Cedar plantations as habitat for Japanese squirrels in the cool temperate zone

Authors: Honda, Suzuka, and Saito, Masayuki U.

Source: Journal of Vertebrate Biology, 72(23002)

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/jvb.23002

Journal of Vertebrate Biology

Open Access

J. Vertebr. Biol. 2023, 72: 23002

DOI: 10.25225/jvb.23002

RESEARCH PAPER

Cedar plantations as habitat for Japanese squirrels in the cool temperate zone

Suzuka HONDA[1] and Masayuki U. SAITO[2*]

[1] *Graduate School of Agricultural Sciences, Yamagata University, Tsuruoka, Japan; e-mail: su92.tomokuma@gmail.com*

[2] *Faculty of Agriculture, Yamagata University, Tsuruoka, Japan; e-mail: saito.ume@gmail.com*

Received 8 January 2023; Accepted 3 February 2023; Published online 30 March 2023

Abstract. In this study, we determine whether coniferous plantations in the cool temperate zone of northeast Japan, with few natural evergreen forests, can serve as a habitat for Japanese squirrels. We also examine whether Japanese squirrel habitat use in cedar plantations varies based on forest structure. Our results showed that the relative frequency of squirrel occurrence, determined by camera traps and the number of feeding signs, was significantly higher at cedar forest survey sites than other forest types. The best generalised linear model for frequency of occurrence included the number of standing trees, canopy openness and understory visibility, while the best model for the number of feeding signs included total basal area, canopy openness and the number of walnut trees. The results suggest that cedar plantations within the study area serve partially as a habitat for squirrels, replacing natural evergreen trees. Furthermore, squirrel habitat use differed between cedar plantations based on forest structure, confirming the importance of a diverse forest structure for squirrels. Therefore, when considering the conservation and management of small arboreal mammals that use such plantations, they must include diverse structures to facilitate their use as a habitat.

Key words: arboreal mammal, conifer, forestry, habitat selection, northeastern Japan, *Sciurus lis*

Introduction

Forest plantations established through artificial silviculture are now prevalent worldwide. The establishment of such plantations represents a marked alteration in land use, with trees often planted in areas where existing forests have been cleared or areas of abandoned agricultural land or grassland. Additionally, such plantations often comprise just one or two tree species for harvesting. They are planted at uniform intervals, resulting in forests with simple species compositions and spatial structures (Food and Agriculture Organisation of the United Nations 2020). Over the past decade, research has revealed that such forest plantations negatively impact biodiversity, species populations and the functional characteristics of various wildlife taxa (Iglesias-Carrasco et al. 2022).

However, it is not always the case that forest plantations are detrimental to all wildlife. For example, coniferous plantations with dense understory vegetation can provide a habitat for herbivores such as Japanese serows (*Capricornis crispus*) and Japanese hares (*Lepus brachyurus*) (Tsujino & Yumoto 2014). Furthermore, Japanese macaques (*Macaca fuscata*) have been observed using young coniferous plantations as feeding habitats, suggesting that appropriate thinning can increase food resources favourable to these primates (Sakamaki et al. 2011, Sakamaki & Enari 2012), while Katsumata et al. (2008) reported that the abundance of two Japanese field mouse species (*Apodemus speciosus*

* *Corresponding Author*

and *A. argenteus*) was higher in coniferous plantations than in secondary broad-leaved forests, possibly as fallen trees generated during thinning provide a three-dimensional hiding place on the forest floor. It is important to remember, therefore, that some species may selectively use forest plantations and, as such, they deserve evaluation as wildlife habitats. Furthermore, such evaluations will provide information for future forest management that promotes coexistence between wildlife and human production activities (Iglesias-Carrasco et al. 2022).

Forest plantations can pose a significant threat to species with limited mobility, such as amphibians, reptiles, small mammals, and many invertebrates (Iglesias-Carrasco et al. 2022), and in such animals, adaptive behaviour is likely to be critical. However, there have been few studies on the impacts of forest plantations on taxa with limited mobility. Furthermore, since organisms often respond strongly to changes in microhabitats, the simplified structure of monoculture forest plantations may significantly impact arboreal more than terrestrial animals (Iglesias-Carrasco et al. 2022). In this study, we focus on the Japanese squirrel (*Sciurus lis*), an arboreal mammalian species endemic to Japan, and the role of coniferous plantations in its habitat selection, thereby contributing to our understanding of how small arboreal mammals respond to plantation forests and their conservation management.

Some previous studies have examined the importance of evergreen forest, mixed forest and broad-leaved forest as habitats for Japanese squirrels, several of them noting the importance of walnut (*Juglans ailantifolia*) and pine trees (e.g. *Pinus parviflora*) as a primary food resource (Tamura 1998, Yatake et al. 1999, Yatake & Tamura 2001, Tamura et al. 2006, Kobayashi et al. 2009, Harashina et al. 2013). Japanese squirrels typically use natural evergreen forests as nesting and resting sites (Tamura et al. 2006) and rarely use coniferous plantations in the presence of natural evergreen or mixed forests (Tamura 1998), which provide a greater diversity of food resources and more complex hierarchical structures more suitable for resting and nesting sites. Recently, however, it has been suggested that coniferous plantations may be important as drey sites in cool temperate zones where natural evergreen forests are scarce and that Japanese squirrels may selectively use coniferous plantations in snowy environments (Honda & Saito 2021, Honda et al. 2022). In these areas, therefore, coniferous plantations may not be harmful sites for Japanese squirrels but rather represent an essential part of their habitat. The habitat requirements of Japanese squirrels include continuous forest vegetation and canopy for movement, a complex canopy of evergreen trees that provide food resources, resting and nesting sites, and sparse understory vegetation that allows for easy movement and predator detection during ground use (Yatake et al. 1999). However, not all natural environments will fulfil these conditions; thus, habitat use by Japanese squirrels may vary depending on forest structure.

