



The retrieval of food hoarded by red squirrels inhabiting an urban park

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Abstract

Food hoarding is a useful evolutionary adaptation which strongly affects animal fitness. However, its effectiveness depends on the trade-off between costs of gathering supplies and the benefits of using them by a hoarder when other food is hardly available. A field experiment conducted between November and April in a large urban park in Warsaw (Poland) showed that the survival rate of hazelnuts *Corylus avellana* hoarded by red squirrels *Sciurus vulgaris* was very low – about half of nuts disappeared from caches within one day, and after 50 days the probability of nut survival was 0.01. The survival rate of hazelnuts cached by squirrels was lower than these hidden in control caches. This difference suggests that squirrel-made caches were recovered by caching individuals and/or robbed by pilferers, both conspecific and heterospecific, more successfully than man-made caches. Moreover, survival rates of nuts deployed in control caches in clumps of trees were lower than in the open space areas avoided by squirrels. The probability of nut survival in a squirrel cache and in the control cache increased with the increasing proportion of days with frost as frozen soil limit squirrel access to cached nuts. The probability of nut survival in a squirrel cache and in control cache in the clumps of trees increased over the study period. We discuss whether food hoarding in the environmental conditions of an urban park where animals are oversupplied with food by humans is beneficial for squirrels or if it is an unimportant imprinted behaviour which does not increase their fitness.

Keywords *Sciurus vulgaris* · Behaviour · Caches · Field experiment

Introduction

Food hoarding is an important evolutionary adaptation of many animal species – it enables to overcome periodic or unpredictable variations in food availability, affects animals' survival and reproduction and enhances fitness (Smith and Reichmann 1984; Vander Wall 1990). It is related to high environmental variability, therefore, it is more common at higher latitudes than in tropical areas (Smith and Reichmann 1984). In temperate regions, food caching takes place mostly in the period when food supplies are available (summer and autumn) and prior to when they are scarce

and required (winter and spring). Among stored food types, seeds are cached most commonly and for the longest times, because of their adaptations to dormancy and their concentrated energy reserves (Smith and Reichmann 1984). The way in which food is hoarded may differ according to the hoarder species. Scatter-hoarding, unlike larder-hoarding, is placing single food items in storage sites distributed throughout the home range; however, some intermediate hoarding patterns can also be distinguished and environmental factors may have an effect on hoarding plasticity (Hurly and Robertson 1990; Zong et al. 2014). If hoarders have low abilities to protect food, they will mainly use scatter-hoarding.

There is a wide occurrence of food hoarding in mammals (Smith and Reichmann 1984; Sherry 1985; Vander Wall 1990), and particularly among the species of *Sciuridae* family. In red squirrels *Sciurus vulgaris*, which are typical scatter-hoarders, food hoarding is an adaptive foraging strategy to preserve temporarily abundant resources for future periods of food shortage. In winter and spring, cached food represents a large part of a red squirrel's diet, and the number

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of recovered tree seeds cached by squirrels positively affects their body mass, survival and reproductive output (Wauters et al. 1995; Wauters and Casale 1996).

Red squirrels successfully inhabit urban parks, where they adapt to alternative food resources such as supplemental anthropogenic feeding and where they alter their behaviour to receive food from people (Krauze-Gryz et al. 2021). In urban conditions, red squirrels are offered various sources of supplemental food, mostly walnuts, hazelnuts and peanuts, but they also pilfer bird feeders which hold sunflower seeds and other grains (Babińska-Werka and Żółw 2008; Reher et al. 2016). Being provided food by humans has a direct effect on squirrels' feeding habits and movement patterns (Reher et al. 2016). Squirrels inhabiting urban parks hoard food given by people but their hoarding behaviour, similarly to squirrels inhabiting forests, changes seasonally – nuts are eaten mostly in spring (when there is a shortage of other high energy food) and stored in autumn (Moller 1983; Kostrzewa and Krauze-Gryz 2020). The type of food given also affects squirrel behaviour – most of unshelled nuts (walnuts and hazelnuts) are cached rather than eaten at once (Tamura et al. 1999; Kostrzewa and Krauze-Gryz 2020). In general, red squirrels are able to store great amount of seeds and in populations which receive supplemental feeding each individual can cache several thousand food items per year (Shuttleworth 2000). This volume of food is larger than the volume of food cached by squirrels which do not have access to supplemental feeding (Wauters and Casale 1996). In energy terms, the animals receiving supplemental foods can cache 4–7 times as much as those which are not (Shuttleworth 2000).

