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Original paper

Influences of weather conditions, natural food abundance, and the spacing of feeders on the feeding-table use by Japanese squirrels *Sciurus lis* in a suburban forest

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Abstract. The purpose of this study was to examine the influences of seasonal and annual changes in weather conditions, natural food abundance (pine seeds), and the spacing of feeders on the use of walnuts on feeding tables by Japanese squirrels (*Sciurus lis*) in a suburban forest in Nagoya City, in summer (Jul–Aug) and autumn (Sep–Oct) from 2019 to 2021. Feeder-use increased in severe weather conditions, i.e., low temperature and heavy rain in both seasons, and decreased in summer of the year when pine-seeds were abundant. Feeders were used more in autumn for hoarding before the winter. The intervals among eight feeding tables were widened during the study from c. 100 m in 2019–2020 to c. 300 m in 2021. In the years when the feeders were placed at short intervals, we found two behavioral modifications due to the supplemental feeding: a concentrated distribution of many individuals in 2019 and exclusive occupation by a particular female in 2020. In contrast, in 2021 with the feeding tables placed at wider intervals, the distribution of individuals expanded over the entire study area, and the use of supplementary feeding decreased, while seed consumption increased.

Key words: home range, pine seed, squirrel, supplemental feeding, walnut.

Arboreal mammals such as squirrels are susceptible to forest fragmentation because of their limited ability to move outside of forested areas (Tamura 2001; Koprowski 2005). The Japanese squirrel (*Sciurus lis*) is endemic to Japan, distributed from Honshu Island to the Kyushu and adjacent islands (Ohdachi et al. 2015). They mainly feed on the seeds of plants such as Manchurian walnut (*Juglans mandshurica*) and Japanese red pine (*Pinus densiflora*, hereafter red pine), and sometimes on fruits, shoots, flowers, mushrooms, and insects (Yatake and Tamura 2001; Nishi et al. 2014). However, their numbers have declined throughout Japan as a result of fragmentation and degradation of forested habitats (Yatake 2001), and they are now listed as an endangered species in western and southern Japan (Ministry of the Environment 2020).

Supplementary feeding, installing nest boxes, planting trees, and establishing eco-bridges have been conducted for the conservation of fragmented squirrel populations (Yatake 2001). Supplementary feeding, in particular, is a simple and effective method for conservation in environments where food resources are scarce (Reher et al. 2016; Turner et al. 2017). However, some studies of Eurasian red squirrels (*S. vulgaris*) have revealed negative effects of feeding such as increased competition, predation, and disease spread due to concentrated distributions of individuals (Shuttleworth 2001; Wauters et al. 2002; Chantrey et al. 2014). As shown in some primate species (van Noordwijk and van Schaik 1987; Dubuc and Chapais 2007), feeding tables in small patches may be exclusively occupied by certain socially dominant individuals of squirrels. In a previous study, we detected inbreeding in this population via genetic analysis using microsatellite DNA (Inoue et al., in press); this inbreeding could be a result of the concentrated distribution of feeders. Therefore, we need to examine how supplementary feeding maximizes the positive effects of supplemental resources while minimizing the

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negative effects of their intensive use (Fingland et al. 2022). The effects of feeding on squirrels' behavior have been shown for home range (Reher et al. 2016), activity duration (Thomas et al. 2018), foraging (Shuttleworth 2000), antipredation behaviour (Uchida et al. 2021), and reproductive performance (Rézouki et al. 2014). However, these studies have not evaluated the influence of weather conditions, natural food abundance, and spacing of feeders.

We predict that feeder-use should increase when the conditions of weather and/or natural food abundance are severe and decrease when feeders are widely spaced. To test these predictions, this study is aiming at examining the influences of seasonal and annual changes in these factors on the use of feeding tables by Japanese squirrels in a suburban forest in Nagoya City, where the squirrel population has declined (Nawa and Noro 2015). In this study, we investigated the use of feeding tables with automatic infrared video cameras and the distribution of home ranges with radiotelemetry for each individual. We then analyzed how their use of feeding tables changed with seasonal and annual changes in weather conditions and natural seed production. We also examined how the squirrels' use of feeders changed when the feeding tables were moved to different places to spread. Based on these results, we discussed the effects of supplemental feeding for the conservation of squirrels inhabiting a suburban forest.

