traits differ with habitat type and resource availability, so this supports the variation in personality in heterogenous landscapes (Santicchia et al., 2018). In this study, we focused on red squirrels from a busy urban park, with an abundant supply of supplemental food, and also a rich natural food base. As we showed in a similar study (Krauze-Gryz et al., 2021), squirrels from this population (as opposed to those living in the forest) had smaller home ranges, spent a considerable part of their time on the ground, interacted with park visitors by approaching and taking food, and their diet seemed to be dominated by human-delivered food items. By keeping in mind individual variations within the population, we wanted to check if individual squirrels modified their behaviour to a similar ex-

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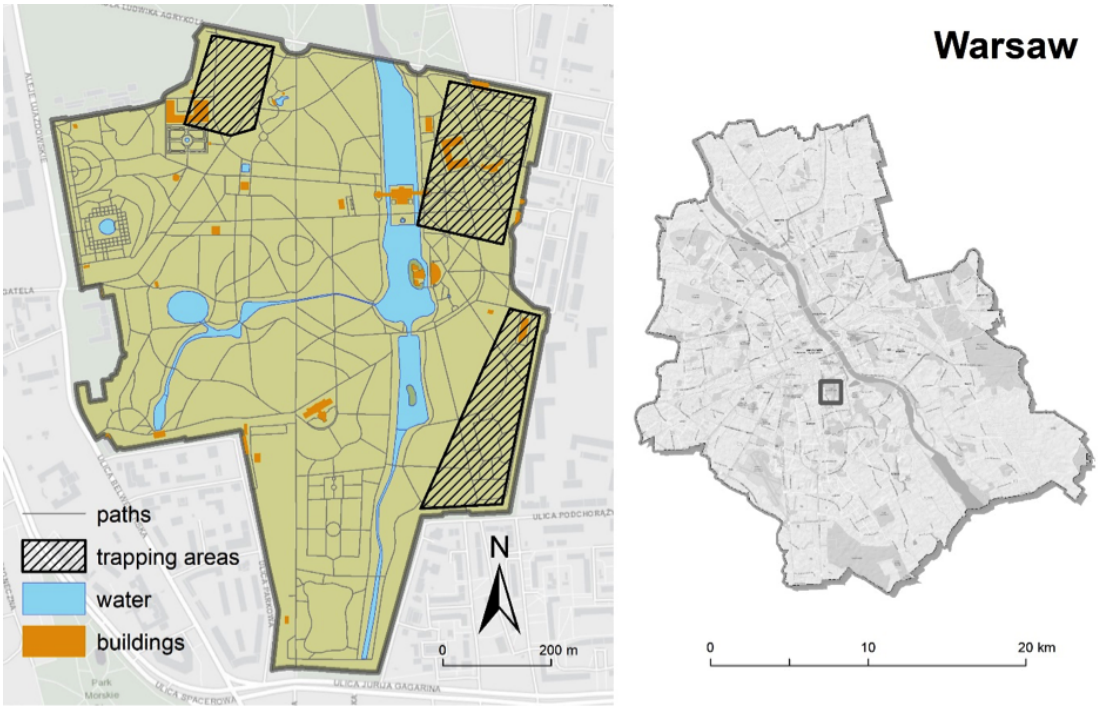

Figure 1 – Study area (Łazienki Park) in Warsaw (Poland). Approximate locations of red squirrel trapping areas are shown.

tent. Increased boldness is one of the main modifications of behaviour in urban animals, and this changes their reactions to human presence, e.g., in the form of a reduction in flight initiation distance (Uchida et al., 2019). This, in turn, may be beneficial, as humans in urban habitats are often a source of supplementary food (Krauze-Gryz and Gryz, 2015; Kostrzewa and Krauze-Gryz, 2020). In our study, we compared the proportion of time spent on the ground between individuals and checked if this correlated with behavioural responses towards people (i.e., positive vs. negative reactions) and home range characteristics (core area size and number of nuclei). We hypothesised that high intraspecific competition in a very dense population leads to the formation of various feeding strategies. Squirrels who are more habituated to human presence, assumingly bolder ones, are less arboreal and react more positively to people (as they often provide a food source). On the contrary, individuals who react to people with alert or escape behaviours, forage mostly in the trees to avoid interaction with humans.