Food hoarding behaviour in squirrels has been mostly studied in enclosures and outdoor arenas (e.g., Jacobs and Liman 1991; Vander Wall et al. 2008), urban parks (e.g., Leaver et al. 2007) and rarely in natural habitats (e.g., Zong et al. 2014) mostly due to methodological difficulties – it is very hard to follow the fate of natural caches over an extended period of time. Red squirrels inhabiting urban parks live in conditions much different from these in managed and natural forests – they are usually supplied with large amounts of food by people, live in high densities and compete for food with corvids. Therefore, their hoarding behaviour and utilization of cached food can be strongly affected by factors that do not occur or are restricted in forest habitats. However, urban park conditions give an opportunity to study squirrel hoarding behaviour in more natural conditions than experiments in enclosures. Squirrels are free ranging, have an unlimited space that can be used for caching food, interact with conspecifics and heterospecifics. Red squirrels inhabiting urban parks are usually well habituated to human activity, therefore their food hoarding behaviour is relatively easy to observe. It has been analyzed

in several studies (e.g., Kostrzewa and Krauze-Gryz 2020; Krauze-Gryz et al. 2021) but some new questions concerning food hoarding in human managed habitats can still be asked. One of them concerns the recovery rates of hoarded food and the amount of food taken from caches by pilferers. In squirrels, hoarding behaviour evolved as a profitable adaptation and is strongly imprinted. However, in modified ecological conditions its adaptive role may be reduced or even maladaptive if the hoarded food resources are not consumed by a hoarder. Therefore, the main question arises – is food hoarding in conditions of oversupply and high intra- and interspecific competition still beneficial for squirrels? In other words, is it better to invest the energy as a hoarder, pilferer or just a consumer?

It has been demonstrated that hoarded food is mainly retrieved by the hoarder based on its memory and olfactory cues, and probably to a lesser extent, by conspecific and/or heterospecific competitors (Vander Wall and Jenkins 2003; Vander Wall et al. 2006). The proportion of cached food retrieved by hoarders and/or discovered by pilferers may vary considerably according to numerous environmental factors, but it is very difficult to distinguish between these possibilities under natural conditions. However, estimates of the proportion of caches retrieved by a hoarding animal versus the proportion discovered by pilferers can be obtained using artificial caches (Vander Wall et al. 2006). The aim of our study was to estimate the survival rate of hazelnuts hoarded by red squirrels in a large urban park, analyse variation of this rate over winter period in relation to snow cover and temperature and compare it with the survival rate of nuts hidden by man in artificial caches. We hypothesize that survival rate of nuts hoarded by squirrels should be lower than survival rates of nuts in artificial caches because squirrel-hoarded nuts can be retrieved both by hoarders and pilferers, whereas these hoarded by man only by pilferers.

Materials and methods

Study area

The field experiment was conducted between 13th November 2020 and 18th April 2021, in the Skaryszewski Park (52.242 N, 21.055E), Warsaw, Poland. The park, established between 1906 and 1922, covers 55.5 ha. It is intensively visited by people throughout the year (up to 10 000 people daily in warm weather). The park is a mosaic of grassland (lawns and meadows, 25% of the area), clumps of trees and shrubs, tree-lined avenues, rose garden and several ponds connected with canals (11.3 ha). Due to the parks' age, in many places trees compose over hundred years old growths, and offer many natural shelters such as hollows and cavities.

In 2008, 100 years old tree stands covered 43% of the park area (Romanowski 2016). The park is well maintained and managerial activities are undertaken there (meadows are being mowed, fallen leaves collected in autumn, new trees planted). There is a variety of tree and shrub species in the park (162 taxa), both native and non-native. Deciduous plants predominate but several areas with coniferous trees (spruce *Picea* sp.) and shrubs (common yew *Taxus baccata*) exist.

