Weight operated see-saw feeding hoppers are not selective for red squirrels when greys are present

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Feeding hoppers are not selective for red squirrels when greys are present

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ABSTRACT

The competition for food resources between the native red squirrel and the introduced American Eastern grey squirrel is well known, and can lead to the extinction of the native species. Providing supplementary food resources for the red squirrel, by adopting selective feeding hoppers, has been proposed as a possible support for the short term conservation of native populations, but studies that investigate its effectiveness have not yet been performed. In this study we evaluate the effectiveness of the feeding hoppers, in terms of selectivity towards the smaller native species, quantifying their utilization by the two species in sympatry and allopatry.
Feeding hopper were not selective toward the native species. The success in the attempts to enter the hoppers was 95% for red and 86% for grey squirrels. The 50 hazelnuts provided during each feeding session, covering the energetic requirements of an individual for 6 (reds) or 3.5 (greys) days, were consumed in 45:43 ± 38:26 hh:mm by red and 31:07 ± 37:18 hh:mm by grey squirrels. The average weight of grey squirrels that entered the feeding hopper (490 ± 47 g) was higher than the calibration weight of the see-saw floor (400 g). This highlights an incorrect functioning of the system, also related to a learning behaviour of the animals. Structural modification of the feeding hoppers should be considered to obtain a real selectivity according to species before their implementation in the conservation of red squirrel populations.
However feeding hoppers were selective in feeding squirrels, excluding the access to food supplies by other species. Therefore they can be used with success in supplementary feeding studies or behavioural and ecological studies, especially if combined with camera traps and individually marked animals.

Keywords

Sciurus vulgaris, *Sciurus carolinensis*, competition, supplementary feeding, activity pattern.

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Introduction

The introduction of non-native species is a widely known issue in biological conservation (Manchester and Bullock, 2000; Simberloff, 2005): changes in ecosystems due to the establishment of introduced species may have dramatic consequences, often leading to the decline, or even extinction, of native taxa (Vié et al., 2009; Collen et al., 2012).

A well known case of replacement competition between native and introduced species is related to the introduction of the Eastern grey squirrel (*Sciurus carolinensis*) in Great Britain, Ireland and Italy. This species, native to North America, is causing a progressive rarefaction of the Eurasian red squirrel (*Sciurus vulgaris*) (Martinoli et al., 2010; Bertolino et al., 2014a; Gurnell et al., 2014) and is exerting an impact on forestry through tree debarking (Dagnall et al., 1998; Bertolino et al., 2008). The substitution carried out by the grey squirrel is mainly based on interspecific competition for food resources (e.g., Kenward and Hodder, 1998; Wauters et al., 2002a, 2002b; Gurnell et al., 2015). The utilization of the same feeding resources may reduce the daily energy intake of the red squirrel, with a decrease of both female breeding success and juvenile body growth/recruitment (Wauters et al., 2001; Gurnell et al., 2004). Bryce et al. (2001) considered the daily energetic requirement and the mean body weight of both squirrel species and proposed a theoretical competition coefficient, whereby one grey squirrel will use up to 1.65 times the food energy required by a red squirrel. These factors generate a reduction of native squirrel fitness and, as a consequence, the progressive decrease of population size. In Great Britain the competitive exclusion is also mediated by a squirrel poxvirus, carried by grey squirrels and lethal to red squirrels (Sainsbury et al., 2000; Tompkins et al., 2003; Shuttleworth et al., 2014). In Italy, both macro-parasite spillover and spillback processes between grey and red squirrels occur (Romeo et al., 2014, 2015).