Materials and methods

Study area

The study site was located on Mt. Togokusan (198 m in altitude, approximately 120 ha in total area) in the northeastern part of Nagoya City (35°15'22"N, 137°03'11"E). The vegetation was a mixed forest of coniferous and broadleaved species, dominated by Japanese chinquapin (*Castanopsis cuspidata*) and Japanese cedar (*Cryptomeria japonica*). Red pine, which produces seeds that squirrels consume, grows in the southern part of the study area (Fig. 1b).

In the study area, a local volunteer group, the Moriyama Squirrel Study Group, installed eight feeding tables (30 cm × 35 cm × 5 cm, made of cypress wood), attached with 3 mm diameter ropes at 120 cm height to the sides of tree trunks c. 10–30 m away from the forest trails. At each feeding table, 80 pieces of walnuts have been supplied in the morning on Saturday every week since 1998 (Ohtake et al. 2017). The food supply at each table is restocked within a five-minute period without any

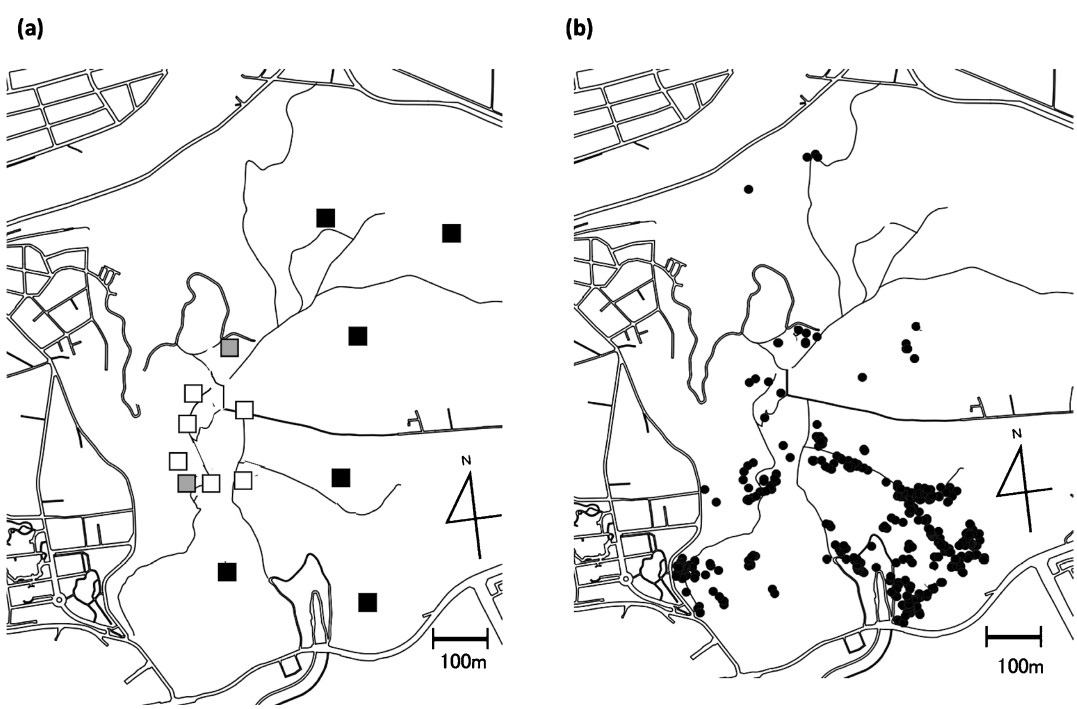

Fig. 1. (a) Locations of feeding tables. Squares indicate the location of the feeders in 2019 and 2020, circles indicate the location of the feeders in 2021 (gray squares indicate that the locations were the same during all three years). and (b) Locations of Japanese red pines (*Pinus densiflora*). Black circles indicate the location of native Japanese red pines and squares indicate the location of the survey points.