Sullivan et al. (2009) and Sollmann et al. (2015) reported that forest structure affected habitat use by small forest-floor mammals, and similar phenomena have been observed in arboreal squirrels. Samaras & Youlatos (2010), for example, found that red squirrels (*Sciurus vulgaris*) preferred to use the middle and upper reaches of the forest canopy, while Flaherty et al. (2012) and Dylewski et al. (2016, 2021) showed that forest structure characteristics, such as canopy closure, number of trees, distance to open areas, understory vegetation, number of tree species and tree diameter at breast height (DBH), all influenced forage site selection in red squirrels. Canopy closure is especially important for arboreal squirrels (Smith & Mannan 1994) as it enhances tree connectivity and reduces ground movement, thus mitigating predation risk (Flaherty et al. 2012). When on the ground, however, arboreal squirrels often use logs and fallen trees as movement routes, foraging sites and hiding places from predators (Douglass & Reinert 1982, Bakker 2006, Cudworth & Koprowski 2011, Minami et al. 2019). Thus, forest structure is crucial when examining habitat use by arboreal squirrels in planted forests.

In this study, we verify whether coniferous plantations in the cool temperate zone of northeast Japan, where natural evergreen forests are scarce, serve as a habitat for Japanese squirrels. To this end, we conducted camera-trap and feeding sign surveys in Japanese cedar (*Cryptomeria japonica*) plantations, Japanese beech (*Fagus crenata*) forests and mixed forests and compared habitat use by Japanese squirrels across these forest types. If squirrels selectively used Japanese cedar plantations, then we also examined whether their habitat use varied according to the purpose of use and forest structure. Based on these results, we discuss the potential role of Japanese cedar plantations as a habitat for Japanese squirrels.

Material and Methods

Study area

This study was conducted in the Kaminagawa Experimental Forest (Faculty of Agriculture,