While Great Britain and Ireland are islands, the presence of the grey squirrel in Italy poses a serious threat to the red squirrel in most of Europe (Tattoni et al., 2006; Bertolino et al., 2008; Di Febbraro et al., 2013). For this reason, management actions have been recently started to eradicate or control the Italian populations of the grey squirrel (Bertolino et al., 2014b; Bertolino et al., 2015). The conservation of viable red squirrel populations mainly relies on the numerical control of the grey squirrel, performed by trapping and removing the animals or by shooting them (Huxley, 2003; Schuchert et al., 2014). In Great Britain, the conservation of the red squirrel is also based on the long-term management of strongholds reserves; large conifer forests are managed to increase suitability for the native species and subject to systematic grey squirrel control programs (Parrott et al., 2009; Shuttleworth et al., 2012).

Competition being mainly based on a better exploitation of food resources by the grey squirrel, a supplementary artificial feeding for red squirrel has also been proposed as a possible conservation measure for the native species (Gurnell and Pepper, 1991; Gurnell, 1996). In Great Britain, the Forestry Commission developed a supplementary feeding hopper system, specific for the conservation of the red squirrel (Pepper, 1993). The feeding hopper was designed to feed red but not grey squirrels, adopting a lever system based on the weight of the animals. Adult grey squirrels (weight 400-720 g: Harris and Yalden, 2008) are nearly 60% heavier than red squirrels (240-400 g in Europe: Bosch and Lurz, 2012); therefore, to limit the entrance in the feeding hopper to the red squirrels and the lighter young grey squirrels should be possible. The supplementary food resources, available for red squirrels in sympatric areas with grey ones, should conceptually prevent the decrease of individual body mass and, consequently, increase reproductive success and survival probability of the animals with positive effects at the population level. The discovery of the role of the squirrel poxvirus in the competition between the two species has prevented the use of this supplementary feeding system in Great Britain. In fact, the presence of a feeding point could increase the number of contacts between the two species, increasing the probability of disease transmission (Rushton et al., 2000). By contrast, in Italy, cases of infection from squirrel poxvirus have never been recorded (Lurz et al., 2005; Bertolino S. and Wauters L. unpublished data) and therefore the use of the feeding hopper is not hindered. The selectivity of the feeding system for red squirrels has not been formally tested yet. If feeding hoppers are proven to be effective, the implementation of the supplementary feeding system may be evaluated as a conservation measure for the red squirrel, both in areas where grey squirrels are removed and in areas recolonized by the red squirrel.

Aim of this study was to evaluate the selectiveness of the feeding hopper toward the red squirrel, by quantifying its utilization by the native and the introduced species, both in sympatric and allopatric areas. Selection at the entrance and food consumption, in terms of food and energy intake, in relation with the time necessary for the squirrels to feed, were analysed. We further evaluated how a feeding hopper system could be used to study the daily activity pattern for arboreal species.

Material and methods

Feeding hopper

Feeding hoppers used in this work are like those described by Pepper (1993). They have (Fig. 1): *i)* an entrance and a tunnel which allows squirrels to reach the food, with a see-saw floor calibrated at a fixed weight of 400 g; *ii)* a reservoir of food resources; *iii)* an outside platform to help squirrel to enter inside the feeding hopper. The calibration of the see-saw floor was verified with progressive weight for each feeding hopper. The feeding hoppers were placed on tree trunks at about 1.70 meters from the ground, supervised by a camera trap (models: LTL Acorn 5310, IDS Multipir 12 HD, Scout Guard SG550) to record squirrels and their activity (Rovero et al., 2013). Camera traps were set to record videos of 1-2 minute length with no gap between each recording, to allow a continuity of the video during the animal activity. A weighing scale was placed on four feeding hoppers to estimate the weight of the grey squirrels approaching the hoppers. During the research, it has not been possible to mark the animals so as to allow their individual recognition in video.

Thirteen feeding hoppers were placed in six study areas: 2 areas occupied only by the grey squirrel, 1 area occupied only by the red squirrel, and 3 areas where both species occurred (Fig. 2). The number of feeding hoppers in each area and the number of days left in place varied at each study area (Table 1).