human-squirrel interaction. These feeders had been placed at intervals of c. 100 m in a small area in the northwestern part of the study area until 2020 (Fig. 1a). To study the effects of feeder spacing on the squirrels' use of feeding tables or natural resources, and home ranges, the eight feeders were moved in 2021 to intervals of c. 300 m throughout the study area (Fig. 1a). This interval was determined based on the size of female home ranges for this species (Tamura 2004); a circular area with a 150 m radius is c. 7 ha, which is almost the size of female home range.

Field observation

Individuals were captured in May–July 2019, June 2020, and January–June 2021 using existing cage traps (15.5 cm width × 26.0 cm depth × 11.0 cm height) that had been affixed to the feeders for capture since their installation. Captured individuals were weighed using a spring scale, and sex and age (adult/juvenile) were determined based on a visual assessment of external reproductive morphology (Nishi et al. 2011). Subsequently, the squirrels were fitted with collars (1 g in weight, 2 mm in width) with a small transmitter (weight 10 g, Wildlife Materials International Inc., Illinois, USA). The animals selected to be fitted with the devices were adults weighing ≥ 200 g so that the total device weight was less than 5% of the individual's body weight. Individuals were identified by the color of their collar.

The home ranges of individuals equipped with transmitters were surveyed by three persons on sunny or cloudy days during 05:00–18:00 h every week during July–October of 2019–2021. The direction of the individual was determined at a minimum of 30-min intervals using a receiver (R410, Advanced Telemetry Systems Inc., Minnesota, USA) and a Yagi antenna (H-4EL, Ham Center Sapporo, Sapporo, Japan). Out of the 18 individuals with transmitters, the nine individuals with sufficient data of location were plotted on a map in QGIS ver. 3.8.0 (https://qgis.org/ja/site/forusers/download.html), and the outermost contour method was used to estimate their home range (95%) and core area (50%) for each summer (July–August) and autumn (September–October) season.

Resource utilization at feeding stations and native red pines

Automatic infrared video cameras (400-CAM066, Sanwa Supply Co., Ltd., Okayama, Japan) were set up near the eight feeding tables to record the individuals' behavior on the tables. The camera SD card was exchanged approximately every week, and the data were examined on (1) the date and time that squirrels appeared at the feeder, (2) the presence/absence and color of the collar for individual identification, and (3) the squirrels' behavior at the feeder, such as foraging or consuming of walnuts, and dominance-related interactions such as chasing, attacking and vigilance to other individuals.

The total number of consumed walnuts on the feeding table was determined as the supplied number (80 pieces) minus the sum of the remaining number every week. During July–October 2019, cone production of red pines was examined using seed traps placed at five locations under the canopy (Fig. 1b). The traps were polyester nets (0.3-mm mesh) with an opening of 1 m × 1 m and a depth of 60 cm, fixed at a height of 1 m using four poles. During July–October in 2020 and 2021, a 10-m squared survey quadrat (100 m^2) was placed at each of the same five locations. The numbers of all fallen cones that showed squirrel-feeding signs were counted weekly, and the cones counted were removed from the quadrats. The location of red pines within the study site was determined using GPS (eTrex30J, GARMIN, Schaffhausen, Switzerland) and plotted on a QGIS map (Fig. 1b).

Statistical analysis

For the number of walnuts consumed by squirrels on the feeding tables and the number of consumed pinecones, Wilcoxon's signed-rank test was used to examine differences between years, and U-test was used for between-season differences each year. The Bonferroni method was used for *P*-value correction in multiple comparisons.