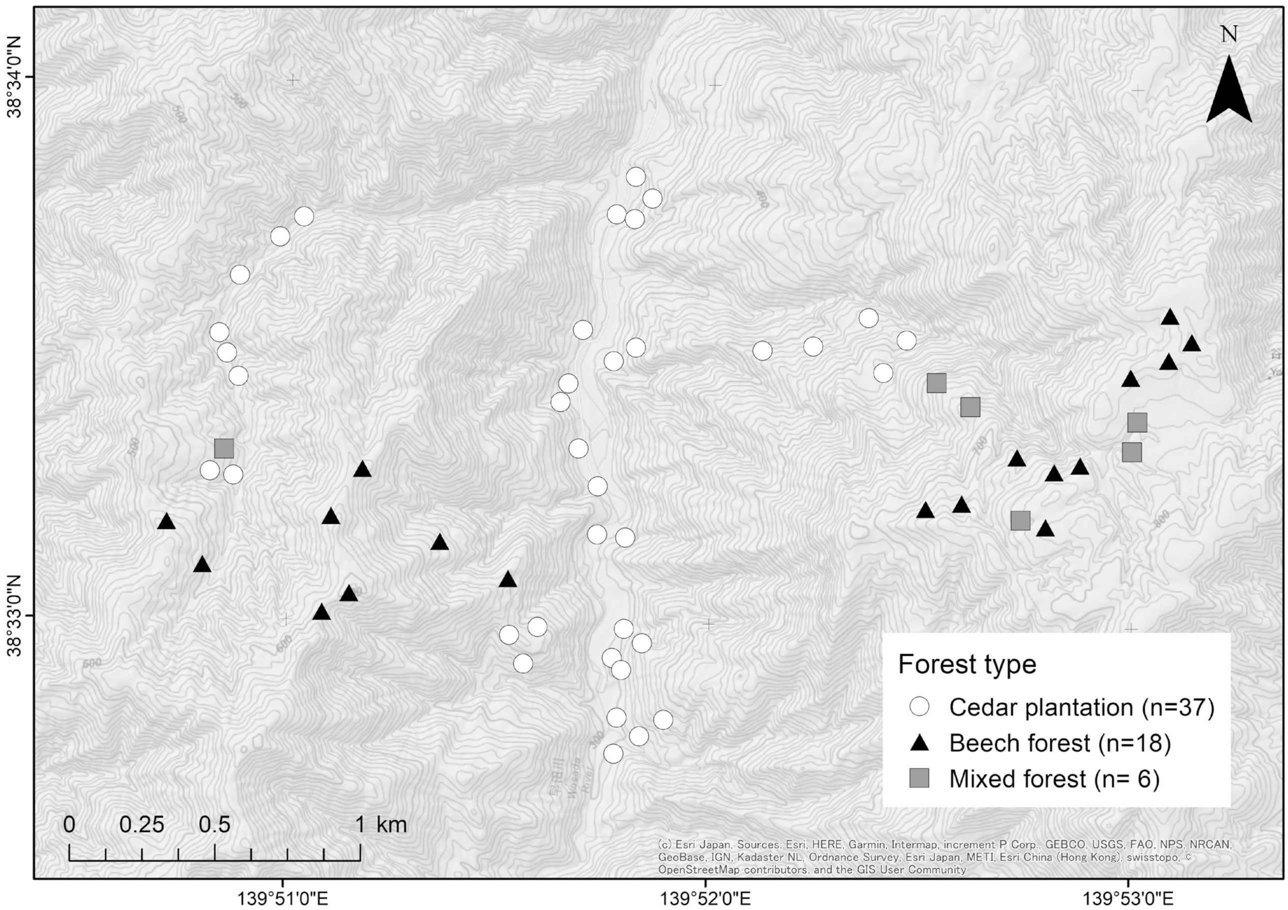

Fig. 1. Location of the survey sites.

Yamagata University at Tsuruoka City, Yamagata Prefecture; 139°52′ N, 38°34′ E; Fig. 1). The forest covers an area of 753 ha and ranges in elevation from approximately 230 to 850 m. The region lies within the cool temperate zone, with an average annual temperature of 10.3 °C and an annual precipitation of 3,476 mm (values for 2021 from a meteorological observation point within the experimental forest). The study area is subject to heavy snowfall, with an annual maximum snow depth of approximately 200 to 300 cm. The dominant forest types in the area include Japanese beech forests, Japanese oak (*Quercus crispula*) forests, Japanese cedar plantations, and mixed forests. Within the study area, a small number of broad-leaved tree species, such as the Japanese horse chestnut (*Aesculus turbinata*), Japanese whitebark magnolia (*Magnolia obovata*) and Japanese walnut, sometimes occur within and around the cedar plantation.

For the field survey, we established 61 15 × 15 m plots, 37 in cedar plantations (18 to 107 years), 18 in beech forests and six in mixed forest. Though the study plots were arbitrarily selected to allow for differences in forest structure, the distance between plots was set at least 100 m apart, based on a daily movement range of Japanese squirrels of approximately 200 to 400 m (Yatake & Tamura 2001), thus ensuring that individuals would select habitats within their range of activity.

Camera trap survey

While Japanese squirrels are small arboreal mammals, they also use the ground for movement (Yatake 2016, Honda et al. 2022). To investigate ground use by Japanese squirrels in each survey plot, we conducted camera trap surveys using BTC-6HD-APX infrared sensor cameras (Browning, USA) between July and October 2021, installed approximately 1.2 m above the ground. To account for seasonal changes, we divided the survey period into two smaller periods, i.e. July-August (ten days) and September-October (15 days), then combined the data from these two periods for each plot. As Yatake & Tamura (2001) suggested that Japanese squirrels follow almost fixed movement paths for commuting between foraging and nesting sites, we installed the cameras in different directions during each survey period to avoid biased shooting ranges. The camera was set to take five consecutive photographs per detection, with a one-minute interval between events. Photographs of squirrels taken within 30 minutes of the preceding photograph were treated as sequential behavioural events of the same individual and excluded from the dataset (see O'Brien et al. 2003, Watabe & Saito 2021). We then divided the total frequency of separate observations by the number of camera days to obtain the relative frequency of occurrence of Japanese squirrels in each survey plot.

Feeding sign and forest structure surveys

The field survey to investigate feeding signs and forest structure occurred between October and November 2021. As walnuts are a significant food resource for Japanese squirrels (Tamura 1998, Tamura et al. 2006), we assessed the value of each survey plot as a foraging site by examining the presence of walnut feeding signs. Per similar studies on Eurasian red squirrels (Flaherty et al. 2012), we randomly established ten 2 × 2 m subplots within each survey plot and counted the number of walnut feeding signs in each. As Japanese squirrels break walnuts into two pieces along the suture lines to eat them, we counted each broken half as one feeding sign. The total number of feeding signs in each subplot was then recorded as the number of signs in the respective survey plot.

To assess forest structure within the cedar plantations, we collected data on the number of standing trees, DBH (cm), canopy openness (%), number of fallen trees, visibility of understory vegetation (%) and prevalence of walnut trees, all of which have previously been studied in relation to arboreal squirrels (Bakker 2006, Flaherty et al. 2012, Dylewski et al. 2021). We also measured the number of standing trees and DBH for all trees with a DBH > 3 cm within each survey plot. Using these measurements, we calculated the basal area (BA, m^2) of each tree and the total BA (TBA, m^2) for the plot. To determine the degree of canopy openness, we took hemispheric photographs 1.2 m above the ground using a Coolpix P5100 digital camera with an FC-E8 fisheye lens (Nikon, Japan) on cloudy days between July and September 2021. We then used CanopOn2 image analysis software (Takenaka 2009) to calculate the degree of canopy openness. We counted all those broken near the root or base for the number of fallen trees. To assess visibility in the understory vegetation, we marked five points at 20 cm intervals from the ground (i.e. up to 1 m) and observed them from 10 m away, repeating this process five times at 1 m intervals. The percentage of points visible was then used as an index of visibility. Finally, we counted the number of walnut trees within each survey plot and in the 35 × 35 m area surrounding it, following the methods of previous studies on the feeding and hoarding habits of Japanese squirrels (Tamura 1997, Deguchi et al. 2017).