Each feeding hopper was supplied once a week with 50 hazelnuts. Videos from the camera traps were recovered in the meantime and the feeding hopper inspected to check for residual hazelnuts. Hereafter, each weekly maintenance period is considered as a single sampling period (*SP*). The fixed number of hazelnuts allows the comparison of the time-series and the daily activity pattern among species and seasons. We recorded the following variables during the screening of the videos: the squirrel species approaching the hopper; the number of squirrels fallen after the activation of the see-saw floor, both during the entrance or exiting from the feeding hopper; the time required for the consumption of the hazelnuts. Four time-series were recorded for each *SP*: *i)* the time between the resources supply and the consumption of the first hazelnut (T_{fh}); *ii)* the time for the consumption of all the hazelnuts (T_{tot}), from the first entrance in the feeding hopper to the last one; *iii)* the effective time for the consumption of all the hazelnuts (T_{eff}), taking away from T_{tot} the periods when the squirrels were not in or around the feeding hoppers; *iv)* the total time spent inside the feeding hopper by a species (T_{ins}). These time-series were analysed through non-parametric tests (Chi-square, Mann-Whitney) to assess differences between species.

Time-series were also analysed through a circular statistical method (Mahan, 1991) to compare the activity in the feeding site between the two species and the seasons of the year. The Rayleigh test was used to evaluate the distribution of the squirrel activity patterns: differences from a uniform distribution and concentration of the hours of activity. The Watson-Wheeler test was used to assess differences in the activity patterns between species and seasons. The data available allowed the analysis of the seasonal utilization during a year for the red squirrel, while the comparison between the two species was performed throughout the autumn, winter and early spring season, when contemporary data were available.

For each study area, a utilization index *Ui* ranging from 0 (no utilization) to 1 (maximum utilization) was calculated for the two species, by considering the number of *SP* in which a squirrel was recorded in feeding activity over the number of *SP* in which the hoppers were available for the squirrels to feed (removing the *SP* with camera trap problems or different species utilization).

Daily energy intake

One hundred shelled hazelnuts were weighed with an analytical balance after a drying process at 80 °C for 48 hours to evaluate the energy provided by 50 hazelnuts. The mean energy nutrient value for 50 hazelnuts was calculated by multiplying the weight of the mean dry matter with the energy standard reference value for the hazelnuts, which corresponds to 6.28 kcal/g (National Agricultural Library, 2015).

The daily energy requirements for the squirrels (mean daily energy intake of 347 kJ for the red squirrel and 574 kJ for the grey squirrel) were derived from Bryce et al. (2001).

Results

The sampling success was nearly half of the sampling effort: on 274 overall *SP*, only 164 (60%) could be analyzed. The other *SP* were not considered for various reasons: *i)* feeding hoppers were not used by the squirrels and the hazelnuts were not eaten; *ii)* the camera traps did not work properly; *iii)* feeding hoppers were used, though in rare cases, by other animal species (0.96 % by *Glis glis*, 0.48 % by genus *Apodemus* spp.).

Overall, the red squirrel accessed the feeding hopper 2629 times, falling 8 times (0.30%) because of the see-saw floor; the grey squirrel accessed the feeding hopper 2428 times, falling 46 times (1.89%). Although grey squirrels fell down significantly more often than reds (χ^2 = 28.73, df = 1, p < 0.001) they succeeded entering in the vast majority of attempts. Exiting from the hopper red squirrels fell 103 times out of 2621 occasions (3.93%) and grey squirrels 863 out of 2382 (36.23%) a highly significant difference (χ^2 = 833.6, df = 1, p < 0.001). However, falling while exiting did not affect the squirrel's possibility of feeding, because they fell with the hazelnuts in the mouth. Red squirrels consumed 2506 hazelnuts (95.3% of the access attempts led to acquire a hazelnut) and grey squirrels 2086 hazelnuts (85.9%; difference between species χ^2 = 6.66, df = 1, p < 0.05) (Fig. 3). The mean weight of the grey squirrels that entered inside the feeding hoppers was 490 ± 47 g, with extreme values of 400 g and 600 g. The utilization index *Ui* for the two species for each feeding hopper is reported in Table 1.

