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REVIEW

Ecology and conservation of the Japanese flying squirrel *Pteromys momonga*

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Abstract. Flying squirrels have important roles in ecosystems, dispersing seeds and spores. However, flying squirrel species, which strongly depend on old mature forests, have declined in abundance due to the logging of mature forests. Guidelines for the conservation of flying squirrels have been developed, but it is vital to have an accurate understanding of their ecology to revise the guidelines to be more effective. The Japanese flying squirrel (*Pteromys momonga*, JFS), endangered in wide areas of Japan, is one of the flying squirrel species for which the least ecological information is available. This paper reviews individual reports and attempts to address knowledge gaps in JFS ecology to facilitate conservation strategies. Of particular importance is the fact that JFS uses planted Japanese cedar (*Cryptomeria japonica*) for nesting, gliding and winter forage, and JFS habitat may be strongly influenced by human activities such as forestry. Plantations are regularly logged, so management of plantations needs to be implemented with attention to the JFS habitat. It was also found that some ecological information necessary to develop guidelines for conservation, such as diet, gliding ability, and home-range size, is missing. Clarification of these issues is an important task.

Key words: food content, habitat use, nest site, plantation, reproduction

Introduction

Gliding mammals can be divided into three main groups: flying squirrels, gliding marsupials, and colugos. Flying squirrels are the most diverse and widely distributed of these, inhabiting Asia, Europe, and North America (Jackson 2012) and playing essential roles in ecosystems as seed and spore dispersers (Maser et al. 1985, Nandini & Parthasarathy 2008) and as essential prey for predators vulnerable to environmental changes (Carey et al. 1992, Fryxell et al. 1998, Byholm et al. 2012). As such, they are of worldwide conservation interest (e.g. Smith et al. 2005, Koli 2016, Selonen & Mäkeläinen 2017). Flying squirrels are strongly reliant on old-growth forests and are sensitive to the isolation of forests (Smith 2012). They have experienced declines in abundance due to the logging of mature forests (Hokkanen et al. 1982, Holloway & Smith 2011). Although guidelines for their conservation have been developed, it is important to gain an accurate and comprehensive understanding of their ecology to revise the guidelines and make them more effective (Santangeli et al. 2013).

In Japan, three species of flying squirrels have been described: Japanese giant flying squirrel (GFS, *Petaurista leucogenys*), Japanese flying squirrel (JFS, *Pteromys momonga*), and Siberian flying squirrel (SFS, *Pteromys volans*) (Ohdachi et al. 2009). Japan is comprised of four main islands: Hokkaido, Honshu, Shikoku, and Kyushu, and the fauna inhabiting these islands vary along the Blakiston's Line

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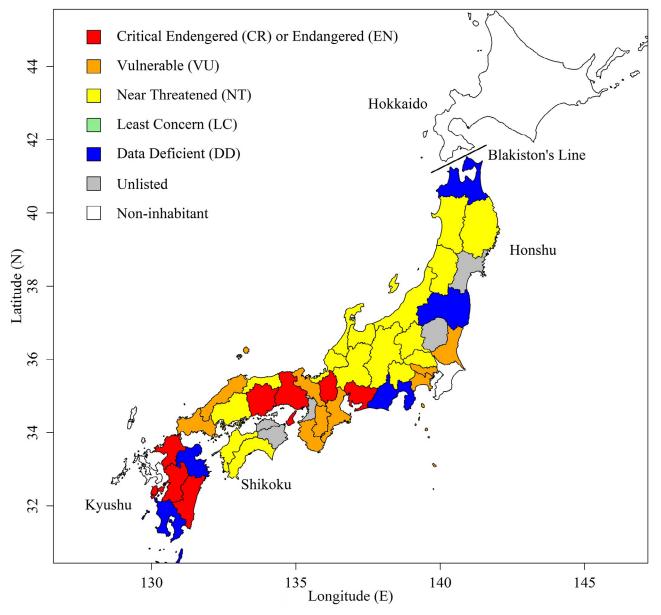


Fig. 1. Prefectural Red List rank of Japanese flying squirrel (JFS) in Japan. Since some prefectures do not distinguish between Critically Endangered and Endangered, the colour of both ranks is unified here. There is no prefecture that ranked JFS as Least Concern.