Statistical analysis

All analyses were conducted using R v.3.6.3 (R Development Core Team 2020). Using the "exactRankTests" package in R, the Wilcoxon rank-sum test was used to compare differences in Japanese squirrel habitat usage between forest types based on the relative frequency of squirrel occurrence and the number of walnut feeding signs. Multiple comparisons were then adjusted using Holm's method. To assess the effect of forest structure on squirrel habitat use within the cedar plantations, we constructed a generalised linear model (GLM) with squirrel frequency of occurrence and number of walnut feeding signs as response variables and

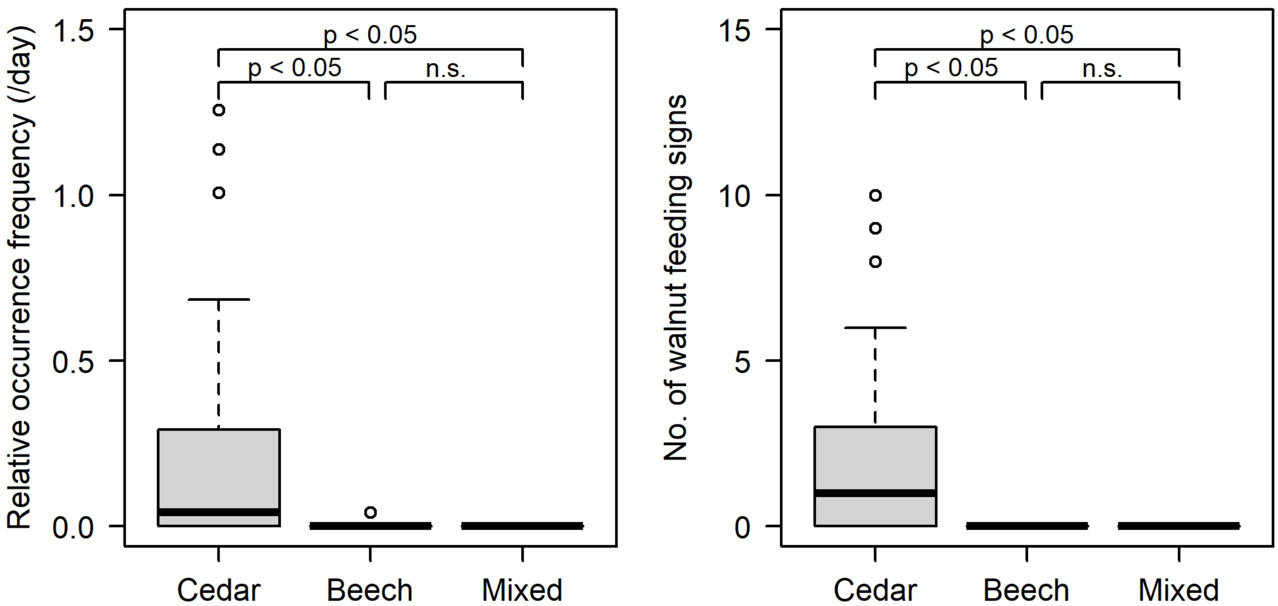

Fig. 2. Boxplots for relative frequency of occurrence of Japanese squirrels using camera traps (left) and number of Japanese walnut feeding signs (right) in each forest type.