To investigate the factors affecting feeding table use by individuals, we performed a generalized linear mixed model (GLMM) using Poisson distribution and log link function for the summer (July–August) and autumn (September–October) seasons, respectively. In each analysis, the number of visits by squirrels to the feeding tables was used as the response variable, and mean temperature, mean wind speed, total precipitation for each day (Appendix), pine-cone abundance per week, and sex (male = 1; female = 0) were used as explanatory variables. To evaluate the different spacing of feeders between years, year difference (2021 year = 1, other years = 0) was also used as an explanatory variable. Individual differences were assumed to be random variable effects. Continuous explanatory variables were scaled and were selected so that the variance inflation factor (VIF) was < 10.

Meteorological data for Nagoya City were obtained from the Japan Meteorological Agency (https://www.data.jma.go.jp/obd/stats/etrn/index.php, Appendix). All statistical analyses were performed using R 4.0.2 (R Core Team 2020).

Results

Feeding table use and home ranges of individuals

During the three years, F1 was observed in three years and M3 in two years, but the other individuals in only one year. In 2019, six individuals were observed to use the eight feeding tables, which were placed in a small area in the northwestern part of the study area. F1 used the tables the most frequently, i.e., contributing to 54–91% of the visits by all individuals at six of the eight tables, and 60% in total (Table 1). The four individuals (F1, F2, M1, and M2) for which home ranges and core areas could be determined via telemetry were all active around the feeding tables (Fig. 2a). In 2020, five individuals were observed to use the feeding tables, which were placed as in 2019. F1 used the tables more frequently than in 2019, i.e., 68–97% at six of the eight tables and 74% in total (Table 1). Two individuals (F4 and M4), whose home ranges and core areas could be estimated, were active in the southeastern part of the area where feeding tables were placed, in both summer and autumn (Fig. 2b). In 2021, when the intervals among feeding tables were widened, eight individuals were observed to use feeding tables. Most individuals contributed to more than 30% of total visits by all individuals to each table, and table usage was almost evenly distributed among the tables for all individuals, although two tables (I and J) in the northern part of the study area, which was dominated by cedar plantation forest, were not used by any individuals (Table 1). Of the three individuals whose home ranges and core areas could be estimated, F5 was mainly active in the northern part, F6 in the southeastern part, and M7 in the northwestern part, indicating that the overall distribution of the species had expanded so as not to overlap among individuals (Fig. 2c).