Material and methods

Study area

We carried out our study in Warsaw, the capital city of Poland, which has approximately two million inhabitants. It is located in the central part of the country, a region that is affected by 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 amount of precipitation is 600 mm per year; and the mean ambient temperature ranges from −4 °C in January to 18 °C in July, but the minimum temperature may drop below −30 °C and the maximum may rise above 35 °C.

The research was carried out in an urban park (the Royal Łazienki Museum) of 76 ha, located in the central district of Warsaw (Fig.1). It is a representational area, with numerous old trees, which provided a rich, natural food base (Babińska-Werka and Żółw, 2008), with historical buildings, as it was founded in the 17th century. It is very popular with tourists and local inhabitants. Here, squirrels are one of the main park attractions, and are fed with nuts by visitors (Krauze-Gryz and Gryz, 2015; Kostrzewa and Krauze-Gryz, 2020). The population density of red squirrels is around 2 ind./ha (Babińska-Werka and Żółw, 2008).

Trapping and radio-tagging

The population was monitored by radio-tagging. To trap squirrels for radio-tagging, we used 25 Tomahawk traps (51x15x15 cm), placed on the ground or in trees on a wooden platform. The traps were partly covered by dark plastic to give the squirrels shelter from rain or snow. Traps were pre-baited with unshelled hazelnuts and walnuts for at least seven days and then baited and set for five days. They were set at dawn and checked after approximately 2–4 hours, depending on the temperature, and secured for the night so they did not end up being closed. Trapped squirrels (Supplementary material S1) were flushed into a wire mesh handling cone (Lurz et al., 2000) to minimise stress during handling. Newly trapped individuals were weighed, sexed and marked with numbered metal ear tags of 2x8 mm (National Tag&Band Co.) and radio tags (Biotrack transmitters with temperature sensor, 8–9 grams, less than 3% of individual body mass). The signal range of the transmitters was usually between 100 and 400 m, depending on the weather, season, and squirrel position (in a tree or on the ground). The batteries in the radio transmitters lasted for up to eight months. Temperature sen-

Table 1 – Squirrel ID, radiotracking time and number of radio locations (fixes) collected for each squirrel included in the study (M-male, F-female) in the urban park (Łazienki Park, Warsaw).

Squirrel ID	Sex	Radiotracking time	# of fixes	
			Spatial analysis	Behavioural observations
1	M	Oct 2012–Feb 2013	181	129
3	M	Nov 2012–Mar 2013	193	151
10	F	July–Nov 2012	66	26
11	F	May 2012–Feb 2013	181	91
12	F	Sept 2012–Feb 2013	67	46
17	M	Nov 2012–May 2013	131	72
20	F	May–Sept 2012	103	63
28	F	May–Nov 2012	121	61
31	M	Sept–Oct 2012	50	29
32	M	Sept 2012–Apr 2013	80	61
34	M	Sept 2012–Jan 2013	90	66
41	F	Nov 2012–Apr 2013	122	85

sors in radio tags allowed for identification if a squirrel was active or in a drey.

Radio-tagging was done four times between May 2012 and Nov 2012. Overall, 15 individuals were tagged, but sufficient data were collected for 12 squirrels (six males and six females) and only those were included in the analysis (Tab. 1). Squirrels were followed (monitored) for 2 to 9 months (5.5 months on average) between May 2012 and May 2013 (Tab. 1). In some cases, a new radio-tag was provided when the battery failed. We followed the radio-tagged squirrels (using Y-4FB 150-152MB TELEVILT antenna and Telonics TR-5 receiver) until the death of the animal or the failure of the transmitter battery. Radio transmitters were removed from animals recaptured at the end of the study, but four individuals were lost and could not be recaptured.