The mean weight of the dry matter for a shelled hazelnut was 1.52 ± 0.08 g. Considering the reference value of 6.28 kcal/g, 50 hazelnuts provide an energetic value of 475.98 ± 4.73 kcal, equal to 1992.84 ± 19.80 kJ. Considering the mean daily energy intake for the two species derived from

Bryce et al. (2001), the 50 hazelnuts provided by a feeding hopper ensured the energetic requirements for 5.74 ± 0.06 days for a red squirrel and 3.47 ± 0.03 days for a grey squirrel.

The overall time for hazelnuts consumption T_{tot} was higher for the red than for the grey squirrel (Table 2, U = 1854, p < 0.01), while the effective time for consumption T_{eff} was higher for grey squirrels (U = 3907, p < 0.001). No statistical differences were detected between the species in the other two time-series analysed, T_{fh} and T_{ina}. The squirrels start to use the feeding hoppers mainly the day after the resource supply, but there are cases of earlier (00:33 h:mm) or later utilization (164:50 h:mm).

The Rayleigh test confirms that the squirrels' activity is concentrated during the daylight (Table 3). In the red squirrel activity pattern, the length of the resultant vector r is different among seasons, according to the changes in the photoperiod: r is higher in winter when the day length is shorter, indicating a concentration of the squirrel activity during fewer hours; intermediate in autumn and spring; lower in summer when the day length is longer, indicating a dispersion of the squirrel activity among more hours. The mean daily squirrel activity on the feeding hopper is represented together with the rose diagram, which highlights the daily periods of utilization by merging the observation in time groups (Fig. 4). Significant differences in the daily activity pattern between red and grey squirrel are shown (Watson-Wheeler test: U^2 = 25.51, p < 0.001). The red squirrel use the feeding hoppers mostly from 8:00 to 14:00, while the grey squirrel has two daylight activity peaks, from 8:00 to 9:00, from 15:00 to 17:00 and a lower but constant utilization from 9:00 to 15:00. Significant differences in the red squirrel activity pattern were also detected among seasons: summer, autumn and winter differs between them (summer-autumn: U^2 = 11.23, p < 0.01; summer-winter: U^2 = 29,68, p < 0.001; autumn-winter: U^2 = 15.18, p < 0.001); spring only differs from winter (U^2 = 18.83; p < 0.001).

Discussion

The feeding hoppers tested in this study were proven to be not selective for the red squirrel, allowing also the entrance of grey squirrels. We observed statistical differences between the two species by comparing the access attempts and the hazelnuts consumed, but these differences do not guarantee any selectivity toward the native species. In most of the occasions grey squirrels which attempted to reach the food resources came out from the hoppers with a hazelnut in the mouth.

The mean weight of grey squirrels which entered inside the hoppers was higher than the calibration weight of the see-saw floor, thus emphasizing the incorrect functioning of these systems. More than half the individuals weighed more than 500 g with an upper extreme value of 600 g, suggesting that adult grey squirrels may enter inside the feeding hoppers. Furthermore, a learning behaviour was observed in some grey squirrels: animals which felt during the first attempts, sometimes reached the food resources in following efforts. A possible explanation of this phenomenon is that grey squirrels may learn to place the front legs further into the see-saw floor, reducing the distance between fulcrum and effort: with a shorter lever the power exerted by the weight is reduced. Therefore, a structural modification of the feeding hoppers may increase the sensitivity of the selective see-saw floor. For instance, a modification in the length of both the tunnel entrance and the see-saw floor, so that squirrels are forced to exert their weight on the initial part of the platform (lever with more distance between fulcrum and effort), would make more difficult their use by grey squirrels. If the selectivity will increase, then the feeding hoppers could be used in areas where the grey squirrel is removed or in areas of new recolonization by the red squirrel, to help the short-term survival of the red squirrel population, as recommended by many authors (Gurnell & Pepper, 1991; Gurnell, 1996; Kenward and Hodder, 1998). However, a long-term strategy based on supplemental feeding would not only be expensive, but also lead to the maintenance of man-dependent populations of squirrels; therefore, it should be discouraged.