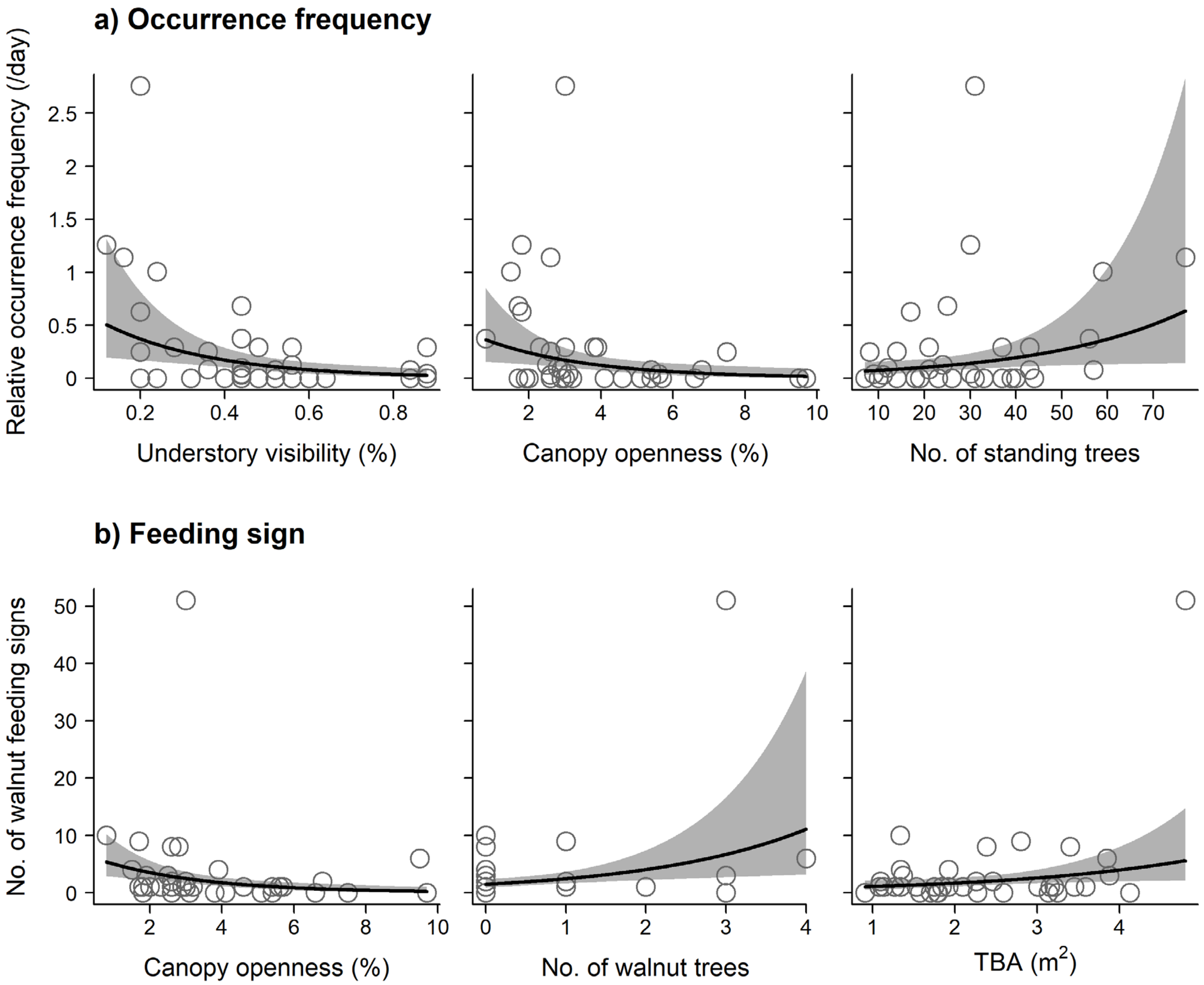

Fig. 3. Scatter plots and response curves for each variable in the best GLMMs for Japanese squirrel frequency of occurrence (a) and feeding signs (b). The grey area represents the 95% confidence intervals for the best GLMM prediction. Aside from the variables of interest, mean values were used throughout when drawing the response curve of each prediction. TBA = total basal area.

forest structure variables (i.e. number of standing trees, TBA, canopy openness, number of fallen trees, visibility of understory vegetation, and number of walnut trees) as explanatory variables. We assumed a negative binomial distribution for the response variables and checked for multicollinearity among the explanatory variables ($|r| < 0.7$, Dormann et al. 2013). Model selection was based on Akaike's information criterion corrected for small-sample bias (AICc), and the relative importance of the variables was determined using the standardised regression coefficients of the best model. In each case, the analyses were conducted using the "MASS" and "MuMIn" packages in R.

Results

A total of 1,658 camera days yielded 258 Japanese squirrel occurrence events. The squirrels were detected in 22 of the 61 survey plots, 21 of which were cedar forests and one a beech forest. Walnut feeding signs were observed in 27 of the 61 survey plots in cedar forests.

There was a significant difference in the relative frequency of occurrence between cedar and other forest types using both camera traps and the number of walnut feeding signs (Wilcoxon rank-sum test, $P < 0.05$; Fig. 2). No significant differences were found between Japanese beech and mixed forests ($P \geq 0.05$).

GLM model selection identified the number of standing trees, canopy openness and understory visibility as the most influential mode variables for squirrel frequency of occurrence (Table 1), with all three variables showing significant differences ($P < 0.05$; Table 2). Variable importance analysis indicated that visibility and canopy openness had a greater impact than the number of standing trees (Table 2). The best model suggested that Japanese squirrels had a higher frequency of occurrence in areas with more standing trees, closed canopies and poor visibility (Fig. 3).

The best models for the number of feeding signs were TBA, canopy openness and the number of walnut trees (Table 1), with all three variables in the best model showing significant differences ($P < 0.05$; Table 2). Based on standardised regression coefficients, variable importance analysis revealed that canopy openness had the greatest relative impact, followed by the number of walnut trees and TBA (Table 2). The number of feeding signs tended to be higher in areas with a greater TBA, closed canopies and a higher presence of walnut trees (Fig. 3).

Discussion

In our study, Japanese squirrels showed a clear preference for Japanese cedar plantations as habitat over other forest types in the study area (Fig. 2). The use of evergreen forest as habitat, and Japanese cedar in particular compares well with previous findings (Tamura 1998, Yatake et al. 1999). Evergreen forests with year-round canopy cover provide small arboreal mammals with the means to conceal their nests and reduce the risk of predation by raptors (Selonen et al. 2016). Given that most evergreen forests in the study area are cedar plantations, these areas are likely suitable for Japanese squirrels. Moreover, the difference in results between frequency of occurrence and feeding signs (Tables 1, 2) suggests that Japanese squirrels utilise forest structure within cedar plantations differently.