Squirrels were monitored from 8 to 21 (on average 14 days per month), at different times of day. An individual squirrel was located once per day, and its location was recorded with a GPS receiver (Garmin 62sc) with an accuracy of approximately 5 m. Locations were estimated while homing in on the radio signal. When a squirrel was located, its activity (active or in a drey) and position (on the ground, in the tree) were determined, and then it was observed for five minutes to assess its behaviour (more than one type of behaviour could be recorded for each fix). The recorded behaviours were as follows: foraging (not related to humans)—searching, handling, recovering stored food, caching or eating any food that was not seen to be taken from humans; travelling—movements not related to food or any interactions; self-grooming; inter- and intraspecific interactions (not including humans, mainly corvids, such as rooks (*Corvus frugilegus*), hooded crows (*Corvus cornix*) or feral pigeons (*Columba livia* f. *urbana*); resting outside the drey; interactions with people—any kind of behaviour related to human presence, such as alert, escape, approaching and begging for food, taking food from people (eating or caching it). Behavioural observations were carried out only when an animal was clearly visible. Twice a month, we followed the squirrels from dawn to dusk, trying to locate each squirrel every hour. During this whole-day monitoring period, only squirrel positions and their activity were recorded, with no behavioural observations being carried out. A minimum of 30 radio locations for each animal were used to describe the home range of a squirrel (Wauters and Dhondt, 1992; Lurz et al., 2000; McCleery et al., 2007). When a squirrel remained in a drey, its location was taken for analysis (Di Pierro et al., 2008) only once per day.

Analysis

Home range analyses were performed using Ranges8 software (Anatrack Ltd., Wareham, UK) (Kenward et al., 2008). Minimum convex polygons (MCP) of 100% were calculated for each squirrel using coordinate data. Core areas were estimated by cluster analysis using nearest neighbour distances. The objective core areas option was used, in which locations with nearest neighbour distances beyond the normal distribution were excluded as outliers (Kenward et al., 2014). Statistical analysis were performed with mixed effects logistic regression in R (`Lme4` package). Two separate models were built. In the first model, the effect of sex (SEX), core area size (CORE) and the number of nuclei (NUCLEI) (as an explanatory variable) on the position of animals (ground vs. tree as binary dependent variable) was analysed. We marked all records in which squirrels were observed in the trees as one and all records in which squirrels were observed on the ground as zero. The IDs of squirrels were set as a random effect to account for the repeated sampling of individual animals. The second model analysed factors that can potentially explain the reactions of squirrels to humans. In this model, positive reactions to humans (approaching and/or taking food) were marked as one and other reactions (alert and/or escape behaviours) were marked as zero. The explanatory variables in the model were as follows: sex (SEX), squirrel position (in a tree vs. on the ground (POSITION)), core area size (CORE) and the number of nuclei (NUCLEI). All the explanatory variables were set as grouping factors. The POSITION was set in a similar way as in the first model. CORE was divided in two groups: squirrels with smaller core areas (up to 1 ha) and squirrels with larger core areas (over 1 ha). NUCLEI was similarly divided in two groups: smaller number of nuclei (up to 3) and larger number of nuclei (over 3). We did not analyse the MCP in the model, because squirrels with higher MCP also had a higher core area. Similar to the first model, the ID of an individual squirrel was set as a random effect. In both models, we performed a model selection based on hypothesis (Burnham and Anderson, 2002). All possible model permutations were performed and, finally, the models were ranked according to their Akaike weights (ω_i). The principle of model selection was lower AIC values.

Results

Although all the squirrels (n=12, Tab. 1) spent a considerable amount of time on the ground, we found out that this proportion differed for individual squirrels (Fig.2). There were six squirrels who spent most of their time on the ground (60–71% of records), while another three individuals were recorded as mostly staying in the trees (they were recorded on the ground for only 15–28% of fixes) (Fig.2). The sex of squirrels did not influence the position (in a tree vs. on the ground) of the animals. In other words, the frequency of records in the trees and on the ground was similar for both sexes. Squirrels who were more often observed in the trees occupied smaller core areas with fewer nuclei (Tab. 3). Both variables significantly explained the position of squirrels (in a tree vs. on the ground), but the core area was more important in the explanation of squirrel position, because the Akaike weight was higher for the CORE-only model (Supplementary material S2). Nevertheless, the fixed factors presented a relatively small contribution to the model (marginal pseudo R square equalled 0.15 and conditional pseudo R square was 0.12).

For all individuals, interactions with humans were observed frequently, accounting for 16 to 45% of recorded behaviours. The share of other behaviours differed between individuals, but, on average, foraging was the other dominant activity in most cases (10–56% of records of behaviour) (Fig.3). Individual squirrels reacted towards people in

Table 2 – Home range estimates for individual radio-monitored red squirrels in the urban park (Łazienki Park, Warsaw). Sex: M—male, F—female.