The Skaryszewski Park is inhabited by many vertebrate species, including the red squirrel *Sciurus vulgaris*, which is a common rodent in the park. In 2015, squirrel numbers were estimated to be up to 100 individuals and population density between 2 and 3 individuals / ha (Romanowski 2016), which is very high compared to forest habitats (e.g. Andrén and Lemnell 1992), but also many other urban parks in Warsaw (Romanowski 2016). Squirrels are unevenly distributed all over the area. They usually stay close to the oldest tree stands or areas with spruce trees. In winter, squirrels keep close to bird feeders and the main park lanes where most people walk and the probability of getting food is highest. Squirrels avoid open space with no trees to climb in an emergency. This is mainly due to the fact that entering with dogs is allowed in the park, and despite they ought to be leashed, owners often let them free. Among many other animal species inhabiting the park, corvids and rodents, such as hooded crow *Corvus cornix*, rook *C. frugilegus*, jay *Garulus glandarius*, field striped mouse *Apodemus agrarius*, yellow-necked mouse *A. flavicollis* and common rat *Rattus norvegicus* may compete with red squirrels for food.

Experimental design

In the study area red squirrels are used to human presence as they are notoriously fed by visitors, mainly with hazelnuts and walnuts. Feeding is most intensive between autumn and spring. The flight initiation distance is very low and squirrels often take food directly from peoples' hands. Squirrels consume the received nuts on the spot or cache them nearby. During the study, squirrels were given hazelnuts in evenly distributed sites all over the park and their caching activity was observed (if a nut was consumed, the next one was given after consumption or another squirrel was attracted by the observer). An observer did not follow a squirrel but watched its behaviour from a distance of several meters. Squirrels cached nuts by burying them in the soil, litter or under fallen leaves. Caching was easy to recognize – squirrels used their forelimbs to dig and while burying a nut they made characteristic movements. The search for a proper place to cache a nut lasted from a few seconds up to a few minutes, and squirrels could make several attempts to hide a nut until they decided to do that. When a nut was cached

and a squirrel moved away, an observer approached the place. A small wooden marker with a red painted tip and its own number was stuck into the ground, always 20 cm to the south from the cache (compass and ruler were used). After being stuck into the ground, the size of the exposed part of a marker was 3 cm x 1 cm. Location of a buried nut was also recorded with GPS.

To create the control sample, hazelnuts were cached randomly all over the park in two different types of habitats – clumps of trees and in open space areas (lawns and meadows), far from the trees, during the same days when nuts were given to the squirrels. This spatial distinction was made due to the fact that squirrel activity in tree-covered areas was very high, whereas open space areas were avoided. Nuts were shallowly buried in the soil and litter, similarly to the way squirrels do. Location of nuts in artificial man-made caches was marked in the same way as in the case of nuts cached by squirrels.

Squirrel caches and control caches were checked by an observer between one day and 50 days after a nut had been cached (mean time for squirrel caches 17.3 days, SD = 13.4; mean time for control caches in clumps of trees 16.7, SD = 11.4; mean time for control caches in open space areas 10.7, SD = 8.8) and the presence or absence of a nut in a given cache was recorded. Each cache was checked only once, as reburying caches increases the probability that they will be pilfered due to the additional olfactory cue of human scent (Duncan et al. 2002). Therefore, each uneaten nut was removed from the cache and its survival time was registered (in days). If a cache was empty, the time elapsed between nut burying and the check of the cache was calculated (also in days). Caches were checked randomly, so as to have various exposure time of cached nuts.

We assumed, similarly as Vander Wall et al. (2006), that removal of real caches represented the activity of the hoarder squirrel and the activities of pilferers (other squirrels and other species), whereas the removal of artificial caches represented the activities of pilferers only.

Statistical analysis

All analyses were performed in R version 4.0.2 (R Core Team 2021), using packages lme4 (Bates et al. 2015). The survival probability of nuts was analyzed using generalized linear models (GLM) with binomial error distribution including four explanatory variables: cache type (1- squirrel cache, 2- control deployment in clumps of trees, and 3- control deployment in open space areas), number of days that have elapsed between nut caching/deploying and the check of a cache, proportion of days with frost, and consecutive month (from November to April). As days with frost and snow cover highly correlated, we decided to use

Table 1 Number of squirrel made caches, control caches, caches found and not found over time, catches with nut present and missing