Kenward et al. (2005) developed another type of selective and automatic feeding system, based on the individual identification with passive integrated transponders (PIT tags). This method is for sure selective, because animals which could reach the food resources are only those with the PIT tag implant. However, this technique cannot be used in the conservation of red squirrel populations on a large scale, due to the necessity to continuously trap and PIT mark a high number of squirrels.

The feeding hoppers used for this study were selective in feeding squirrels, excluding the access to food supplies by other animal species, such as other arboreal rodents or birds. Therefore they can be used with success in supplementary feeding studies or behavioural and ecological studies, especially if combined with camera traps and individually marked animals. The estimation of the energy intake ensured by food resources, in relation with the time spent by the squirrels in feeding, could be a crucial parameter for the evaluation of the food hoarding behaviour and the energetic budget of a species (Macdonald, 1997; Goheen and Swihart, 2003). In our work, the mean time spent by the squirrels for the consumption of all the hazelnuts T_{tot} is lower than the mean time of energy intake ensured by the hazelnuts, due both to food hoarding and simultaneous frequentation of the feeding hopper by different individuals. Both species were able to collect in one day the 50 hazelnuts that covered the energetic requirements of an individual for 6 (reds) or 3.5 (greys) days. The presence of marked animals might allow further studies on this behavioural aspect, enabling the evaluation of the daily energy intake consumed by each individual. Despite the higher value of T_{tot} recorded for the native species, the effective time for the consumption of all the hazelnuts T_{eff} is lower for the red than for the grey squirrel. This could be due to the different behaviour observed in the feeding site for the two species. The red squirrel generally approached the feeding hoppers with high speed and agility, while the grey squirrel was slower and wandered more near the feeding site.

Both species are known to be typically diurnal (Wauters & Dhondt, 1987; Wauters et al., 1992; Wauters, 2000); the mean peaks in activity rhythms around feeding sites were located around midday. Koprowski (1994) reported a bimodal activity pattern from spring to autumn for the grey squirrel, with peaks of about 2 h after sunrise and 2-5 h before sunset, and an unimodal pattern in winter, with a peak of 2-4 h before sunset. This was also found by Wauters et al. (2002b) in mixed red-grey sites in Italy. Tonkin (1983) and Wauters et al. (1992) described a similar activity pattern for the red squirrel, with the difference of an unimodal winter activity peaking in late morning. Our results confirmed these activity patterns. However, our data suggested differences between the two species in timing of major activity around the hoppers. This is in contrast to earlier studies which, using radiotracking, demonstrated a high degree of overlap in activity patterns of the two species (Wauters et al., 2002b; Gurnell et al., 2015). These differences between studies could be due to activity around hoppers not reflecting the complete active period of the two species, but rather differences in spatial foraging behaviour and/or foraging decision making processes.

We also observed a differentiation of the red squirrel activity pattern among seasons. In agreement with previous studies, the winter activity showed an unimodal pattern from 8:00 to 13:30, and this distribution was significantly different from the distributions of the other seasons (Tonkin, 1983; Wauters et al., 1992). In spring and summer, we observed a bimodal activity pattern, while in autumn a high utilization in the morning and a low frequentation before sunset was detected, similar to studies carried out in Belgium and N. Italy (Wauters et al., 1992, 2002b; Wauters, 2000). Furthermore, the quantity of time spent by the squirrels while feeding was different among seasons, in relation with the changes in the photoperiod. The length of the resultant vector r indicated a high concentration of the feeding activity during few hours for the winter season, while lower values of r during the other seasons indicate a feeding activity more distributed throughout the day. The minor number of data available for the grey squirrel did not allow us a comparison on the activity pattern among seasons.