The best GLM for frequency of occurrence, reflecting ground use, and the number of feeding signs, reflecting foraging sites, showed closed canopy to be a key feature (Table 2, Fig. 3). Closed canopies will facilitate predator avoidance for the squirrels, which face natural enemies such as raptors (northern goshawks, *Accipiter gentilis*; eastern buzzards, *Buteo japonicus*) and carnivores (red foxes, *Vulpes vulpes*; Japanese martens, *Martes melampus*) (Nishigaki & Kawamichi 1996, Nakamura et al. 2001, Yatake & Tamura 2001), while ground use is likely to be influenced by the closed canopy's ability to reduce predation risk from predatory raptors (Selonen et al. 2016). Japanese squirrels have also been reported to forage frequently in the forest canopy layer (Yatake et al. 1999). As a closed canopy is a safe foraging site that protects from ground and aerial predators, it is likely to have a higher concentration of feeding signs.

Japanese squirrels were also observed more frequently in areas with poor visibility or thriving understory vegetation (Table 2, Fig. 3). As with the American red squirrel (*Tamiasciurus hudsonicus*), Japanese squirrels

Table 1. Selected variables for the higher ranking GLMs (i.e. with ΔAICc < 2 by model selection in each response variable). "○" indicates that the variable was selected for the model. TBA = total basal area.

Model rank	Variable						AICc	ΔAICc
	No. of standing trees	TBA	Canopy openness	No. of fallen trees	Understory visibility	No. of walnut trees		
Frequency of occurrence								
1	○		○		○		188.0	0.0
2			○		○		188.4	0.4
3	○		○		○	○	188.5	0.5
4	○		○		○		188.8	0.8
5	○		○		○	○	188.9	0.9
6			○		○		189.1	1.1
null model							197.5	9.5
No. of feeding signs								
1		○	○			○	155.8	0.0
2		○	○	○		○	156.2	0.4
3			○			○	156.9	1.1
4	○	○	○			○	157.4	1.6
null model							171.5	15.7

Table 2. Coefficients for the best GLMs explaining each response variable. TBA = total basal area.

Variable	Standardised regression coefficient	Standard error	*P* value
Frequency of occurrence			
Intercept	–2.012	0.257	< 0.001
Understory visibility	–0.820	0.271	0.002
Canopy openness	–0.744	0.285	0.009
No. of standing trees	0.534	0.249	0.032
Feeding sign			
Intercept	0.657	0.204	0.001
Canopy openness	–0.762	0.237	0.001
No. of walnut trees	0.541	0.199	0.007
TBA	0.434	0.196	0.026

may make a trade-off between ease of movement for visual concealment, despite generally avoiding dense vegetation (Bakker 2006). On the ground, Japanese squirrels face predation risks from raptors and carnivores (Nishigaki & Kawamichi 1996, Nakamura et al. 2001, Yatake & Tamura 2001); thus, they are likely to choose areas with poor visibility to better escape predators. In addition, proximity to trees further reduces predation risk due to the availability of arboreal escape routes (Bakker 2006), explaining the Japanese squirrels' habit of moving from tree root to tree root when on the ground (Nishigaki & Kawamishi 1996). These results suggest that Japanese squirrels prefer to use the ground in areas with high tree density, where escape to trees is readily accessible.

The number of feeding signs of walnuts, a primary food resource for Japanese squirrels (Kato 1985, Tamura 2011, Nishi et al. 2014b), was higher in areas with nearby walnut trees (Table 2). Deguchi et al. (2017) found that Japanese squirrels forage within 10 m of food collection locations, with Tamura (1997) reporting an average hoarding transport distance of 18.3 meters. These findings suggest that Japanese squirrels forage close to food collection locations, supporting the significance of distance from walnut trees, their primary food source. In addition, areas with higher TBA were also selected as foraging sites, though they were of lesser importance than canopy openness and the number of walnut trees (Table 2). Japanese squirrels frequently forage in the forest canopy layer (Yatake et al. 1999) and choose foraging sites based on safety and canopy openness and height (Deguchi et al. 2017). A higher TBA signifies a more mature forest stand, and Japanese squirrels may prefer such stands as foraging sites due to their developed canopy layer and thicker, sturdier branches.

Our findings suggest that Japanese squirrels in the cool temperate zone actively select cedar plantations and that their use varies depending on forest structure. As Japanese squirrels do not hibernate, the presence of evergreen trees within their range is important (Honda et al. 2022) as such trees are often used as nesting sites due to their suitability for concealment (Yatake et al. 1999, Yatake & Tamura 2001, Nishi et al. 2014a, Honda & Saito 2021). In northeast Japan, however, the predominant forest vegetation type is cool-temperate, with few natural evergreen and beech forests dominating on that side facing the Sea of Japan (Okitsu 2000). In our study area, therefore, Japanese cedar plantations serve as partial habitat for squirrels, replacing natural evergreen trees. However, Japanese squirrels also require major food resources such as walnuts close to their habitat, and while the squirrels can forage for cedar leaves and bark (Nishi et al. 2014b), cedar plantations may offer limited food resources for squirrels due to their low species diversity. Nevertheless, our results suggest that Japanese cedar plantations can serve as habitat when walnut trees are nearby.