Cache type	Total	Not found	Found	Nut present	Nut missing
Caches with hazelnuts hoarded by squirrels	859	181	678	149	529
% from all	100	21.1	78.9		
% from found			100	22.0	78.0
Control caches in clumps of trees	793	58	735	340	395
% from all	100	7.3	92.7		
% from found			100	46.3	53.7
Control caches in open space areas	506	114	392	343	49
% from all	100	22.5	77.5		
% from found			100	87.5	12.5

Table 2 Output from the top generalized linear model describing effects of id, the number of days that have elapsed between nut caching/deploying and the check of a cache (N days), proportion of days with frost (Frost) and consecutive month (Month; 1–November – 6–April) on probability of hazelnut survival. Id: S – nuts cached by squirrels, T – nuts deployed in the clumps of trees, L – nuts deployed on the lawns

Variables	Estimate	SE	Z value	P	
Intercept	-0.7684	0.1979	-3.883	0.0001	***
N days	-0.0885	0.0141	-6.283	> 0.0001	***
Frost	1.8830	0.4755	3.96	0.0001	***
Month	0.1739	0.0364	4.772	> 0.0001	***
Id S vs. T	0.5085	0.2260	2.250	0.0244	*
Id S vs. L	2.8515	0.3821	7.463	> 0.0001	***
N days: id S vs. T	0.0608	0.0163	3.726	0.0002	***
N days: id S vs. L	0.0172	0.0300	0.573	0.5666	
Frost: id S vs. T	-2.0269	0.5985	-3.387	0.0007	***
Frost: id S vs. L	0.1269	1.7186	0.074	0.9412	

in the model only the frost variable. In the model, we also included interaction between cache type and the three other variables. We checked the residuals, the overdispersion of the model using the performance package (Lüdtke et al. 2021). Some squirrel and control caches were checked even after about a 100 day-long exposure but due to the small sample size after the 50th day of exposure, nut survival rates were calculated and shown for a 50 days-long period. We computed model support using Akaike's information criterion with a correction for the small sample size (AICc), and we evaluated the strength of the evidence for each model using normalised Akaike weights (Burnham and Anderson 2002). We selected the model with the smallest ΔAICc as the best among all compared models.

Results

Between November and April, we managed to record and mark 859 caches in which hazelnuts given to squirrels were hoarded, we created 793 control caches placed in clumps of trees and 506 in open space areas. The number of caches that could be found after a certain time (some could not be found due to disappearance of the markers), as well as the number of remaining nuts, differed between squirrel made caches, control caches in clumps of trees and in open space areas (Table 1).

Model selection showed that the most parsimonious model ($\text{AICc}=1879.7$, Akaike weight=0.974) for the probability of nut survival contained the number of days,

the proportion of days with frost, caches type, as well as two-way interactions between caches type and the number of days, and between caches type and the proportion of days with frost (Table 2). The second competitive model was 8.17 AICc units worse ($\text{AICc}=1887.9$, Akaike weight=0.016) than top model. The probability of nut survival was lower in squirrel caches than in both types of control caches (Fig. 1; Table 2), and the probability of nut survival in control caches in clumps of trees was lower than in open space areas. The probability of nut survival in squirrel and control caches decreased over time, but nuts cached by squirrels were disappearing from the caches significantly faster than nuts hidden randomly in a control cache in the clumps of trees (Fig. 1; Table 2). After one day, the probability of nut survival in a squirrel cache was about 0.47 ($\text{CI}=0.38\text{--}0.55$), whereas in a control cache in the clumps of trees it was 0.57 ($\text{CI}=0.50\text{--}0.64$), and in open space areas almost all deposited nuts remained (0.94, $\text{CI}=0.87\text{--}0.97$). After 50 days, the probability of nut survival in a squirrel cache was 0.01 ($\text{CI}=0.004\text{--}0.033$), in the control cache in the clumps of trees 0.25 ($\text{CI}=0.16\text{--}0.38$), and in open space areas 0.32 ($\text{CI}=0.07\text{--}0.75$). The probability of nut survival in a squirrel cache was positively related to the proportion of days with frost, and increased from 0.19 ($\text{CI}=0.15\text{--}0.23$) in periods without frost to 0.56 ($\text{CI}=0.38\text{--}0.72$) in periods in which proportion of the days with frost was 0.9. It was significantly different than in control caches in the clumps of trees, where survival decreased only slightly from 0.48 ($\text{CI}=0.44\text{--}0.51$) in periods without frost to 0.44 ($\text{CI}=0.31\text{--}0.60$) in periods in which proportion of the days with frost