between Hokkaido and Honshu (Fig. 1). GFS and JFS are endemic species in Japan, found south of the Blakiston's Line in Honshu, Shikoku, and Kyushu Islands. In contrast, SFS is found in Hokkaido Island north of the Blakiston'tabls Line but is also distributed in a wide area of the Eurasian Continent. The Hokkaido population of SFS is thought to have separated from the Eurasian population during the Holsteinian interglacial (Oshida et al. 2005) and is treated as an endemic subspecies, P. volans orii. Ecological information pertaining to these species was reviewed in "The wild mammals of Japan" (Ohdachi et al. 2009) and was subsequently revised in 2015 (Ohdachi et al. 2015). The GFS is more readily observable than the other two flying squirrels due to its larger size and vocalizations. In addition, the

fact that the GFS is found in shrine forests on flatland is probably a significant factor. Thus, the ecology of GFS has been actively studied since the 1980s (Ando & Imaizumi 1982, Ando et al. 1983) and has been reviewed in great detail (Kawamichi 2015). Research on SFS has seen a marked increase in the rate of investigation since the 1990s (Yamaguchi & Yanagawa 1995, Yanagawa 1999), with discoveries still being made frequently (Suzuki et al. 2013, Suzuki & Yanagawa 2019, Murakami et al. 2021). In particular, the ecology and conservation of SFS as a flagship species in the Eurasian Continent have been studied in depth (Selonen & Mäkeläinen 2017). The ubiquity of SFS in urban and sub-urban forests on flatlands makes it a species that is easy to observe, which has likely been a contributing factor to the

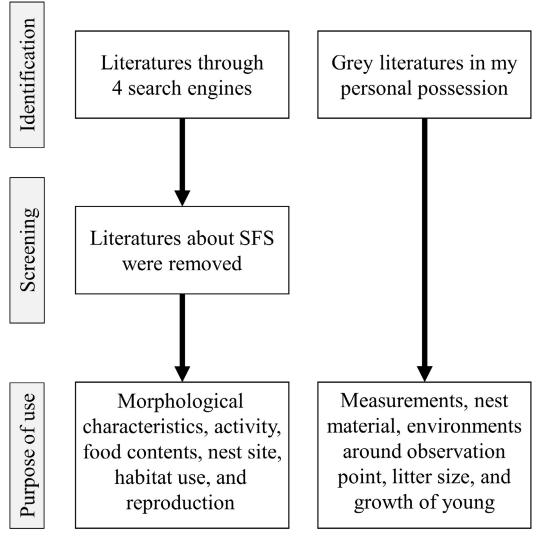


Fig. 2. Flowchart of the literature search.

advancement of the research. In contrast, although there were a few records of behavioural observations in captivity (Tezuka 1959, Ando et al. 1985), little was known about the ecology of JFS.

JFS has been categorized as of Least Concern on the IUCN Red List. The Ministry of the Environment of Japan has not placed JFS on the red list. Although JFS has been found in some prefectures, 88% of the prefectural governments are concerned about its potential extinction (Fig. 1). This is partly due to the difficulty in its detection, as its actual range is likely to be small. Direct observation of JFS is challenging due to their habitat preferences; JFS inhabit steep mountainous regions. However, the development of survey methods, such as nest box (Ando 2005) and camera trapping (Suzuki & Ando 2019), have enabled researchers to collect field data and have yielded new ecological insights. However, the findings on the ecology of JFS have often been reported simply as case studies and have never been discussed

comprehensively. This paper reviews individual reports and attempts to address knowledge gaps in JFS ecology to facilitate conservation strategies.

