Ecology and conservation of an endangered flying squirrel in plantations

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Abstract: Flying squirrels have important roles in ecosystems, serving as dispersers of seeds and spores. However, logging of mature forests has led to a decline in the abundance of species which depend heavily on old-growth forests. While guidelines have been developed to conserve flying squirrels, an accurate and comprehensive understanding of their ecology is necessary to ensure the effectiveness of these guidelines. The Japanese flying squirrel (*Pteromys momonga*, JFS) is one of the flying squirrel species with the least ecological information, yet developments in survey techniques have enabled an increase in recent habitat information. This paper reviews JFS ecology, such as activity, diet, nest site, reproduction, and habitat use, based on individual field observations and provides information of habitat conservation. The results suggest that JFS is one of the most prolific species of flying squirrels, and is strongly dependent on Japanese cedar (*Cryptomeria japonica*) and cypress (*Chamaecyparis obtuse*) plantations. The population growth rate of JFS, which has a similar litter size to the field mouse, does not appear to be significantly lower. Consequently, its high reproductive potential cannot be identified as the cause of its threatened status in many parts of Japan. I consider that that plantations offer an important opportunity for habitat conservation that could improve insufficient conservation practices. Japanese cedars, which provide both nesting sites and nesting material, with cavity should not be cut, and if cutting is unavoidable, alternative nest

boxes should be installed. Furthermore, based on the gliding capabilities of related species, logging practices that create gaps of 1.8 times or more the height of the trees at the forest edge should be avoided. Currently, internationally, there is great interest in management regimes of plantations which promote biodiversity for conservation of endangered species. My review indicates that coniferous plantations with native broad-leaved trees can serve as a habitat for the endangered flying squirrel. I hope that this paper will be useful in the conservation of JFS habitat through the use of plantations.

1. 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, Maser & Trappe, 1985; Nandini & Parthasarathy, 2008) and as essential prey for predators vulnerable to environmental changes (Carey, Horton & Biswell, 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 and Mäkeläinen 2017). Flying squirrels are strongly reliant on old-growth forests, and are sensitive to isolation of forests (Smith, 2012). They have experienced declines in abundance as a result of logging of mature forests (Hokkanen, Törmälä & Vuorinen, 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 in order 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).

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 flatland shrine forests is probably a major factor. Thus, the ecology of GFS has been actively studied since the 1980s (Ando & Imaizumi, 1982; Ando, Funakoshi & Shiraishi, 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 new discoveries still being made frequently (Suzuki, Sagawa & Yanagawa, 2013; Suzuki & Yanagawa, 2019; Murakami, Kikuchi & Oshida, 2021). In particular, the ecology and conservation of SFS as a flagship species in the Eurasian Continent has been studied in depth (Selonen & Mäkeläinen, 2017). The ubiquity of SFS in flatland urban and sub-urban forests make it a species that is easy to observe, which has likely been a contributing factor to the advancement of the research. In contrast, little progress had been made on at the time. Although there were a few records of behavioral observations in captivity (Tezuka, 1959; Ando, Shiraishi & Uchida, 1985), nothing was known about the ecology of JFS.

Direct observation of JFS is challenging due to their habitat preferences, with

GFS and SFS residing in shrine and urban forests, while JFS inhabit steep mountainous regions. In recent years, however, the development of survey methods, such as nest box (Ando, 2005) and camera trapping (Suzuki & Ando, 2019), have enabled researchers to collect data in the field and have yielded new ecological insights. This paper reviews these individual reports and attempts to address gaps in our knowledge of JFS ecology, to facilitate the development of conservation strategies for JFS.

2. Distribution and red list rank

Japan is comprised of four main islands: Hokkaido, Honshu, Shikoku, and Kyushu, and the fauna inhabiting these islands vary along the Blakiston's Line 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 to the north of the Blakiston's 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. v. orii*.