The utilisation of habitat in cedar plantations by Japanese squirrels was found to vary based on forest structure, thus indicating a need for forests of varying age and structure as suitable habitat for the species. At present, approximately half of the cedar plantations in Japan are of an age optimal for logging (Forestry Agency 2020); consequently, extensive logging of such forests is likely to lead to a decrease in Japanese squirrel habitat. However, reforestation of these sites will have little impact on the ability of Japanese squirrels to escape aerial predators until the trees have matured and the canopy layer has developed. Additionally, research has shown that the height of Japanese squirrel nests ranges from 4 to 18 m (average 10 m), with the average height of nesting trees being 16 m (Yatake & Tamura 2001) and the minimum ground height of tree-based resting sites being around 4 m (Yatake et al. 1999). This finding implies that, following reforestation, the forest may not function as a resting or nesting site for Japanese squirrels for an extended period. Thus, when considering the conservation and management of small arboreal mammals that use forest plantations, such as the Japanese squirrel, it is vital to adopt a mosaic forest management approach to create plantations with diverse structures, supporting their use as a squirrel habitat.

Acknowledgements

We thank the staff of the Experimental Forest of Yamagata University and the Associates of Yamagata University for supporting our field survey. The procedures used in this study were all in accordance with the national laws of Japan. The authors declare no competing interests.

Author Contributions

S. Honda and M.U. Saito designed the study, S. Honda undertook data collection and analysis, and S. Honda and M.U. Saito wrote the manuscript. Both authors have accepted responsibility for the entire manuscript content and approved its submission.

Literature

Bakker V.J. 2006: Microhabitat features influence the movements of red squirrels (*Tamiasciurus hudsonicus*) on unfamiliar ground. *J. Mammal. 87: 124–130.*

Cudworth N.L. & Koprowski J.L. 2011: Importance of scale in nest-site selection by Arizona gray squirrels. *J. Wildl. Manag. 75: 1668–1674.*

Deguchi Y., Kamimizu A. & Nishi C. 2017: Selection of feeding location after food collection of the Japanese squirrel in Takamatsu Park, Morioka, Iwate Prefecture. *Bull. Iwate Univ. For. 48: 41–46. (in Japanese with English summary)*

Dormann C.F., Bacher S., Buchmann C. et al. 2013: Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography 36: 27–46.*

Douglass N.J. & Reinert H.K. 1982: The utilisation of fallen logs as runways by small mammals. *Proc. Pa. Acad. Sci. 56: 162–164.*

Dylewski Ł., Jagodziński A.M., Tomaś Ł. et al. 2021: Forest stand structure and cone crop affect winter habitat use by Eurasian red squirrel (*Sciurus vulgaris*). *For. Ecol. Manag. 502: 119705.*

Dylewski Ł., Przyborowski T. & Myczko Ł. 2016: Winter habitat choice by foraging the red squirrel (*Sciurus vulgaris*). *Ann. Zool. Fenn. 53: 194–200.*

Flaherty S., Patenaude G., Close A. & Lurz P.W.W. 2012: The impact of forest stand structure on red squirrel habitat use. *Foresty 85: 437–444.*

Food and Agriculture Organization of the United Nations 2020: Global forest resources assessment 2020. Download on 26 December 2022. *https://www.fao.org/3/I8661EN/i8661en.pdf*

Forestry Agency 2020: Annual report on forest and forestry in Japan. Download on 26 December 2022. *https://www.rinya.maff.go.jp/j/kikaku/hakusyo/r1hakusyo/attach/pdf/zenbun-19.pdf (in Japanese)*

Harashina K., Goto M., Takahashi H. & Nishi C. 2013: Habitat use of the Japanese squirrel, *Sciurus lis*, in a patchy woodland land-scape: a case study of the Isawa Alluvial Fan, Iwate Prefecture. *Mamm. Sci. 53: 257–266. (in Japanese with English summary)*

Honda S. & Saito M.U. 2021: Drey site selection of Japanese squirrels in the cool temperate zone: evaluation at multiple spatial scales. *Landsc. Ecol. Manag. 26: 45–52. (in Japanese with English summary)*

Honda S., Saito M.U., Watabe R. & Watanabe K. 2022: Winter habitat selection of Japanese squirrels in a snowy region of northeastern Japan. *Landsc. Ecol. Eng. 18: 421–428.*

Iglesias-Carrasco M., Wong B.B.M. & Jennions M.D. 2022: In the shadows: wildlife behaviour in tree plantations. *Trends Ecol. Evol. 37: 838–850.*

Kato J. 1985: Food and hoarding behavior of Japanese squirrels. *Jpn. J. Ecol. 35: 13–20.*

Katsumata T., Sato A., Sugawara I. & Uehara I. 2008: Habitat selection of rodents in coniferous forest and broad-leaved forest. *Kanto J. For. Res. 59: 243–246. (in Japanese)*