Squirrel ID	Sex	100% MCP area (ha)	Core areas Area (ha)	Core areas % of fixes	# nuclei
1	M	3.98	1.89	91	2
3	M	2.20	0.96	94	3
10	F	2.86	0.95	87	3
11	F	1.81	0.48	92	9
12	F	1.71	0.22	89	2
17	M	1.96	0.74	88	3
20	F	1.44	0.49	89	6
28	F	1.03	0.38	94	3
31	M	1.61	0.65	94	3
32	M	2.35	0.72	92	3
34	M	2.06	0.66	87	3
41	F	1.22	0.40	87	5

Table 3 – Effect of A) squirrel position (in the tree vs. on the ground) (POSITION) and core area size (⩽1 ha vs. >1 ha) (CORE) on squirrels' positive reactions to humans (approaching and/or taking food) and B) core area size (⩽1 ha vs. >1 ha) (CORE) and the number of nuclei (⩽3 vs. >3) (NUCLEI) on squirrel position (in the tree vs. on the ground), in mixed effects logistic regressions (for model selection, see Supplementary material S2 and S3); all *p*-values are statistically significant.

	Source	β-values	Sandard error	z-values	*p*-values	Odds ratio
A	Intercept	−2.678	0.684	−3.914	<0.001	0.069
	POSITION (tree)	−2.203	0.267	−8.251	<0.001	0.110
	CORE (>1 ha)	2.409	0.763	3.157	<0.01	11.120
B	Intercept	1.234	0.300	4.116	<0.001	3.435
	CORE (>1 ha)	−1.659	0.318	−5.226	<0.001	0.190
	Nuclei (>3)	−0.701	33.460	−2.096	<0.05	0.496

different ways (Fig.4). There were five individuals who mostly reacted positively (approached people and/or took food from them; more than 80% of records, 97% maximum). In contrast, for four individuals the negative reactions towards people were dominant (an escape and/or alert behaviour), while three of them were never observed to react positively to people. In the case of three individuals, both types of reactions were observed in more even proportions. Squirrels had small home ranges (100% MCP ranging from 1.0 to 3.9 ha), but these were below 2 ha in the case of seven individuals (Tab. 2). Core areas were below 1 ha in all but one case, with 2 to 9 nuclei. A positive reaction to humans was significantly explained by the squirrel's position (POSITION) and core area size (CORE). The model selection procedure excluded the sex of the animals (SEX) and the number of nuclei (NUCLEI) (Supplementary material S3). The fixed factors of the model presented quite a large contribution to the model when comparing them to the random factors, as the marginal pseudo R square equalled 0.4, whilst the conditional pseudo R square was 0.53. The chance of a positive reaction to humans was significantly lower when the squirrel was in a tree, but individuals with larger core areas showed positive reactions to humans significantly more frequently (Tab. 3). The POSITION factor seemed to be more important in the explanation of squirrel behaviour, because the Akaike weight was higher for the POSITION-only model (Supplementary material S3).

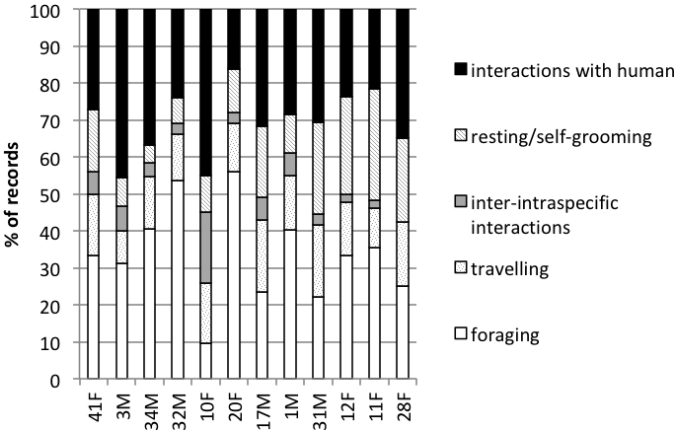

Figure 3 – Behaviours of radio-monitored individual squirrels (squirrel ID and sex-M/F are given) (percentage of records when a given behaviour was observed) in the urban park (Łazienki Park, Warsaw). The behaviours of active and visible squirrels were recorded. Foraging: feeding on any food that was not seen to be obtained from people, food handling, caching, cache recovery. Interactions with humans: any kind of activity involving people. Number of records of behaviour for each individual (ID-number of records): 41–114, 3–195, 34–84, 32–71, 10–31, 20–68, 17–98, 1–144, 31–36, 12–42, 11–93, 28–40.