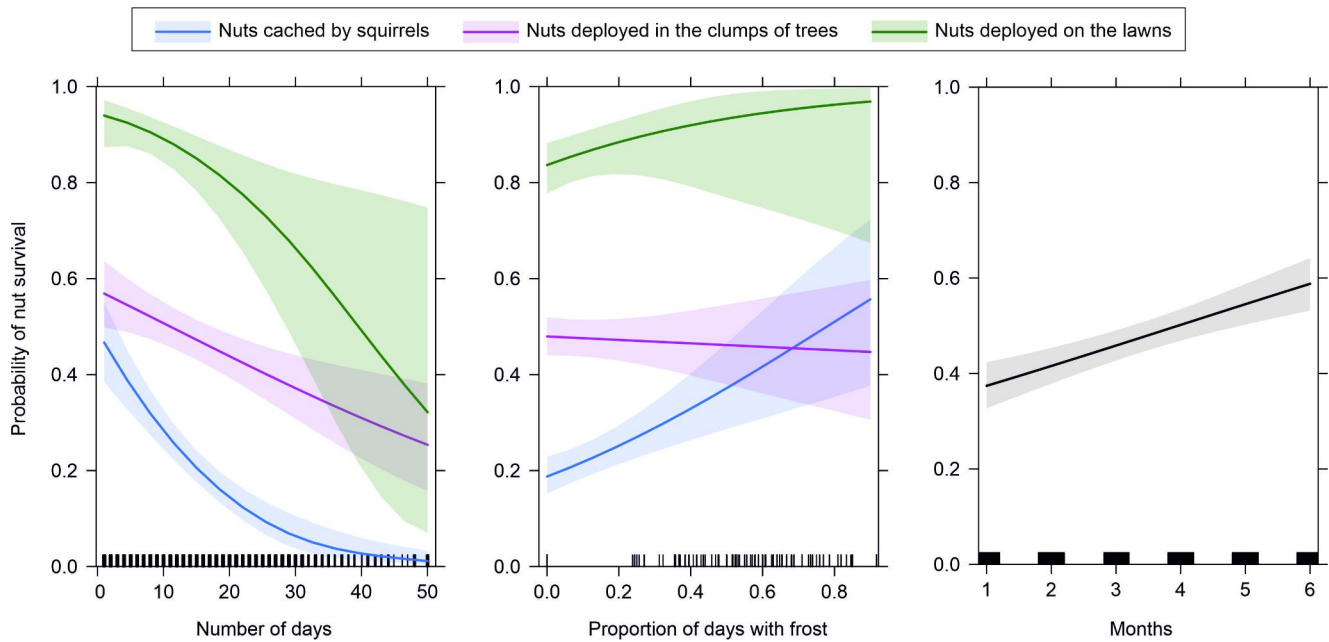


Fig. 1 Probability of hazelnut survival in relation to: number of days that have elapsed between nut caching/deploying and the check of a cache, proportion of days with frost, consecutive month (1-November – 6-April) estimate from the top model

was 0.9 (Fig. 1; Table 2). The probability of nut survival in a squirrel cache and in control cache in the clumps of trees increased in consecutive months during the study period from November (0.37; CI=0.33–0.42) to April (0.59; CI=0.53–0.64) with no interaction between cache types (Fig. 1).

Discussion

In this study we have proved that majority of hazelnuts hoarded by red squirrels in an urban park in cold season is being quickly retrieved from the caches. We also found evidence that probability of nut survival is significantly lower for nuts cached by squirrels than for those hidden in artificial caches. This suggests that the majority of nuts cached by squirrels was found and consumed by them. This assumption can be supported by the fact that in open space areas, where squirrels were not active, survival rate of nuts in artificial caches was higher than in tree clump areas inhabited by squirrels. Food stored by squirrels can either be retrieved by the hoarder or pilfered, but it is difficult to distinguish between these possibilities. In our study, some hazelnuts were definitely found and retrieved from the caches (both squirrel- and man-made) by animals other than squirrels. In the open space areas most likely by hooded crows and rooks, in the areas with tree and shrub cover by hooded crows, jays, mice and rats. The proportion of nuts robbed by crows and other pilferers from squirrel and artificial caches remains unknown, but the recorded differences