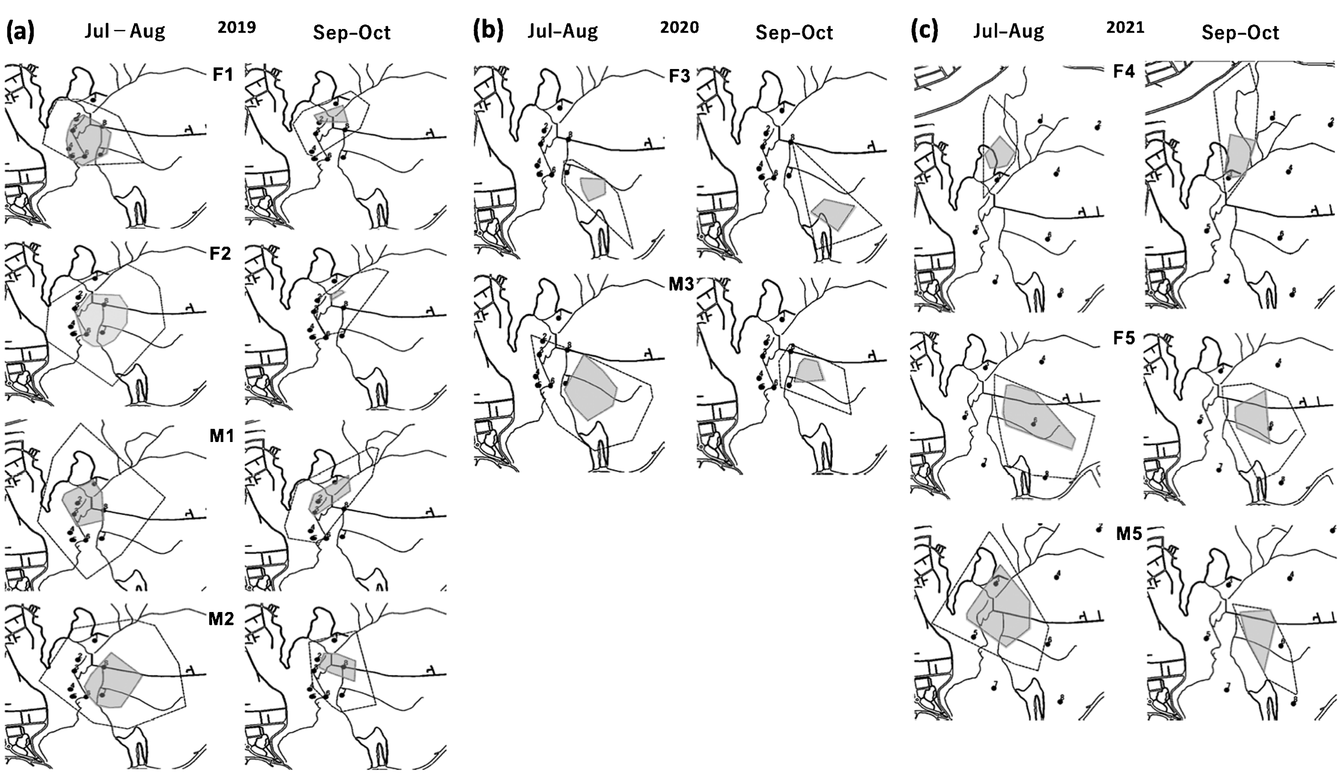

Fig. 2. Distribution of the home range (area enclosed by the outer line) and core area (gray area enclosed by the inner line) in July–August and September–October as estimated by radio-tracked Japanese squirrels (*Sciurus lis*) in 2019–2021. Black dots indicate the location of feeding stations.

Table 1. Number of times that eight different feeding tables were used by individual Japanese squirrels from 2019 to 2021

	2019										2020										2021							
	Feeding tables										Feeding tables										Feeding tables							
	A	B	C	D	E	F	G	H	TL		A	B	C	D	E	F	G	H	TL		J	A	K	D	L	M	N	TL
F1	8	34	89	39	19	87	62	3	341	F1		26	7	3	44		8		88	F1				13			0	13
		2	93	255	299	306	327		1282			316	432	330	357	268	178		1881					353				353
F2	1					222	44	1	268																			
									0																			
F3						54	7	65	126																			
						10	149	13	172																			
M1	22	2	1						25																			
	98	13	9	30	10	1			161																			
M2	26	7	6		11	9	5	114	178																			
		2	3	32	32	35	11	50	165																			
M3	1							2	3																			
										F4		20			29			8	57									
												5					10		15									
										M4	84	27		1					112	M4		1	1		17		82	101
											27			1			12		40				22		57		100	179
										M5	3	10	1					6	20									
											41	34	55	37	51	1	1	7	227									
										M6	64	30	8	8	1	1			112									
											10	33	13	6	3	7			72									
																				F5		29						29
																						133						133
																				F6							100	100
																									9		157	166
																				F7				234		40	150	424
																								118		282	217	617
																				F8								0
																										249		249
																				M7					6			6
																						18		2				20
																				M8		23		2				25
																						124		75	40			239
SM	156	60	201	356	371	724	605	248	2721	SM	233	501	516	386	485	277	236	21	2655	SM	18	328	23	797	129	614	850	2759

Upper in Jul–Aug and lower in Sep–Oct for each individual (M = male, F = female). SM = summed number of visits. TL = total number of visits to all feeders for each individual. The intervals among eight feeding tables were widened during the study from c. 100 m in 2019–2020 to c. 300 m in 2021.

Over the three years, dominance-related interactions (such as aggression and escape) were rarely observed between any individuals on the feeding tables, but vigilance to other individuals was frequently observed.