Three species of flying squirrels have been documented to have a strong reliance on forested environments. Basically, GFS and SFS are found in lowland to montane zone habitats, while JFS inhabits montane to sub-alpine zones. It has been vaguely assumed that habitats of GFS and JFS are separated by altitude. In recent years, however, GFS was found in sub-alpine zone (2,160 m) in Nagano Prefecture (Kikuchi, 2015). In contrast, JFS has been documented to inhabit a wide range of elevations (Table 1) and has been found at low elevations of a few hundred meters (Yanagawa et al., 1996; Yano, 2009; Okazaki, 2012). It is becoming increasingly evident that the two species have a rare sympatric occurrence, as reported from Fukushima Prefecture (590-960 m), Kanagawa Prefecture (500-910 m), and Tokyo metropolitan area (240 m, 310 m, 440 m, 500 m, 650 m, and 830 m) in the Honshu Island (Yamaguchi, Yuzawa & Yuzawa, 2004; Aoki et al., 2006; Suzuki et al., 2008; Asari, 2012; Iwasaki, 2012; Okazaki, 2012; Suzuki & Ando, 2019) and Kagawa Prefecture (650 m) in Shikoku Island (Yano, 2012). Thus, there appears to be no clear division in the distribution of the two species by elevation, with considerable overlap observed.

The exact distribution range of JFS remains uncertain, but there is no its presence in Chiba Prefecture in Honshu Island and Nagasaki and Saga Prefectures on Kyushu Island. In IUCN red list, JFS has been ranked for least concern. JFS has not described in red list of Ministry of the Environment of Japan. 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. In fact, JFS is not widely found in mountains, but is localized in certain hotspot areas (Suzuki et al., 2008).

3. Morphological characteristics

The head and body (HB) and tail (TL) lengths and hind-foot length (HF) excluding claws of JFS range from 139 to 200 mm, 95 to 140 mm, and 32 to 39 mm, respectively (Ohdachi et al., 2009), while SFS had values of 130 to 167 mm, 92 to 118 mm, and 32 to 36.5 mm, respectively. Although JFS is slightly larger than SFS, both species are difficult to distinguish visually due to their similar size.

Many illustrated books report the body weight (BW) of JFS as ranging from 150 g to 220 g (e.g. Jackson 2012; Ohdachi et al. 2015). However, I believe these values are overestimates. HB and BW of 15 JFS (Suzuki, 2006) are presented in Table 2. While the HB measurements were in agreement with previous knowledge, the BW of almost all individuals were less than 150 g. Of those, two female individuals had offspring, and those weights were 134 g and 146 g, respectively. Moreover, in the western area of Honshu Island, the BW of 16 adult females and 29 adult males ranged from 108 to 173 g (average of 149.4 g) and from 100 to 165 g (132.5 g), respectively (Kobayashi, 2012a).

In Shikoku Island, BW of dead female and male was 117 g and 120.7 g, respectively (Yano, 2009). Furthermore, in Kyushu Island, mean BW of 3 females and 2 males was 144.8 g and 131.5 g, respectively (Okubo et al., 2015). Generally, across all islands where JFS inhabit, their BW is typically less than 150 g. Thus, JFS can be considered mature enough to weigh less than 150 g for the following reasons: females weighing less than 150 g have offspring, and there is sexual dimorphism in body weight and female are slightly larger than male (Kobayashi, 2012a). Because minimum body weight of pregnant female in alive was 108 g (Table 2), Therefore, I suggest revising the weight of adult JFS from 100 g to 173 g, which is approximately 20-30% lighter than previously described. This discrepancy is of particular significance, as it risks misidentifying a mature adult as a subadult.

The tail of JFS is flattened in shape, differing from the rod-shaped tail of GFS. Additionally, JFS possess gliding membranes between their forelimbs and hind limbs, as well as cartilaginous spurs extending from the outside of the wrist, thus providing an increased surface area of gliding membranes (Ando & Shiraishi, 1984).

4. Nocturnal activity

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 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. During my observation of 4 gliding events, I was unable to calculate the glide ratio (vertical drop / horizontal glide distance) due to my inability to ascertain the landing point. However, given that SFS with similar body size have an average glide ratio of 1.7-2.0 (Asari, Yanagawa & Oshida, 2007; Suzuki, Asari & Yanagawa, 2012; Suzuki & Yanagawa, 2019), it is likely that JFS possess a comparable gliding capacity. Furthermore, camera trapping has revealed that JFS are often photographed on trunk of Japanese cedar (*Cryptomeria japonica*) with a high tree height, suggesting that JFS may prefer these trees as landing sites for gliding (Suzuki & Ando, 2019).