Discussion

Urban animals tend to behave differently from individuals of the same species in more natural environments (Lowry et al., 2013; Sol et al., 2013; Gryz and Krauze-Gryz, 2018, 2019). Despite arboreal foraging being thought of as a fixed behaviour in red squirrels (Kenward and Hodder, 1998), we found that this trait could not be attributed to all individuals in our study. Generally, squirrels in Łazienki Park, one of the biggest and most busy parks in Warsaw, spent a high proportion of time on the ground (when compared to other populations that inhabited urban forests), approached people and begged for food (Krauze-Gryz et al., 2021). However, this proportion between individual squirrels differed, i.e., some squirrels were mainly arboreal while other spent most time on the ground. This did not differ between sexes, but squirrels who spent more time in the trees occupied smaller core areas and with fewer nuclei. We also found that squirrels reacted differently towards people: some reacted positively, approached them and took food, while others reacted with alert and/or escape behaviours. This positive reaction was attributed to squirrel position (squirrels who were recorded as being on the ground more often reacted more positively to people). It may be assumed that such behaviour is beneficial, as squirrels on the ground are more visible, and thus more likely to be offered food.

Behavioural plasticity is an important characteristic for species' success in urban, human-modified habitats (Lowry et al., 2013). Urban animals adapt to living at high densities (Francis and Chadwick, 2012), and also in close contact with people. In the case of grey squirrels, a positive association between density and intraspecific aggression was found (Parker and Nilon, 2008). However, a negative reaction to frequent stimuli would be costly and result in high stress hormone levels, which, in turn, can be detrimental to an individual (Łopucki et al., 2013). Thus, individuals living in the city should minimize the physiological cost of social interactions (Łopucki et al., 2013). Higher boldness is one of the most prevalent behavioural modifications in urban animals, which resulted in more habituation to humans and a reduction in vigilance. In an urban park, where people often gain an affinity with wildlife and feed squirrels (e.g., directly from their hands), increased tolerance to humans is an advantage (Uchida et al., 2019). Indeed, a study on eastern grey squirrels claimed that with more exposure to humans, squirrels may have learned that they are not threatening and could be beneficial (Engelhardt and Weladji, 2011). However, this is a trade-off, as such behaviour exposes a squirrel to predation risks. Nevertheless, it was shown that although, for urban squirrels, the flight initiation distance was shorter (Uchida et al., 2016), they were able to assess the risk level attributed to different objects (like humans or predator models; Uchida et al., 2019). This ability to assess risk correctly may be the reason why squirrels have managed to successfully colonise urban areas worldwide (Uchida et al., 2019), even with numerous threats, such as the high density of urban predators, e.g., corvids (Mazgajski et al., 2008) or free-roaming domestic cats (*Felis catus*; Krauze-Gryz et al., 2017), which are also typical in our study area.

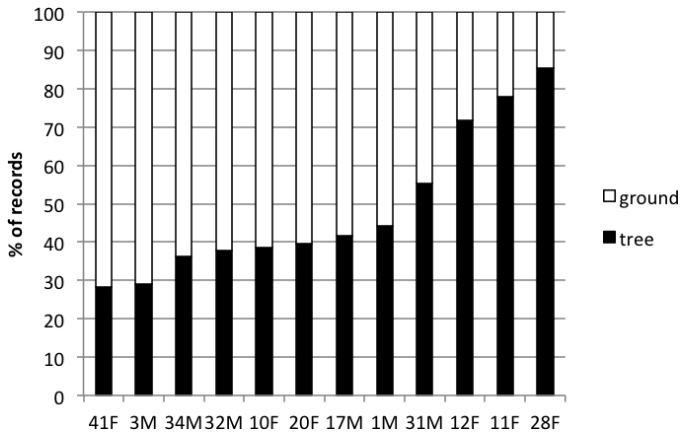

Figure 2 – Proportion of records when individual active squirrels (squirrel ID and sex—M/F are given) were recorded in the trees (as opposed to the ground) in the urban park (Łazienki Park, Warsaw). For the number of records for each individual radio-monitored squirrel, see Tab. 1.