Consumption of walnuts and pine seeds

The number of walnuts consumed per year was significantly larger in 2019 than in either 2020 (T_{18} = 1, P < 0.001) or 2021 (T_{18} = 2, P < 0.001) but not significantly different between 2020 and 2021 (T_{18} = 32, P > 0.1) (Fig. 3a). Comparing between seasons in each year, the number of walnuts consumed in autumn was significantly higher than in summer in 2020 ($U_{9,9}$ = 1, P < 0.001) and 2021 ($U_{9,9}$ = 2, P < 0.001) but not significantly different in 2019 ($U_{9,9}$ = 35, P > 0.1). In seed trap surveys conducted in July–October 2019, no dropped pinecones were collected in any of the five traps set. In quadrat surveys conducted in July–October 2020 and 2021, the number of dropped cones reached a maximum in August and then decreased during September–October (Fig. 3b). The number of consumed pinecones was greater in 2021 than both 2019 (T_{18} = 0, P < 0.001) and 2020 (T_{18} = 10.5, P < 0.001), and more were consumed in 2020 than 2019 (T_{18} = 0, P < 0.001) (Fig. 3c). Comparing between seasons in each year, there was no significant difference between summer and autumn in 2019 ($U_{7,9}$ = 31.5, P > 0.1), 2020 ($U_{7,9}$ = 23.5, P > 0.1), or 2021 ($U_{7,9}$ = 26, P > 0.1).

In the GLMM results (Table 2), the feeder-use increased with lower temperature, higher precipitation and lower wind velocity in both summer and autumn. When pinecones were abundant, feeder-use decreased in summer but increased in autumn. Females used more feeding tables than males in summer, while no difference was found between sexes in autumn. In both seasons, the frequency of feeder-use was lower in 2021 than the other two years.

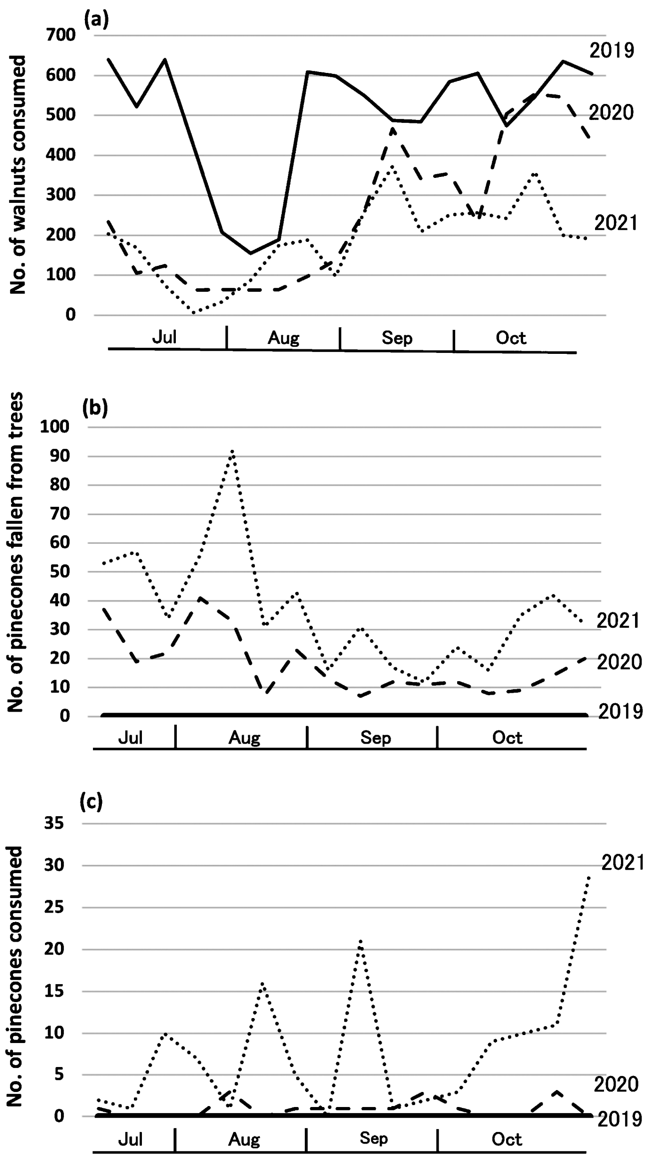

Fig. 3. Seasonal changes in numbers of (a) consumed walnuts, (b) fallen pinecones, and (c) consumed pinecones during 2019–2021.