JFS activity peaks vary seasonally, with two peaks in temperate seasons and three peaks in cold seasons (Suzuki & Ando, 2017). The first peak is observed within 2 h after sunset, the second around midnight and the third, only in cold seasons, before sunrise. Despite the observed increase in rest periods during the cold (short daylength) season (Okubo et al., 2014), it is still unknown which behaviors (e.g. foraging, grooming or moving) JFS engages in during its active period.

5. Food contents

JFS are considered to be folivorous, 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). In addition, while captive JFS have been observed to forage on sweet potato (*Ipomoea batatas*) (Tezuka, 1959), it is unlikely that free-ranging JFS exhibit this behavior since they are arboreal and do not dig in the soil. Captive JFS have also been reported to forage on Asian hazel (*Corylus heterophylla*) and Japanese green alder (*Alnus firma*) (Kurota, 1941), but the part, such as leaf, bub, and 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, there is only one recorded instance of JFS foraging on

Japanese zelkova (*Zelkova serrata*) (Okazaki, 2012). From winter to early spring, however, feces of JFS have been found to contain pollen of Japanese cedar (Ichikawa et al., 2004; Iwasaki & Takahashi, 2009).

Herbivores of smaller body size require more protein and energy per unit body mass than larger species (Demment & Van Soest, 1985). Furthermore, arboreal mammals that have adapted to folivory tend to have a longer alimentary tract (Chivers & Hladik, 1980). The cecum length per HB of the GFS (0.85 and 0.89) with large body size (approximately 1,000 g) is longer than that of SFS (0.56) (Mitsuzuka & Oshida, 2018). In contrast, the cecum length per HB of JFS averages 0.74 (Table 2; N = 5, SD = 0.176). This indicates that the JFS has a digestion capacity that is intermediate between the GFS and the SFS. This is consistent with the view that the GFS has a higher digestive capacity than the JFS (Okubo et al., 2015).

Given the importance of food availability in determining animal distribution (Lurz, Garson & Wauters, 2000) and its role in optimizing animal survival (Pyke, 1984), t 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 food contents is urgently needed. In contrast, the food contents of GFS have been studied in greater detail, with 139 species of plants from 47 families identified (Kawamichi, 2010) as well as chemical-based food selections (Ito et al., 2016; Ito, Tamura & Hayashi, 2017; Ito & Hayashi, 2020). Additionally, the food contents of SFS are relatively well known, with 16 species of plants from 7 families identified by direct observation (Fujimaki, 1963; Yanagawa, 1999; Asari, Yamaguchi & Yanagawa, 2008; Nambu & Yanagawa, 2010). The large disparity in the amount of knowledge regarding the food contents of JFS compared to the other two species is likely attributable to the difficulty in directly observing JFS foraging in steep mountain environments, in contrast to the other two species which inhabit urban forests and/or shrine and temple forests. Nevertheless, recent findings based on DNA analysis of SFS feces (Murakami, Kikuchi & Oshida, 2021) suggest that food contents of JFS can be identified. Feces of JFS accumulate at the base of trees with cavities, where JFS nest (Iwasaki & Takahashi, 2009). Moreover, due to the ease of collection of SFS feces by placing umbrellas upside down at the base of trees with cavities (Suzuki, Mori & Yanagawa, 2011), it is likely that JFS feces could similarly be collected. Consequently, identifying food content of JFS by feces may be more feasible than direct observation.