Material and Methods

A flowchart of the literature search is shown in Fig. 2. I conducted an exhaustive search of the literature related to JFS using four search engines, such as Google Scholar, PubMed, Citation Information by the National Institute of Informatics, and NDL DIGITAL COLLECTIONS, because it is suggested that more than two databases should be used for a comprehensive search of the literature (Atkinson & Cipriani 2018). Only species names were used as search terms to ensure a comprehensive search of the literature on JFS: Japanese flying squirrel, *P. momonga*, and four Japanese names, such as "Nihon momonga", "Honshu momonga", "Hondo momonga", and "Momonga". However, not only JFS but also SFS is called Momonga in Japan. Thus, in

Prefecture	Sex	Head and body length (mm)	Body weight (g)	Cecum length (mm)	Condition
Fukushima	Female	147.5	99.5	132.0	Death
Kanagawa	Female	202.5	134.0	-	Alive
Kanagawa	Female	176.0	146.0	-	Alive
Kanagawa	Female	172.0	122.0	-	Alive
Kanagawa	Female	170.5	162.1	-	Alive
Kanagawa	Female	162.0	118.7	-	Alive
Kanagawa	Female	170.0	116.6	-	Alive
Kanagawa	Female	168.0	110.7	-	Alive
Kanagawa	Female	172.5	108.0	-	Alive and pregnant
Kanagawa	Female	157.0	157.8	-	Alive and pregnant
Kanagawa	Female	174.0	105.6	100.0	Death and pregnant
Kanagawa	Female	156.0	80.0	-	Death
Kanagawa	Male	158.0	94.7	110.0	Death
Yamanashi	Female	167.0	103.7	160.0	Death
Saitama	Female	165.0	91.8	97.0	Death

Table 1. Measurements of Japanese flying squirrels.

the literature, those related to JFS were collected, and those related to SFS excluded.

In addition, the inclusion of grey literature in the review article will improve research accuracy (Atkinson & Cipriani 2018). Thus, grey literature, such as essays and theses describing JFS in my possession, were used, even if they could not be found through the search engines listed above. However, since these references were not peer-reviewed, I did not gather information on the results of statistical analyses but only objective facts such as weight, litter size, and nesting material. From the collected literature, I gathered the following information: measurements of JFS, activity, food contents, nest site, habitat use, and reproduction.

Results and Discussion

Morphological characteristics

The head and body (HB) and tail (TL) of JFS range from 139 to 200 mm and 95 to 140 mm, respectively (Oshida 2009a). Hind-foot length (HF) ranges from 32 to 39 mm, excluding claws. Although JFS is slightly larger than SFS (Oshida 2009b), both species are difficult to distinguish visually due to their similar size. However, these two species can be identified by the difference in mammary number: ten for JFS (Oshida 2009a) and eight for SFS (Oshida 2009b).

Many illustrated books report the body weight (BW) of JFS as ranging from 150 to 220 g (Oshida 2009a, Jackson 2012). However, these values are overestimates. HB and BW of 15 JFS captured in Suzuki (2006) are presented in Table 1. While the HB measurements agreed with previous information, the BW of almost all individuals were less than 150 g. Two female individuals had offspring, and those weights were 134 g and 146 g, respectively. Also, the minimum BW of pregnant females was 108 g (Table 1). In addition, another study also reported a 146 g female giving birth (Kobayashi 2012a). The average weight of three 2-year-old females was reported to be 135.9 g (Okubo et al. 2014). In other words, even individuals weighing less than 150 g are mature. In addition, live males weighed 100 to 165 g, except for young living with their mothers (Kobayashi 2012a, Yano 2009, Okubo et al. 2015). Thus, based on previous reports (Table 1; Kobayashi 2012a, Okubo et al. 2014), I suggest revising the BW of adult JFS to be 108 to 173 g in females and 100 to 165 g in males. These values are approximately 20-30% lighter than previously described. This discrepancy is of particular significance, as it risks misidentifying a mature adult as a subadult.

Movement

The nocturnal activity of the JFS commences shortly after sunset (Suzuki & Ando 2017). Upon leaving the nest, JFS typically defecates in the tree hosting the