In conclusion, the present model of feeding hoppers may not be used as additional or complementary method for the conservation of red squirrel populations where grey squirrels are present. Instead, they could be used successfully in behavioral and ecological studies of arboreal species, as squirrels, especially when combined with methods for individual recognition.

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Table 1

Number of feeding hoppers placed in each study area and number of days left in place. It is also reported the utilization index *Ui* of each feeding hopper for the two species (values just for one species indicate allopatric areas).

Study area	No. of feeding hoppers	Days	*Ui* (Grey squirrel)	*Ui* (Red squirrel)
CN 1	1	130	0.00	0.33
CN 2	1	192	0.11	0.74
TO 1	2	308	absent	0.76 0.29
TO 2	2	139	0.00 0.00	0.80 0.93
TO 3	3	70	0.78 0.00 0.78	absent
TO 4	4	159	0.86 1.00 0.83 0.94	absent

Table 2

Mean values of the time variables for grey squirrel and red squirrel: T_{fh} (time for the consumption of the first hazelnut from the resources supply); T_{tot} (time for the consumption of all the hazelnuts); T_{eff} (effective time for the consumption of all the hazelnuts); T_{ins} (time spent inside the feeding hopper).

		T_{fh} (h:mm)	T_{tot} (h:mm)	T_{eff} (h:mm)	T_{ins} (mm:ss)
Grey squirrel	Mean value	26:03	31:07	3:27	3:18
	SD	30:15	37:18	2:25	1:36
	Min	0:33	0:33	0:31	0:57
	Max	164:50	164:50	11:27	10:52
Red squirrel	Mean value	25:37	45:43	1:42	3:13
	SD	18:40	38:26	0:38	0:57
	Min	0:41	1:20	0:37	0:56
	Max	72:52	164:50	3:14	5:52

Table 3
Summary of the activity pattern analysis: is reported the mean direction with the 95 % confidence intervals (CI), the length of the resultant vector (r) and the Rayleigh's test result (Z) with the p value.

	Mean direction	***CI***	***r***	***Z***	***p***
Grey squirrel	13:11	0:09	0.71	55.07	< 0.001
Red squirrel	11:26	0:06	0.75	114.75	< 0.001
Red squirrel spring season	11:16	0:16	0.72	18.00	< 0.001
Red squirrel summer season	12:54	0:15	0.54	22.13	< 0.001
Red squirrel autumn season	11:43	0:07	0.71	78.00	< 0.001
Red squirrel winter season	10:58	0:08	0.92	31.23	< 0.001

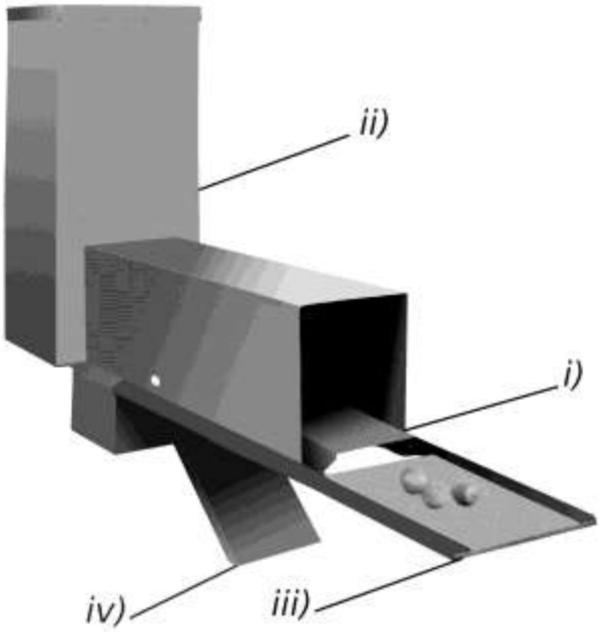

Fig. 1. Selective feeding hopper for squirrels: *i)* entrance and see-saw floor in the non-active position; *ii)* reservoir of food resources; *iii)* outside platform to help the animals to enter the hopper, with hazelnuts to attract them; *iv)* see-saw floor in the active position.