6. Nest site uses

6.1. Nest site selections

JFS uses tree cavity 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. On average, 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., 2011). However, since JFS will also use nest boxes with entrances larger than 3.5 cm (Sakata et al., 2009), it is likely that they will use tree cavities with a similar entrance size. Studies have shown that Japanese cedar cavities are preferred in Kanagawa Prefecture (Suzuki et al., 2011). Additionally, nesting in cavities of Japanese cedar have been confirmed in other areas (Asari, 2012; Iwasaki, 2012; Okazaki, 2012), but they also nest in a cavity of Japanese whitebark magnolia (*Magnolia obovata*) (Iwasaki, 2012). The average height of nesting cavities is 6.2 m (Suzuki et al., 2011). In experiments with nest boxes, JFS tended to prefer nest boxes placed higher (Ookubo & Ando, 2005; Kobayashi, 2014a).

Generally, flying squirrel species have been found to possess multiple nests (Carey et al., 1997; Asari & Yanagawa, 2008; Kawamichi, 2015). In one study, evidence suggested that JFS uses multiple nests, as the same individual was observed in multiple nest boxes (Kobayashi, 2012a). Despite this evidence, the number of nests used by an individual JFS remains unknown.

6.2. Communal nesting

JFS generally exhibit solitary nesting, but communal nesting is observed from autumn to winter (Suzuki et al., 2008; Kobayashi, 2013; Kikuchi, Izumiyama & Oshida, 2022). The number of individuals involved in communal nesting varies from 2 to 9. In SFS populations in Finland, communal nesting is likely associated with mating (Selonen, Hanski & Wistbacka, 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 neccessarily be related to mating. Thus, communal nesting of JFS may not necessarily be aim for mating. Additionally, the hypothesis of communal nesting for thermoregulation has been rejected (Kikuchi, Izumiyama & Oshida, 2022), and the purpose of communal nesting in JFS remains unclear.

6.3. Nest materials

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 not present, JFS will resort to white birch bark and moss (Kakuta, 2006). It is hypothesized that the preference of Japanese cedar bark is likely attributed to its superior waterproofing and insulating properties (Kobayashi, 2012b, 2014b). In captive observations, JFS carried the nest materials into the nest box with its mouth and then striped the materials into narrow pieces inside the nest box (Kakuta, 2006).

7. Reproduction

7.1. Mating seasons and seasonal changes in litter size of JFS

Few confirmed breeding cases of JFS have been reported, with only three birth records (Ohdachi et al., 2015). However, more observations have been made since then, leading to further reproductive information. To date, only one reported mating event has been observed, occurring from January to February (Kikuchi, Izumiyama & Oshida, 2022). Conversely, there are multiple reports of observations of JFS offspring, particularly in Kanagawa Prefecture, central Japan, where they have been found in March and from September to October (Suzuki et al., 2008). Notably, offspring observed on March 12 were neonates, described as hairless and weighing approximately 10 g (Table 2); these are considered to be only a few days old. Furthermore, pregnant females were observed using nest boxes in August (Table 2) and giving birth on August 22 and 28 (Kakuta, 2006). In Tottori Prefecture, western Japan, offspring of JFS were found in nest boxes from April to May and August to October (Kobayashi, 2012a). Specifically, neonates weighing around 7 g and identified on August 13 were observed to be hairless, suggesting they were only a few days old. In Kyushu Island, south western Japan, hairless offspring were found in two nest boxes on August 24 and 26 (Sakata et al., 2009). Although the gestation period of JFS is unknown, 40 to 42 day gestation period for SFS in Russia was reported (Airapetyants & Fokin, 2003), thus suggesting that the mating seasons of JFS likely occur from January to February and in July. Consequently, JFS have two breeding seasons annually, but it is not yet known if the same individuals breed twice a year.