Prefecture	Year	Elevation (m)	Method	Tree species	References
Aomori	1976 to 2016	270 to 300	Direct observation	Tdo, broad-leaved trees	Sasamori & Mineshita (2019)
Aomori	1995	I	Direct observation	Crj, broad-leaved trees	Sasamori & Mineshita (2019)
Aomori	2002	,	Faeces	Tdo	Sasamori & Mineshita (2019)
Aomori	2005	I	Nest box	Crj	Sasamori & Mineshita (2019)
Aomori	2013 to 2017	190	Direct observation	Tdo, broad-leaved trees	Sasamori & Mineshita (2019)
Fukushima	2002 to 2004	350 to 700	Faeces	Crj, Pd, broad-leaved trees	Iwasaki & Takahashi (2005)
Fukushima	2004	1,850	Camera trapping	Am	Iwasaki & Takahashi (2005)
Fukushima	2004	740	Direct observation	I	Yasuda & Yagihashi (2004)
Fukushima	2005	600 to 1,000	Camera trapping	Crj, Fc, Qc, At	Iwasaki (2012)
Fukushima	2005	820 to 1,200	Direct observation and faeces	Crj, Fc, Qc	Iwasaki & Takahashi (2005)
Fukushima	2005	680 to 750	Direct observation and faeces	broad-leaved trees	Iwasaki & Takahashi (2005)
Tokyo	ı	650	Direct observation	Crj, Co, Mo, Fp, Cej, Acer sp.	Okazaki (2012)
Tokyo	1996	310	Direct observation	Crj, Co, Zs, Qm, Caj, Tn	Okazaki (2012)
Tokyo	2000 to 2001	929	Direct observation	Crj, Qc, Acer sp.	Asari (2012)
Tokyo	2002	440	Direct observation	Crj	Iwasaki (2012)
Tokyo	2010	240	Direct observation	Crj, Co, Zs, Cca, Cerasus sp., Caj, Ap	Okazaki (2012)
Kanagawa	1995	I	Direct observation and Nest box	Af, Crj, Co, Broad leaved trees Yamaguchi (1997)	Yamaguchi (1997)
Kanagawa	2001	500	Nest box	I	Yamaguchi et al. (2004)
Kanagawa	2004	650 to 750	Nest box	Crj, Co, Qse, Qa	Ookubo & Ando (2005)
Kanagawa	2005 to 2008	560 to 850	Camera trapping	Crj, Co, Fc, Qse, Af	Suzuki & Ando (2019)
Tochigi	1991 to 1993	650 to 950	Nest box	Fc, Qc	Sato (1997)
Tochigi	1991 to 1993	990 to 1,080	Nest box	broad-leaved trees	Sato (1997)
Tochigi	1991 to 1993	1,160 to 1,450	Nest box	Fc, Td	Sato (1997)
Yamanashi	1981	800	Nest box	Qc, Qse	Ando (2005)
Yamanashi	2007 to 2008	1,350 to 1,600	Camera trapping	Fc, Qc, Bp, Ah	Suzuki & Ando (2019)
Yamanashi	2008	1,074 to 1,399	Camera trapping	Broad-leaved and coniferous trees	Matsubayashi et al. (2009)

Table 2. Records of Japanese flying squirrel.

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Prefecture	Year	Elevation (m)	Method	Tree species	References
Shizuoka	2004 to 2005	830 to 863	Nest box	Crj, Co	Takanaka et al. (2008)
Fukui	1993	930	Direct observation	Qc, Cs, Cb	Matsumura (1995)
Fukui	1995	140	Direct observation	Crj, Co, Qm, Ns	Yanagawa et al. (1996)
Toyama	1997	1,180	Direct observation	Fc	Murayama & Nambu (1998)
Nagano	2016	1,480 to 2,470	Nest box and camera trapping	Qc, Be, Av, Am	Kikuchi & Izumiyama (2020)
Kyoto	1984 to 1991	360	Direct observation	Fc	Nimura et al. (1997)
Shiga	1996	400 to 700	Nest box	Crj, Qc, Qs, Pr, Cco	Ando (2005)
Mie	1978 to 1995	550	Direct observation	broad-leaved trees	Shimizu (2014)
Mie	1997	400	Direct observation	Crj, Co	Shimizu (2014)
Mie	1998	340	Direct observation	Crj, Co	Shimizu (2014)
Mie	2001	400	Direct observation	1	Shimizu (2014)
Mie	2003	200	Direct observation	Crj, Co	Shimizu (2014)
Mie	2005	700	Direct observation	Crj, Co, Qse	Shimizu (2014)
Mie	2005	1150	Direct observation	broad-leaved trees	Shimizu (2014)
Mie	2006	370	Direct observation	Crj, Co	Shimizu (2014)
Mie	2014	470	Direct observation	Crj, Co	Shimizu (2014)
Yamaguchi	1996	500	Nest box	Crj, Co, natural forest	Fukamachi (2004)
Tottori	2010 to 2011	660 to 750	Nest box	Crj, Fc, Qc, Ct, Ic, At, Pr, Af	Kobayashi (2012a)
Ehime	ı	1,000	Direct observation	Crj, broad-leaved trees	Yano (2009)
Ehime	1983 to 1985	1,100 to 1,325	Direct observation	Fc	Yano (2009)
Ehime	1992 to 2005	650	Direct observation	Crj, Co, Zs, Qs, Acer sp., Pr	Yano (2009)
Ehime	1992 to 2008	500 to 800	Direct observation	Crj, broad-leaved trees	Yano (2009)
Ehime	1998	I	Direct observation	broad-leaved trees	Yano (2009)
Ehime	1999	400 to 500	Direct observation	ı	Yano (2009)
Ehime	2004	200	Nest box	Crj, Co	Yano (2009)
Ehime	2004 to 2005	100 to 220	Direct observation and Nest box	broad-leaved trees	Yano (2009)
Ehime	2006	1,030	Nest box	Fc, Qac, Sm, Acer sp.	Furukawa & Miyamoto (2010)
Ehime	2009 to 2010	650	Nest box and camera trapping	Crj, Co, Zs, Qs, Acer sp., Pr	Yano (2009)