in nut survival rates could also be explained by the fact that some pilferers, and particularly hooded crows, can be more successful in finding squirrel caches than man-made caches. Despite some authors suggesting that corvids are not responsible for much cache pilferage (Leaver et al. 2007), we suppose that hooded crows seem to be particularly effective in robbing squirrel caches as they often observe and track squirrels that try to find a proper place to store a nut, whereas it seems rather unlikely that crows are used to nut-caching humans. On the other hand, such an option cannot be excluded because crows also observe humans and learn quickly how to exploit novel food resources. In general, the recorded differences between nut survival rates in squirrel- and man-made caches reflected the proportion of caches retrieved by hoarding squirrels versus the proportion discovered by pilferers in habitat patches inhabited (clumps of trees) and uninhabited (open space areas) by squirrels.

Squirrels can locate buried nuts by their odour, moreover, they can also remember the individual locations of nuts they have cached (Jacobs and Liman 1991). The hoarders seem to be more effective in exploiting their own caches than pilferers because spatial memory gives them a significant advantage over other animals in harvesting cached food (Vander Wall and Jenkins 2003). In an experiment where the seed-hoarders (yellow-pine chipmunks *Tamias amoenus*) remained in the study area, they took real caches 3.4 to 6.5 times faster than artificial caches, but when the caching animals were removed, there were no significant differences in the rates of removal of real versus artificial caches (Vander Wall et al. 2006).

Furthermore, in enclosure experiments, squirrels retrieved significantly more nuts from their own sites than from sites used by other squirrels (Jacobs and Liman 1991). Similarly, in an experimental enclosure, most yellow-pine chipmunks actively searched for food that they had stored before searching for caches to pilfer (Vander Wall et al. 2008). However, several other studies have shown that chipmunks also are very effective pilferers of caches made by other animals (Vander Wall and Jenkins 2003; Vander Wall et al. 2006). In larder-hoarding red squirrels *Tamiasciurus hudsonicus* a majority of individuals stole hoarded food and lost it to stealing, mostly by the neighbours inhabiting adjacent territories (Gerhardt 2005).

Food hoarding rodents can distinguish between nuts they have cached and those cached by conspecifics, on the basis of individually specific olfactory cues. Although squirrels find their own caches easier than caches of other squirrels, they prefer to eat nuts from these made by other individuals thus preserving their own caches (Smith and Reichmann 1984). Therefore, we may assume that in the Skaryszewski Park, squirrel caches were exploited both by the same individuals that established the caches and by conspecifics, but the proportion of their own versus others' caches the red squirrels retrieved remains unknown. In the park, squirrel density was very high and intraspecific competition was intense. Squirrels often remained in close distance from one another, observed other individuals and competed for food given by humans. Squirrels holding nuts were regularly chased by other squirrels. We also observed that under the pressure of conspecifics or hooded crows, squirrels moved hidden nuts to other, probably more safe caches.

Food availability affects the ecology of red squirrels (Wauters et al. 2007, 2008; Selonen et al. 2016), and excess of food can influence their hoarding behaviour in an opposite way (Delgado et al. 2014). Squirrels can reduce their hoarding activity if food is very abundant, as there is no need to have additional food supply. On the other hand, they can intensify food hoarding because their nutritional requirements are fulfilled and they can spend more time and energy on caching available food. The second explanation is more likely and confirmed by some studies. In autumn, when large amounts of food are available, squirrels responded by caching as much and as quickly as possible (Delgado et al. 2014; Kostrzewa and Krauze-Gryz 2020). However, patterns of hoarding behaviour in squirrels are complex and concern not only the amount of cached food but also its quality and care for the choice of a safe cache. It has been observed that during a period of high food availability squirrels cached food with less deliberation compared to a period of food scarcity (Delgado et al. 2014; Kostrzewa and Krauze-Gryz 2020).