While the litter size of JFS is thought to be 2 to 3 (Ohdachi et al., 2015), this estimate is a bit inaccurate. Based on above information (Ohdachi et al., 2015) and 4 additional reports (Kakuta, 2006; Suzuki et al., 2008; Sakata et al., 2009; Kobayashi, 2012a), litter sizes in spring and summer ranged 1 to 2 (N = 4) and 3 to 8 (N = 8), respectively. Furthermore, I observed a single adult and two offspring nesting in a tree cavity in April 2005 (Personal observation). The 28 individuals whose sex was recorded had an even sex ratio of 14:14. Using a generalized linear model with Poisson distribution to compare the litter sizes between the mating seasons based on 54 offspring from 13 samples, the litter sizes in summer (45 offspring; mean = 5.63, SD = 1.51) were approximately three times larger than those in spring (9 offspring; mean = 1.80, SD = 0.45) (Fig. 2; coefficient = 1.139, χ^2 = 12.234, *p*-vale = 0.0005). 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 1-3 (Goldingay, 2000; Hayssen, 2008). The summer litter size of JFS (6.2) is closer to that of Marmotini, which has the largest litter size in Sciuridae (Hayssen, 2008). Although smaller species of flying squirrels often exhibit larger litter sizes (Hayssen, 2008), the maximum litter size (5) of the southern flying squirrel, which has an adult body weight approximately half that of JFS (Fokidis & Risch, 2008), is smaller than the summer litter size of JFS.

Small litter size in flying squirrel species is thought to be an adaptation to gliding locomotion, due to the fact that a mere 3% increase of body weight due to pregnancy is known to decrease gliding ability of GFS (Kawamichi, 2015). The weight of JFS neonates averages 4.6 g (N = 13, range = 3.6 to 5.4) (Kakuta, 2006), which is only slightly lighter than those of northern flying squirrels (*Glaucomys sabrinus*, 5.6 g) (Hayssen, 2008), species that have similar adult body weights to JFS. If there are six fetuses, the mother will gain 27 g prior to giving birth. Assuming that the mother weighs 150 g, pregnancy results in a weight gain of about 18%. Therefore, the larger body weight increase due to pregnancy in JFS compared with other flying squirrel species may have a significantly negative effect on gliding locomotion. Additionally, gliding locomotion may save time for movement, but energy efficiency for horizontal movement is worse than walking when energy cost of climbing trees to glide is taken into account (Byrnes et al., 2011). So, the increased energy expenditure of tree climbing with increased body mass makes locomotion energetically costly. Furthermore, pregnant female flying squirrels (Fokidis & Risch, 2008) have a greater wing loading than non-pregnant females. A higher wing loading leads to an increase in glide speed, which may result in more collisions with trees. It is an intriguing question to explore how JFS circumvents these drawbacks.

In addition, the mechanism driving seasonal changes in litter size is unclear. In SFS inhabiting Finland, food abundance prior to reproduction has a positive effect on litter size (Selonen, Wistbacka & Korpimäki, 2016). As mentioned above, knowledge of the food content of JFS is limited, thus it is unknown how food abundance influences litter size in JFS. Clarifying how food abundance affects seasonal changes in litter size is a necessary next step. Recruitment is a key factor in population fluctuation (Gaillard, Festa-Bianchet & Yoccoz, 1998); thus, elucidating the factors determining litter size will be essential for developing appropriate conservation measures for JFS.

7.2.Growth of offspring

The mean weight of neonates upon birth is 4.6 g, exhibiting gliding membranes and claws (Kakuta, 2006; Kobayashi, 2012a). Ocular opening of neonates typically occurs at 36 days post-partum in captivity (Kakuta, 2006), despite eyes being unresponsive immediately after birth (Suzuki et al., 2008; Kobayashi, 2012a). Furthermore, daily body weight gain of neonates ranges from 1.2 to 1.3 g (Kakuta, 2006).

There is only a single report detailing the behavioral development of JFS in captivity (Kakuta, 2006). From 5 days of age, offspring begin to crawl using their forelimbs. By 21 days, they use both fore and hind limbs to move forward, although their bellies rub the ground. After 26 days, they can walk on the ground, and by 37 days, when their eyes open, they are able to climb the wall of their nest box and emerge from its entrance. At 40-43 days of age, the JFS young are ready to leave the nest and start eating solid food. At around 60 days of age, the offspring show nocturnal activity and are weaned.