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Prefecture	Year	Elevation (m)	Method	Tree species	References
Tokushima	1996	1,100	Direct observation	I	Kawamichi (2009)
Tokushima	2007	730	Direct observation	I	Kawamichi (2009)
Kochi	2007	600 to 840	Direct observation	I	Kawamichi 2009)
Kumamoto	2006 to 2008	680 to 855	Nest box	Fc, Qm, Qac, Acer sp, Af, Ts	Sakata et al. (2009)
Kumamoto	2008	755 to 860	Nest box and camera trapping	Crj, Fc, Qm, Qac, Acer sp, Af, Ts	Sakata et al. (2009)
Kumamoto	2009 to 2010	400 to 480	Camera trapping	Crj, Co, Le, Cc, Qs	Sakata et al. (2011)
Kumamoto	2010	400 to 600	Camera trapping	Le, Cc, Qs, Qac, Qg	Sakata et al. (2010)
Miyazaki	2006	1,000 to 1,607	Direct observation	Crj, Co, broad-leaved trees	Kabemura et al. (2010)
Miyazaki	2007	760	Camera trapping	Crj, Co, Qs, Caj, Af, Ts	Okubo et al. (2009)
Miyazaki	2008	006	Camera trapping	Pd, broad-leaved trees	Yasuda & Kurihara (2009)

Td – Tsuga diversifolia; Pd – Pinus densiflora; Tn – Torreya nucifera; Fc – Fagus crenata; Qs – Quercus salicina; Qse – Quercus serrata; Qa – Quercus acutissima; Qc – Quercus crispula; Qm – Quercus myrsinaefolia; Qac – Quercus acuta; Qg – Quercus gilva; Le – Lithocarpus edulis; Cc – Castanopsis cuspidate; Bp – Betula platyphylla; Be – Betula ermanii; Ct – Carpinus tschonoskii; Zs – Zelkova Tree species: Crj – Cryptomeria japonica; Co – Chamaecyparis obtuse; Tdo – Thujopsis dolaburata; Af – Abies firma; Ah – Abies homolepis; Av – Abies veitchii; Am – Abies mariesii; Ts – Tsuga sieboldii; serrata; Cs – Chengiopanax sciadophylloides; Cca – Cinnamomum camphora; Ns – Neolitsea sericea; Mo – Magnolia obovate; Ic – Ilex crenata; Caj – Camellia japonica; Sm – Stewartia monadelpha; Cb – Clethra barbinervis; At – Aesculus turbinate; Ap – Acer palmatum; Cco – Cornus controversa; Fp – Fraxinus platypoda; Cej – Cercidiphyllum japonicum; Pr – Pterocarya rhoifolia.