Table 2. The results of generalized linear mixed models for the number of times that squirrels visited the feeders

(a) Jul–Aug	Estimate	Std. Error	*z* value	Pr(>|z|)
(Intercept)	0.535	0.491	1.089	0.276
Temparature	–0.532	0.030	–17.613	< 2e-16 ***
Precipitation	0.291	0.021	13.636	< 2e-16 ***
Wind velocity	–0.093	0.029	–3.161	0.002 **
Cone abundance	–0.764	0.063	–12.093	< 2e-16 ***
Sex	–1.399	0.670	–2.088	0.037 *
Year	–0.443	0.163	–2.710	0.007 **

(b) Sep–Oct	Estimate	Std. Error	*z* value	Pr(>|z|)
(Intercept)	0.821	0.901	0.912	0.362
Temparature	–0.094	0.015	–6.456	0.000 ***
Precipitation	0.133	0.010	13.233	< 2e-16 ***
Wind velocity	–0.174	0.015	–11.787	< 2e-16 ***
Cone abundance	0.084	0.026	3.252	0.001 **
Sex	–0.522	1.229	–0.424	0.671
Year	–1.270	0.062	–20.401	< 2e-16 ***

Individual differences were assumed to be random variable effects.
Sex: male = 1; female = 0; Year: 2021 year = 1, other years = 0.
*** P < 0.001, ** P < 0.01, * P < 0.05.

Discussion

Influences of weather conditions, natural food abundance, and the spacing of feeders on the feeding-table use by squirrels

The results showed that feeding table use by squirrels changed depending on weather conditions, natural food abundance, and the spacing of feeders. In both summer and autumn, the feeder-use increased with lower temperature. Walnuts on the feeders were less subject to searching and had a higher calorie content than natural food resources, suggesting that the squirrels' dependence on this food source increased on cooler days. The same relationship between feeder-use and temperature has been reported in forest birds (Cowie and Hinsley 1988; Zuckerberg et al. 2011; Carrascal et al. 2012). Higher precipitation increased feeding table use, both in summer and autumn. On rainy days, the squirrels return to the nest or rest under shelter outside the nest to conserve energy (Ishikawa et al., unpublished data). Thus, the use of walnuts (i.e., providing high foraging efficiency) on the feeding tables may have increased to compensate for the decrease in activity (and therefore foraging) time. Strong winds decreased feeding table use, regardless of the season. Because there is no wind barrier above the feeding tables, the squirrels may have avoided using the feeders during strong winds. The same responses to precipitation and wind velocity have been observed in birds (Cowie and Simons 1991; Zuckerberg et al. 2011).

In 2019 and 2020, when the feeding tables were located at short intervals, the squirrels' feeder-use appeared to change depending on the seed production of red pines. In 2019, when no seeds were produced at all, all individuals were concentrated around the feeding tables. In addition, they depended on the walnuts on the feeders for most of their food resources (Fig. 3), although 60% of walnuts on the feeders were consumed by one female (F1) (Table 1). In 2020, when pine seed production was moderate during the three years, three quarters of the walnuts on the feeders were consumed by one female (F1), and the other individuals moved to the southeast where the pine trees were abundant (Fig. 2). Thus, the placement of feeders in a small area resulted in two different types of behavioral modifications: a concentrated distribution of many individuals in 2019 and exclusive occupation by a particular female in 2020. In contrast, in 2021, with the feeding tables placed at wider intervals, the distribution of individuals expanded over the entire study area (Fig. 2), and the use of supplementary feeding decreased, while seed consumption increased (Fig. 3). Thus, negative effects of the supplementary feeding such as a concentrated distribution of many individuals or exclusive occupation by a particular individual may be reduced.