It takes about 20 days for JFS young to show nocturnal activity after they leave the nest, and similar habits are observed in free-ranging SFS (Suzuki et al., 2016). I In contrast, the offspring of GFS begin to exit the nest at 48 to 61 days of age (Kawamichi 2015; Shigeta et al. 2018), and at this stage, they demonstrate nocturnal habits (Ando and Shiraishi 1985). As the eyes of GFS open at an approximate 36 days of age (Shigeta, Shigeta & Tamura, 2018), JFS and GFS display comparable levels of eye opening and nocturnal activity at corresponding daily ages. Therefore, JFS demonstrate an earlier onset of activity away from the nest than GFS.

8. Habitat uses

A quantitative evaluation of habitat preferences of JFS was conducted based on utilization rate of nest boxes (Suzuki et al., 2008). Results showed that JFS favored mixed forests containing broad-leaved trees, Japanese fir (*Abies firma*), and coniferous plantations of Japanese cedar and cypress (*Chamaecyparis obtuse*). Although not quantitatively evaluated, several reports of JFS observations have been documented (Table 1). It appears that JFS habitats encompass a variety of vegetation, with approximately 60% of their habitats containing plantations of Japanese cedar and cypress. This may be due to the utility of Japanese cedar as a gliding path, winter food item, nest site, and nest material.

JFS has never been surveyed for their home range. At montane and sub-alpine zones where JFS occurs, the terrain is steep and makes tracking small-bodied JFS at night unfeasible. I have attempted to track one JFS with a transmitter attached; however, climbing up and down a steep slope with an antenna proved inadequate to reach the location to which JFS had moved before it relocated again. Consequently, I was unable to elucidate the home range of JFS. Tracking JFS in mountainous areas is highly challenging.

9. Conservation and conclusion

JFS is one of the least ecologically understood species among flying squirrels. Recent observations of the species, however, have been recorded both directly and through the use of nest boxes and camera trapping (Table 1), resulting in a total of 53 papers reviewed in this paper. These observations provide new insights into the ecology of JFS and inform conservation strategies. Remarkably, JFS have been found to have a similar litter size with the Japanese field mouse (*Apodemus argenteus*) (Nakata, 1986; Shibata & Kawamichi, 2009) that is ubiquitous in the mountains of Japan, and the largest among gliding mammals (Goldingay, 2000; Hayssen, 2008). Despite its high reproductive potential, JFS populations are threatened with extinction in many parts of Japan, and the survival rate of adults and offspring remains unknown. Despite the fact that mammals are exposed to terrestrial, arboreal, and aerial predation on the ground, they are only at risk of arboreal and aerial predation in trees. As a result, predation risk in trees is thought to be lower than on the ground (Campos & Fedigan, 2014). Consequently, the population growth rate of JFS, which has a comparable litter size to the field mouse, is not believed to be significantly reduced.

Despite the unknown food contents of JFS, it appears to be more adapted to folivory than SFS, which is widely distributed across urban forests and mountainous areas in Hokkaido. JFS inhabitation appears to be largely unrestricted by food abundance, though not to the same extent as GFS. However, JFS does not inhabit areas with solely Japanese cedar plantations (Suzuki et al., 2008). It is likely that broad-leaved forests are important food resources, and that food plants are necessary within the habitat. Therefore, it is imperative to investigate the food contents of JFS as soon as possible. Although inhabitation of JFS may be locally limited by a lack of food resources, monospecific forest environments such as plantations exist in patches, but never in large areas of mountains, so it is unlikely to be the primary reason for the lack of habitat.

It is evident that the JFS heavily relies on plantations for nesting sites and gliding locomotion. Also, given the clear increase in resting time during the winter, nest materials of Japanese cedar bark with high heat retention would be important for their overwintering. I consider this will be an important aspect of habitat conservation for JFS which currently insufficient conservation practices could be improved. 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. Additionally, given the glide ratio of JFS is estimated to be 1.8, as for the SFS (Suzuki, Asari & Yanagawa, 2012; Suzuki & Yanagawa, 2019), the trees should be felled in a manner that does not create a gap exceeding 1.8 times of the tree height at the edge of the forest.