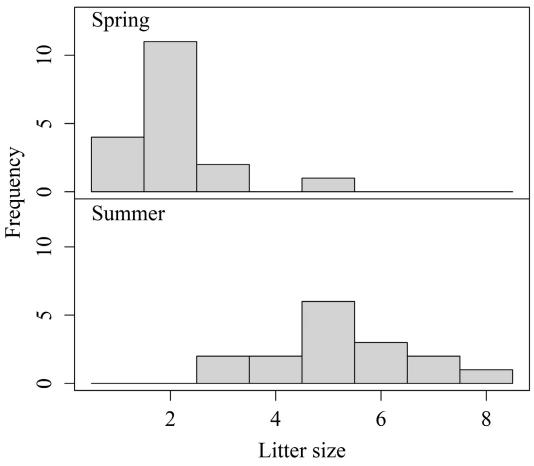


Fig. 3. Histogram showing seasonal changes in litter size of Japanese flying squirrel.

nest or in adjacent trees (Iwasaki & Takahashi 2009). After that, they usually move by gliding, but the details of their gliding ability are not known at all. If the forest is fragmented by logging, the gap size should be based on their glide ratio for JFS habitat conservation. Thus, clarifying the glide ratio of JFS is an important issue and logging based on gliding ability is desired.

However, the movements of JFS may be similar to those of SFS, a closely related species with a similar body size. Given that SFS have an average glide ratio of 1.7-2.0 (Asari et al. 2007, Suzuki et al. 2012, Suzuki & Yanagawa 2019), it is likely that JFS possess a comparable gliding capacity. In addition, the dispersal distances of JFS are unknown, but SFS is observed to move long distances (Selonen et al. 2010). Because dispersal distance is essential information for determining conservation areas and gene flow of the species (Clobert et al. 2004), another critical issue is determining the dispersal distance of JFS.

Camera trapping has revealed that JFS are often photographed on the trunk of Japanese cedar (*Cryptomeria japonica*) with a high tree height (at least 14 m), suggesting that JFS may prefer these trees as landing sites for gliding (Suzuki & Ando 2019). Japanese cedar is in demand as timber because of its straight tree shape. Straight trees may be easier for JFS to land on. In addition, SFS selectively lands on tall trees that allow it to glide farther in the next glide (Suzuki et al. 2012, Suzuki & Yanagawa 2019). JFS would land in a tall tree for the same reason. Straight, tall trees are necessary for habitat as a migration route for JFS.

Food contents

JFS are considered to be folivorous (Oshida 2009a), foraging mainly on leaves, flowers (pollen), buds, seeds, cones, fruits, and bark, with the dietary composition changing seasonally. However, there is little information on the types of plants foraged by JFS, with only a few captive experiments and field observations available. Two JFS captured in the northern part of Honshu Island have been found to forage on leaves of Japanese cedar, cherry (*Cerasus* sp.), and beech (*Fagus crenata*), as well as cones of red pine (*Pinus densiflora*) (Iwasaki & Takahashi 2009). A JFS captured in the central part of Honshu Island was observed to forage on leaves of red (*Quercus acuta*) and sawtooth (Q. acutissima) oaks, young leaves of northern Japanese hemlock (Tsuga diversifolia), and fruit and seed of loquat (Eriobotrya japonica) (Tezuka 1959). Captive JFS have also been reported to forage on Asian hazel (Corylus heterophylla) and Japanese green alder (Alnus firma) (Kurota 1941), but the parts selected, such as the leaf, bud, or seed, is unknown. Insectivory by JFS is controversial, as some records indicate that JFS foraged on orthoptera and beetles (Kurota 1941), while other records suggest the contrary (Tezuka 1959). In the wild, only one recorded instance of JFS foraging on Japanese zelkova (Zelkova serrata) (Okazaki 2012). From winter to early spring, however, faeces of JFS have been found to contain pollen of Japanese cedar (Ichikawa et al. 2004, Iwasaki & Takahashi 2009).

While detailed food contents of JFS are unknown, it is considered that JFS has a lower digestive capacity than GFS (Okubo et al. 2015). Herbivores of smaller body size require more protein and energy per unit body mass than larger species (Demment & Van Soest 1985), and arboreal mammals that have adapted to folivory tend to have a longer alimentary tract (Chivers & Hladik 1980). Mitsuzuka & Oshida (2018) revealed that the cecum length per HB of the GFS (0.85 and 0.89) with large body size (approx. 1,000 g) is longer than that of SFS (0.56), and this means that GFS better adapts to folivory than SFS. Because the caecum length per HB of JFS (Table 1; mean = 0.74, n = 5, SD = 0.176) is located between GFS and SFS, food contents of JFS may also be intermediate between those species.