Squirrels used feeding-tables more in autumn than in summer. The effect of temperature and precipitation on feeder-use by squirrels was expected to be weaker in autumn than in summer, owing to the smaller estimate-values of the scaled variables in GLMM (Table 2). This seasonal difference suggests that squirrels may have used feeding tables for hoarding before the winter (Fletcher et al. 2012).

When pinecones were abundant, feeder-use decreased in summer but increased in autumn. The result in summer can be explained by two reasons that feeder-interval was wider and pine production was more abundant in 2021 than the other two years. However, we could not discriminate which was more important between the feeder-interval and pine production. Moreover, we could not explain why feeder-use increased in autumn with abundance of cone-production. Reher et al. (2016) showed that Eurasian red squirrel's distribution was clustered near feeding tables despite the abundance of natural food. Further ongoing research is therefore needed to examine how feeder-use changes depending on pine seed production.

Supplementary feeding for conservation of squirrels

The lack of any pine seeds collected in the 2019 seed trap survey indicates that annual seed production under natural conditions varied widely. The relationship with environmental factors showed that the use of feeding tables was enhanced in severe weather conditions, such as low temperature and heavy rain. Thus, supplementary feeding may enhance the survival rate of individuals under severe conditions of natural food resources and weather. However, the studies of Eurasian red squirrel have shown that the concentration of several individuals on feeding tables can have negative effects such as inter-individual conflict (Wauters et al. 2002), increased predation risk (Shuttleworth 2001), and the spread of disease (Chantrey et al. 2014). Consequently, supplemental feeding can decrease breeding success (Kopij 2009; Stirkė 2019). In fact, we observed predators such as martens and owls via automatic cameras installed on the feeders during the survey and found collars that had previously been attached to squirrels on the ground near the feeders. Thus, supplementary feeding may create an ecological trap of predation exposure (Robb et al. 2008). Furthermore, in the two years when the feeders were placed in a small area, we found two conflicting negative effects (i.e., the concentrated distribution of many individuals, and exclusive occupation by a particular female). Although breeding behavior was not investigated in this study, a few individuals that occupy the feeders may survive and breed more than others. If such conditions persist for a long period, the risk of population extinction due to inbreeding and reduced genetic diversity is expected in fragmented suburban forests such as the area used in this study. In fact, microsatellite DNA analysis of individuals captured at the same study site revealed that most individuals were genetically homogeneous (Inoue et al., in press). We need future research on the reproduction and survival of squirrels to clarify the effect of supplementary feeding on their fitness.

The results indicate that supplementary feeding for the squirrel conservation in a suburban forest should consider the influences by weather conditions, natural food abundance, and the spacing of feeders. Continuous conservation by feeding will not be guaranteed in the study area because it depends on the activities of nonprofit organizations such as the Moriyama Squirrel Study Group. Therefore, increasing the availability and quality of green spaces would be most beneficial to the long-term conservation of squirrels in suburban environments, even if supplementary feeding is used for conservation in the short term.

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Appendix.

The means and standard deviations (*SD*) of temperatures, total precipitation, and wind speed in summer (Jul–Aug) and autumn (Sep–Oct) from 2019 to 2021

		2019		2020		2021	
		Jul–Aug	Sep–Oct	Jul–Aug	Sep–Oct	Jul–Aug	Sep–Oct
Temparature (°C)	Mean	27.41	23.44	27.89	21.63	27.63	22.00
	SD	2.73	4.15	2.93	4.71	2.20	3.90
Precipitation (mm)	Mean	7.86	6.48	6.75	8.19	10.64	4.74
	SD	12.92	19.58	12.47	18.18	18.57	10.68
Wind speed (m/s)	Mean	2.82	2.89	2.95	2.86	2.82	2.61
	SD	1.05	1.12	0.77	1.00	0.97	0.99