Not only hoarding activity but also recovery rates of cached food can be variable, and food availability is the main factor influencing this variation – the higher food availability the lower cache recovery rates (Zong et al. 2014). In the Skaryszewski Park, survival rate of hazelnuts cached by squirrels was very low – most of them were retrieved from caches just within a few days after being deployed. This suggests that food supplies hoarded by squirrels in an urban park fulfill its basic function to a limited extent, as they are mostly exploited not during the periods of food shortages. In the park, the importance of supplemental food in relation to naturally available food is unknown but amount of food given to animals by visitors in winter season is huge and many natural food resources (acorns, spruce cones) are also available. Therefore, food shortages are rather unlikely, and if they occur their duration is rather short. In natural habitats, squirrels extend the period of food availability by storing nuts, but environmental conditions affect cache recovery and cache pilferage (Vander Wall 2000). The availability of hoarded nuts decreases just in periods of potential food shortages, that is after snowfall and during frost. This fact has been confirmed by the results of our study – survival rates of nuts cached by squirrels were positively correlated with duration of frost (and snow cover) periods. Snow cover and frost prolonged caches' duration time because squirrels and other animals had limited access to buried nuts at that time, and squirrels can reduce their foraging activity at low winter temperatures (Tonkin 1983). We have also found increasing probability of nut survival in squirrel caches and in control caches in the clumps of trees over the whole cold season, which means that cached nuts were being retrieved by squirrels and pilferers most intensively in late autumn and least intensively in late winter and early spring. This may seem somehow confusing, as one would expect that hoarded food supplies should be utilised increasingly to decreasing availability of food resources during cold season. However, as we mentioned above, food in an urban park is supplied mostly by humans and its amount, contrary to natural habitats, may even increase over the winter as people intensify feeding animals from autumn until spring.

Survival rates of nuts hoarded in the Skaryszewski Park are difficult to compare with other results because only a few studies showed fate of squirrel caches and dynamics of their use. For example, nuts hoarded by Japanese squirrels *Sciurus lis* were frequently lost to intraspecific and interspecific competitors – 30% of the caches monitored for 30 days after hoarding were consumed by woodmice, and the other 70% were eaten by squirrels or remained (Tamura et al. 1999). Of these retrieved by squirrels, 46.6% were visited within 3 days, 18.0% after 4–9 days, 6.2% after 10–30 days, and the 29.2% were left hoarded. In our study, the survival rate of nuts cached by squirrels was lower, as about

half of them were gone after one day, and less than 10% remained as long as one month. Very low survival rate of nuts in our study site can result from the fact that squirrels that live at high densities also hoard nuts at densities greater than optimal, and establishing cache densities greater than the optimum would increase the possibility of exploitation by pilfering squirrels (Smith and Reichmann 1984). Nut survival is negatively correlated with density of scatter-hoarded nuts because squirrels recognize differences in nut densities and devote more time to searching in areas with high densities (Stapanian and Smith 1984).

Conclusions

Our research shows only one aspect of food hoarding by red squirrels – the persistence of the caches in conditions of high squirrel and corvid densities in an urban park. In general, survival rate of nuts hoarded by squirrels was very low despite high availability of food delivered to animals by humans. Lower survival rate of nuts cached by squirrels compared to survival rates of nuts in random control caches suggests that nuts cached by squirrels are exploited by them and potential pilferers more intensively than these cached by man. Moreover, differences in survival rates of nuts in control caches located in areas inhabited by squirrels (clumps of trees) and those where squirrels are not active (open space areas) suggests that squirrels are effective in finding nuts even if they are not cached by themselves or conspecifics.

In red squirrels inhabiting forests, food hoarding is an adaptive strategy and individuals that hoard and recover many seeds are more likely to survive and reproduce (Wauters et al. 1995). However, food hoarding is always a trade-off between costs of gathering supplies and benefits of using them when other food is hardly available. Therefore, an open question arises whether food hoarding in environmental conditions of an urban park, with constant food supply, high squirrel and corvid densities, and high storage losses caused by pilferers, is beneficial for squirrels or not? Most animal species that adapt to live in urban ecosystems modify their behaviour (Ritzel and Gallo 2020; Beliniak et al. 2021), but it seems that hoarding behaviour in red squirrel is strongly genetically imprinted, and it cannot be overwhelmed by environmental factors and completely eliminated.

Author contributions MB arranged and conducted field experiment. AZ made statistical analyses, prepared figure and tables. MB and AZ wrote and reviewed the manuscript.

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Data availability Datasets used in the manuscript are available at the request and owned by the corresponding author (Marcin Brzeziński) employed at the Faculty of Biology, University of Warsaw.

Declaration

Ethics approval During the study animals were not trapped, handled, scared or stressed, therefore, ethic approval was not needed.

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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