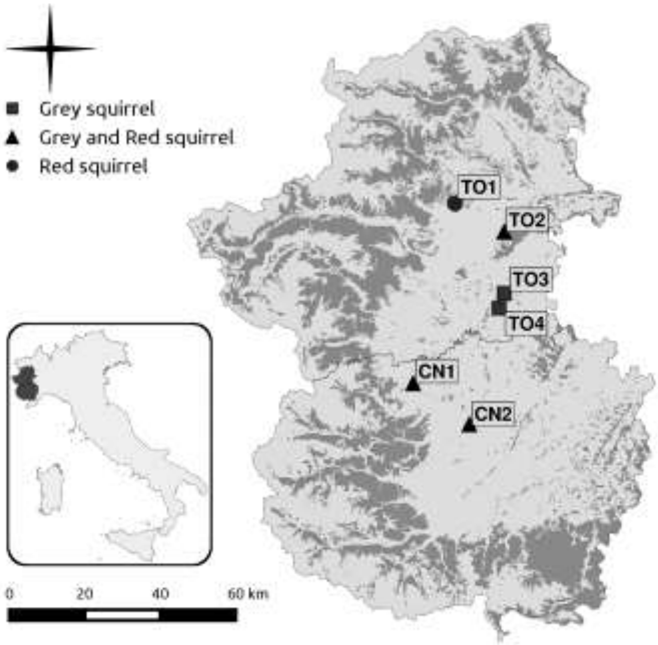

Fig. 2. Location of the six study areas in Piedmont, Italy: one was occupied by the red squirrel (TO 1), two by the grey squirrel (TO 3, TO 4), three by both species (TO 2, CN 1, CN 2).

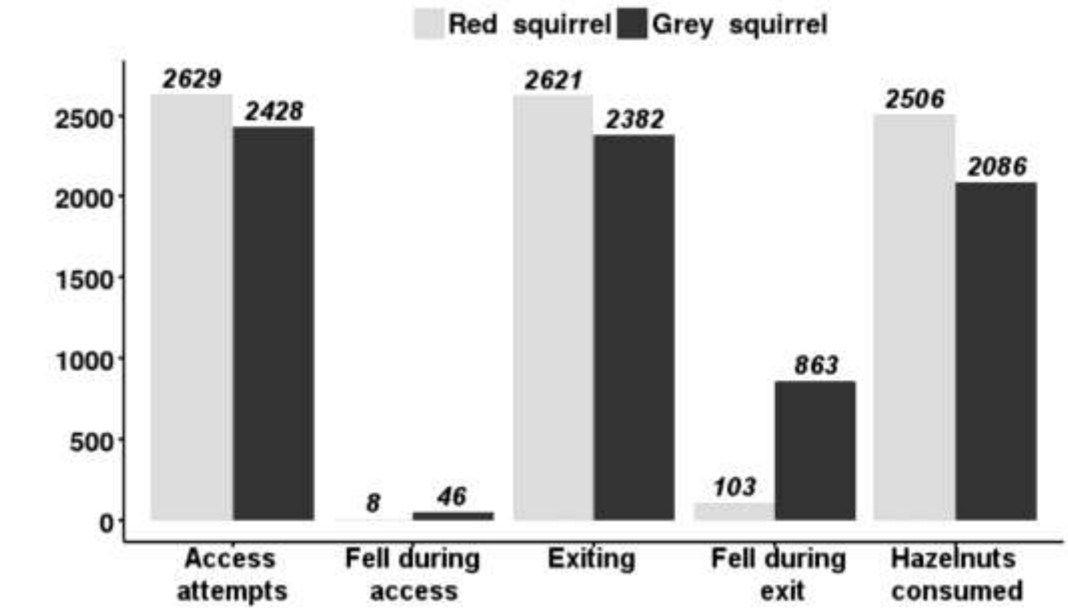

Fig. 3. Utilization of the feeding hoppers by the red and grey squirrel.