Given the importance of food availability in determining animal distribution (Lurz et al. 2000) and its role in optimizing animal survival (Pyke 1984), knowledge of food contents is a critical component of habitat management (Birnie-Gauvin et al. 2017). However, there is limited knowledge of food resources for JFS, and further investigation into their diet is urgently needed. In contrast, the food contents of SFS are relatively well known, with 16 species of plants from seven families identified by direct observation (Fujimaki 1963, Yanagawa 1999, Asari et al. 2008, Nambu & Yanagawa 2010). The large disparity in the amount of knowledge regarding the food contents of JFS compared to the SFS is likely attributable to the difficulty in directly observing JFS foraging in steep mountain environments, in contrast to SFS, which inhabit urban forests. Nevertheless, recent findings based on DNA analysis of faeces (Murakami et al. 2021) suggest that the diet of JFS can be identified. Faeces of JFS accumulate at the base of trees with

cavities, where JFS nest (Iwasaki & Takahashi 2009). Moreover, due to the ease of collecting SFS faeces by placing umbrellas upside down at the base of trees with cavities (Suzuki et al. 2011a), JFS faeces could similarly be collected. Identifying the contents of JFS by faeces may be more feasible than by direct observation.

Nest site uses

JFS uses tree cavities as their primary nesting sites for resting and breeding. Although they are unable to create their own cavities, they utilize cavities created by decaying branches and old nests of woodpeckers. JFS uses multiple nests (Kobayashi 2012a). In addition, JFS generally exhibit solitary nesting, but communal nesting is observed from autumn to winter (Suzuki et al. 2008, Kobayashi 2013, Kikuchi et al. 2022). In SFS populations in Finland, communal nesting is likely associated with mating (Selonen et al. 2014). However, in JFS populations, communal nesting may involve only females or only males (Suzuki et al. 2008, Kobayashi 2013), indicating that the function of communal nesting in JFS may not necessarily be related to mating. The purpose of communal nesting in JFS remains to be determined.

The long and short diameters of the tree cavities used by JFS average 8.2 and 6.9 cm, respectively, with a minimum of 4.6 cm (Suzuki et al. 2011b). However, since JFS will also use nest boxes with entrances larger than 3.5 cm (Sakata et al. 2009), they will likely use tree cavities with a similar entrance size. The average height of nesting cavities is 6.2 m (Suzuki et al. 2011b). In experiments with nest boxes, JFS tended to prefer higher nest boxes (Ookubo & Ando 2005, Kobayashi 2014a). Studies have shown that Japanese cedar cavities are preferred in Kanagawa Prefecture (Suzuki et al. 2011b). Additionally, although JFS nests in a cavity of Japanese white bark magnolia (Magnolia obovata) (Iwasaki 2012), nesting in cavities of Japanese cedar have been frequently confirmed in also other areas (Asari 2012, Iwasaki 2012, Okazaki 2012). Thus, the cavities with an entrance of more than 3.5 cm with openings high on the trunks of Japanese cedar appear to be important for the conservation of JFS.

JFS predominantly utilizes Japanese cedar bark as its primary nesting material (Ando 2005, Suzuki et al. 2008, Sakata et al. 2009). However, if Japanese cedar is absent, JFS uses white birch bark and moss as the materials (Kakuta 2006). It is hypothesized that the preference for Japanese cedar bark is likely attributed to its superior waterproofing and insulating properties (Kobayashi 2012b, 2014b). The preference of JFS for the cedar cavities may be due to the easy availability of nest materials.

Habitat uses

JFS prefer an environment where Japanese cedar and cypress (Chamaecyparis obtuse) plantations and natural broad-leaved forests are adjacent to each other (Suzuki et al. 2008). However, they do not necessarily inhabit only this environment. Although not quantitatively evaluated, several reports of JFS observations have been documented (Table 2). It appears that JFS habitats encompass a variety of vegetation, with approximately 60% of their habitats containing plantations of Japanese cedar and cypress. This situation may be due to the utility of Japanese cedar as a gliding path, winter food item, nest site, and nest material. These reports were mainly based on nest box use, camera trapping, and direct observation. In natural habitats without plantations, the main vegetation seems to be Pinaceae, Fagaceae, and Betulaceae.