Kobayashi A., Kanzaki N., Kataoka T. & Tamura N. 2009: Habitat selection and the selection of Japanese white pine cones (*Pinus parviflora*) by Japanese squirrels (*Sciurus lis*) in the subalpine zone of Mt. Fuji. *Mamm. Sci. 49: 13–24. (in Japanese with English summary)*

Minami Y., Onodera K., Murao N. & Yoshikawa T. 2019: Eurasian red squirrels use woodpiles on the forest floor in eastern Hokkaido. *Nat. Environ. Sci. Res. 32: 21–25.*

Nakamura T., Kanzaki N. & Maruyama N. 2001: Seasonal changes in food habits of Japanese martens in Hinode-cho and Akiruno-shi, Tokyo. *Wildl. Conserv. Jpn. 6: 15–24. (in Japanese with English summary)*

Nishi C., Deguchi Y. & Aoi T. 2014a: Nest use of Japanese squirrels in a suburban forest in Morioka city. *Mamm. Sci. 54: 11–18. (in Japanese with English summary)*

Nishi C., Tadano Y., Deguchi Y. & Aoi T. 2014b: The food habits of Japanese squirrels in a suburban forest of Morioka City, northeastern Japan. *Bull. Iwate Univ. For. 45: 73–80. (in Japanese)*

Nishigaki M. & Kawamichi T. 1996: Japanese squirrel. In: Kawamichi T. (ed.), The encyclopaedia of animals in Japan 1: mammals I. *Heibonsha, Tokyo, Japan: 70–73. (in Japanese)*

O'Brien T.G., Kinnaird M.F. & Wibisono H.T. 2003: Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Anim. Conserv. 6: 131–139.*

Okitsu S. 2000: Phytogeography of the major forests of northern Japan in northeastern Asia. *Geogr. Rep. Kokushikan Univ. 9: 1–11. (in Japanese with English summary)*

R Development Core Team 2020: R: a language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria.*

Sakamaki H. & Enari H. 2012: Activity-specific evaluation of winter habitat use by Japanese macaques in snow areas, northern Japan: implications for conifer plantation management. *For. Ecol. Manag. 270: 19–24.*

Sakamaki H., Enari H., Aoi T. & Kunisaki T. 2011: Winter food abundance for Japanese monkeys in differently aged Japanese cedar plantations in snowy regions. *Mamm. Study 36: 1–10.*

Samaras A. & Youlatos D. 2010: Use of forest canopy by European red squirrels *Sciurus vulgaris* in Northern Greece: claws and the small branch niche. *Acta Theriol. 55: 351–360.*

Selonen V., Varjonen R. & Korpimäki E. 2016: Predator presence, but not food supplementation, affects forest red squirrels in winter. *Ann. Zool. Fenn. 53: 183–193.*

Smith A.A. & Mannan R.W. 1994: Distinguishing characteristics of Mount Graham red squirrel midden sites. *J. Wildl. Manag. 58: 437–445.*

Sollmann R., White A.M., Gardner B. & Manley P.N. 2015: Investigating the effects of forest structure on the small mammal community in frequent-fire coniferous forests using capture-recapture models for stratified populations. *Mamm. Biol. 80: 247–254.*

Sullivan T.P., Sullivan D.S., Lindgren P.M.F. & Ransome D.B. 2009: Stand structure and the abundance and diversity of plants and small mammals in natural and intensively managed forests. *For. Ecol. Manag. 258: S127–S141.*

Takenaka A. 2009: CanopOn2. *http://takenaka-akio.org/etc/canopon2/*

Tamura N. 1997: Japanese squirrels as a seed disperser of walnuts. *Primate Res. 13: 129–135. (in Japanese with English summary)*

Tamura N. 1998: Forest type selection by the Japanese squirrel, *Sciurus lis*. *Jpn. J. Ecol. 48: 123–127. (in Japanese with English summary)*

Tamura N. 2011: Ecology of tree squirrels. *University of Tokyo Press, Tokyo, Japan. (in Japanese)*

Tamura N., Takahashi N. & Satou N. 2006: Habitat variables of the Japanese squirrel identified by regression tree model. *Mamm. Study 31: 1–8.*

Tsujino R. & Yumoto T. 2014: Habitat preferences of medium/large mammals in human disturbed forests in Central Japan. *Ecol. Res. 29: 701–710.*

Watabe R. & Saito M.U. 2021: Diel activity patterns of three sympatric medium-sized carnivores during winter and spring in a heavy snowfall area in northeastern Japan. *Mamm. Study 46: 69–75.*

Yatake H. 2016: Movement on canopy and ground of Japanese squirrels. *J. Jpn. Wildl. Res. Soc. 41: 51–58. (in Japanese with English summary)*

Yatake H., Akita T. & Abe M. 1999: Space use by introduced Japanese squirrels (*Sciurus lis* Temminck) in Shimizu Park. *Mamm. Sci. 99: 9–22. (in Japanese with English summary)*

Yatake H. & Tamura N. 2001: To make guidelines for the Japanese squirrel conservation. III Ecological studies on conserving the Japanese squirrel. *Mamm. Sci. 41: 149–157. (in Japanese)*