Access to stable food sources is crucial as the body mass and condition of squirrels directly relates to reproduction indices (Wauters and Dhondt, 1989, 1995; Wauters et al., 2007; Santicchia et al., 2018). In high-density populations of red squirrels, where encounters between individuals are frequent, body mass tends to increase with age and heavier, older males are more aggressive than lighter, younger ones, with these heavier males more likely to mate (Wauters and Dhondt, 1989; Wauters et al., 1990). In our park, natural food sources were very abundant in the form of seeds of various species of deciduous and coniferous mature trees (Babińska-Werka and Żółw, 2008). Moreover, bird feeders were evenly distributed across the park area, with seeds delivered by park managers and park visitors. Squirrels are attracted to feeders and can benefit from the food supplementation they provide (Starkey and delBarco-Trillo, 2019). Nevertheless, according to our observations, people visiting the park offered food to squirrels mostly directly (Kostrzewa and Krauze-Gryz, 2020). Therefore, squirrels who approached people and were not afraid of close contact (taking food directly form humans' hands) would be more competitive at times when natural food sources are depleted. However, it must be acknowledged

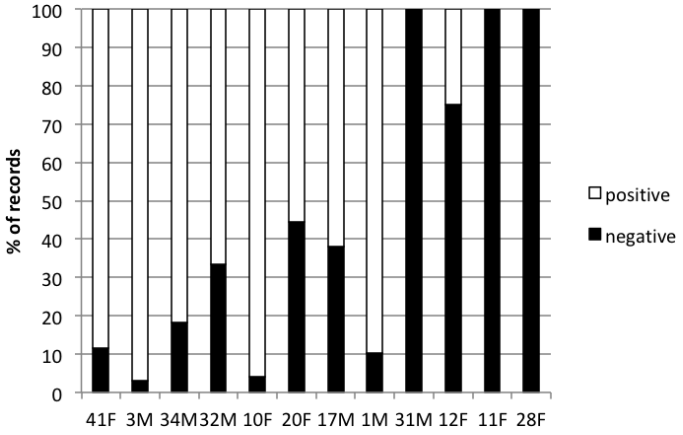

Figure 4 – Reactions towards people of individual radio-monitored squirrels (squirrel ID and sex-M/F are given) in the urban park (Łazienki Park, Warsaw) (percentage of records when a given reaction was observed). Number of records involving human–squirrel interactions for each individual (ID-number of records): 41–43, 3–161, 34–49, 32–24, 10–25, 20–18, 17–42, 1–68, 31–13, 12–12, 11–22, 28–16.

that the frequency of human visits to the park varied throughout the year and was relatively low when unfavourable weather conditions occurred. Thus, a home range with abundant natural food sources might have been crucial for survival in these poor conditions and may have affected the chances of mating (Wauters and Dhondt, 1992, 1995). We found that squirrels who reacted positively to people (i.e., took human-delivered food) had a larger core area size and with higher number of nuclei than other individuals. This may suggest that, in order to obtain food from park visitors, squirrels need to move more, probably in order to travel to the park areas with the highest visitor frequency. This strategy may have its costs, as a negative effect of exploration on reproductive success and survival was found in other studies (Wauters and Dhondt, 1992; Santicchia et al., 2018).

Our results suggest that there were two distinct, adverse feeding strategies utilised by red squirrels in the urban park: human-offered food vs. natural resource exploitation. We may assume that bolder and more experienced squirrels took food from people. However, it is also possible that high intraspecific competition from dominant squirrels (especially in late winter and early spring, when natural food sources are limited) may have affected the spatial use of submissive individuals (Hämäläinen et al., 2018) and forced them to search for alternative (in this case, supplementary) food sources.

To the best of our knowledge, this is the first study that focuses on the behaviour and feeding strategies of individual squirrels in urban conditions. This was a preliminary study with quite a low sample size. Nevertheless, it was clear that differences between individuals occurred. The question is whether these behavioural differences (feeding strategies) affected squirrels' personal attributes (such as body condition, body mass or reproduction indices), and if these effects were consistent over time. This should be investigated further in a study with a higher number of individuals involved. Various personality traits can be beneficial in different environmental conditions (Le Cœur et al., 2015; Santicchia et al., 2018), so it may be expected that seasonal and annual changes in natural food availability may force squirrels to use either (natural vs. supplementary) food source accordingly. Another question is whether this behavioural variation is heritable (Taylor et al., 2012), i.e., if the tendency to explore supplementary, alternative food sources in human-transformed habitats is similar in related individuals.

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 Number of total catches for each individual squirrel

Table S2 Ranking of the models explaining the position of animals

Table S3 Ranking of the models explaining the positive reactions of squirrels to humans