JFS has never been surveyed for their home range. Determining the size of their home range and what type of environment they prefer within the home range is an important issue for their habitat conservation.

Reproduction

JFS have two breeding seasons (spring and summer) per year because their neonates, described as hairless, were found in mid-March (Kakuta 2006) and mid-August (Kobayashi 2012a). The neonates in summer weighed around 7 g. Because The mean weight of neonates upon birth is 4.6 g in captivity and the daily body weight gain ranges from 1.2 to 1.3 g (Kakuta 2006), the neonates must be born within a few days. Although mating has been observed from January to February (Kikuchi et al. 2022), summer mating has probably never been observed. Given the 40 to 42-day gestation period of the SFS (Airapetyants & Fokin 2003), which is almost the same size and belongs to the same genus, there will likely be a mating season in July. However, it is unknown whether the same individuals breed twice a year.

The litter size of JFS vary widely from one to eight (Kobayashi 2012a). Although it has rarely been mentioned, JFS litter size will likely change seasonally. Based on 16 references (Sakaguchi 1957, Shirai 1963, Ueno et al. 1996, Yanagawa et al. 1996, Suzuki 2001, Kakuta 2006, Suzuki et al. 2008, Hosoda 2009, Oshida 2009a, Sakata et al. 2009, Yano 2009, Imaizumi 2012, Kobayashi 2012a, 2019, 2022, 2023) and one personal

observation (two young in spring), the litter size in spring ranges one to five (37 young in 18 litters) and that in summer is three to eight (84 young in 16 litters) (Fig. 3). It should be noted, however, that some offspring may have died prior to the observations, and these litter sizes may be slightly underestimated.

Although seasonal changes in litter sizes are shown in southern flying squirrels (*Glaucomys volans*), average litter sizes for spring and summer were 2.4 and 3.4, respectively (Stapp & Mautz 1991), which is not as large a difference as found in the JFS. The summer litter size of JFS is remarkably large for a flying squirrel species, considering that almost all *Pteromyini species* in the family Sciuridae generally have small litter sizes of one to three (Goldingay 2000, Hayssen 2008). It is unknown why JFS litter size changes seasonally. With such an unusual litter size for an arboreal squirrel, JFS is a vital research target for understanding the evolution of litter size in Sciuridae, and they are worthy of conservation.

Conservation and Conclusions

JFS is one of the least ecologically understood species among flying squirrels. This review highlights knowledge gaps: gliding ability, diet composition, and home range size. In addition, recent observations of the species have been recorded both directly and through the use of nest boxes and camera trapping (Table 2). This review provides some insight into the conservation of JFS; of particular importance is that JFS uses planted Japanese cedar for nesting, gliding, and winter forage. These conclusions indicate that JFS habitat may be strongly influenced by human activities such as forestry.

Despite being generally thought of as having low biodiversity, plantations actually serve as habitats for many species (Brockerhoff et al. 2008). In addition, evidence suggests that plantations have an important role in providing habitat to several endangered species (Brockerhoff et al. 2005, 2008, Barbaro et al. 2009, Berndt et al. 2009). For reasons of human economics, it is impossible to eliminate plantations management altogether. Recently, therefore, regimes of plantations that promote biodiversity have garnered great international interest in the conservation of endangered species (Castano-Villa et al. 2019, Gadoth-Goodman & Rothstein 2020, Jamhuri et al. 2020, Wang et al. 2022).

Plantations are regularly logged, so management of plantations needs to be implemented with attention

to the JFS habitat. For instance, it is preferable to avoid cutting down cavity trees and trees in their vicinity, and if it is inevitable, then a nest box should replace the nest. In addition, the creation of large habitat gaps through thinning should be avoided. Since the glide ability of the JFS is unclear, it is not possible to state here how long of a gap will make it difficult for the JFS to move. Identifying gliding ability is a particularly important issue for developing guidelines for their conservation.

Acknowledgements

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