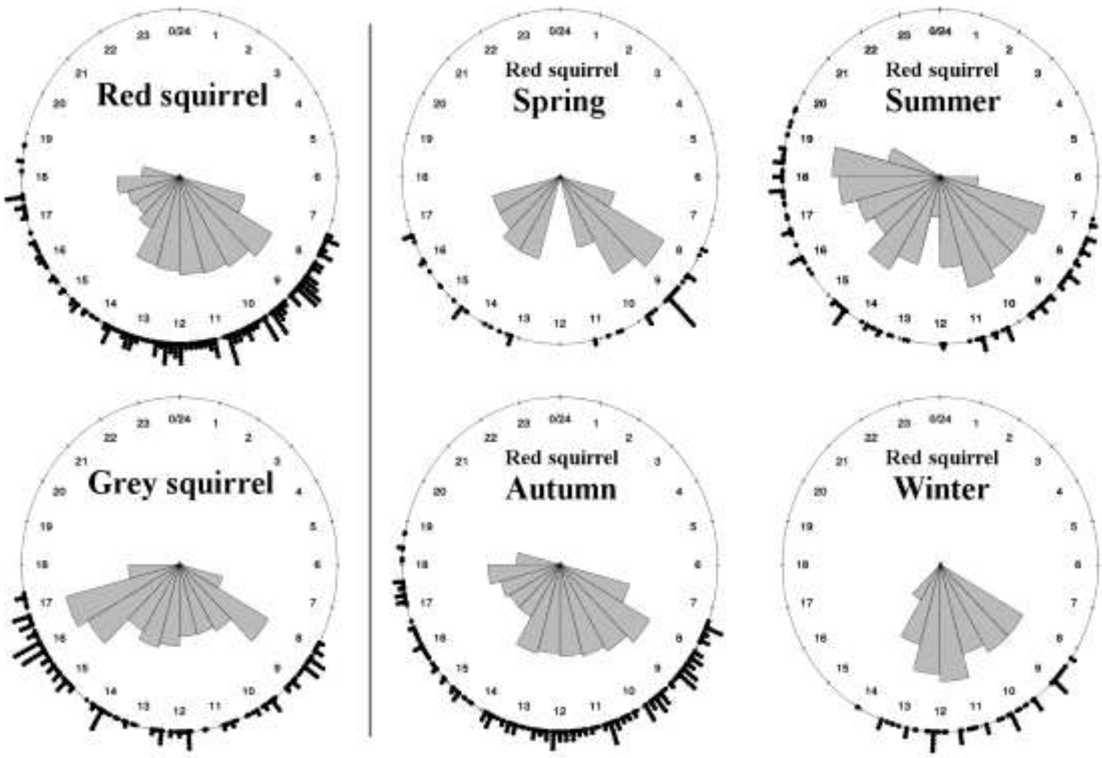

Fig. 4. Daily activity pattern on the feeding hoppers: on the left the activity of the two species during the autumn, winter and early spring seasons; on the right the activity of the red squirrel during the seasons of the year. Inside each circle the rose diagram highlights the daily activity peaks; outside the observations are represented by cumulative points.


2014/11/07 13:47:47
2014/11/07 13:48:04
10/11/2014 12:15:12
10/11/2014 12:15:18


2014/10/05 13:46:50
2014/10/05 13:47:26
01/08/2015 16:22:29
01/08/2015 16:22:40
11/21/2014 12:47:40
11/21/2014 12:47:48
02/09/2015 11:51:07
01/27/2015 14:16:11