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, Berndt & Jactel, 2005; Brockerhoff et al., 2008; Barbaro et al., 2009; Berndt, Brockerhoff & Jactel, 2009). For reasons of human economics, it is impossible to eliminate plantations altogether. Therefore, recently, management regimes of plantations that promote biodiversity have garnered great international interest for conservation of endangered species (Castano-Villa et al., 2019; Gadoth-Goodman & Rothstein, 2020; Jamhuri et al., 2020; Wang et al., 2022). My review implies that coniferous plantations with native broad-leaved trees are suitable habitats for endangered flying squirrels. Ultimately, I hope that this paper will be beneficial for conservation efforts of JFS habitat in plantations.

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Table 1. Environments of habitat of Japanese flying squirrel

Prefecture	Year	Elevation (m)	Method	Tree species	References
Aomori	1976 to 2016	270 to 300	Direct observation	Tdo, broad leaved trees	Sasamori and Mineshita (2019)
Aomori	1995	-	Direct observation	Crj, broad leaved trees	Sasamori and Mineshita (2019)
Aomori	2002	-	Feces	Tdo	Sasamori and Mineshita (2019)
Aomori	2005	-	Nest box	Crj	Sasamori and Mineshita (2019)
Aomori	2013 to 2017	190	Direct observation	Tdo, broad leaved trees	Sasamori and Mineshita (2019)
Fukushima	2002 to 2004	350 to 700	Feces	Crj, Pd, broad leaved trees	Iwasaki and Takahashi (2005)
Fukushima	2004	1850	Camera trapping	Am	Iwasaki and Takahashi (2005)
Fukushima	2004	740	Direct observation	-	Yasuda and Yagihashi (2004)
Fukushima	2005	600 to 1000	Camera trapping	Crj, Fc, Qc, At	Iwasaki (2012)
Fukushima	2005	820 to 1200	Direct observation and feces	Crj, Fc, Qc	Iwasaki and Takahashi (2005)
Fukushima	2005	680 to 750	Direct observation and feces	broad leaved trees	Iwasaki and Takahashi (2005)
Tokyo	-	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)

Table 1. Environments of habitat of Japanese flying squirrel (continued)

Prefecture	Year	Elevation (m)	Method	Tree species	References
Tokyo	2010	240	Direct observation	Crj, Co, Zs, Cca, Cerasus sp., Caj, Ap	Okazaki (2012)
Kanagawa	1995	-	Direct observation and Nest box	Af, Crj, Co, Broad leaved trees	Yamaguchi (1997)
Kanagawa	2001	500	Nest box	-	Yamaguchi et al. (2004)
Kanagawa	2004	650 to 750	Nest box	Crj, Co, Qse, Qa	Ookubo and Ando (2005)
Kanagawa	2005 to 2008	560 to 850	Camera trapping	Crj, Co, Fc, Qse, Af	Suzuki and Ando (2019)
Tochigi	1991 to 1993	650 to 950	Nest box	Fc, Qc	Sato (1997)
Tochigi	1991 to 1993	990 to 1080	Nest box	broad leaved trees	Sato (1997)
Tochigi	1991 to 1993	1160 to 1450	Nest box	Fc, Td	Sato (1997)
Yamanashi	1981	800	Nest box	Qc, Qse	Ando (2005)
Yamanashi	2007 to 2008	1350 to 1600	Camera trapping	Fc, Qc, Bp, Ah	Suzuki and Ando (2019)
Yamanashi	2008	1074 to 1399	Camera trapping	Broad leaved and coniferous trees	Matsubayashi et al. (2009)
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)

Table 1. Environments of habitat of Japanese flying squirrel (continued)

Prefecture	Year	Elevation (m)	Method	Tree species	References
Fukui	1995	140	Direct observation	Crj, Co, Qm, Ns	Yanagawa et al. (1996)
Toyama	1997	1180	Direct observation	Fc	Murayama and Nambu (1998)
Nagano	2016	1480 to 2470	Nest box and camera trapping	Qc, Be, Av, Am	Kikuchi and 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	-	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)

Table 1. Environments of habitat of Japanese flying squirrel (continued)

Prefecture	Year	Elevation (m)	Method	Tree species	References
Ehime	-	1000	Direct observation	Crj, broad leaved trees	Yano (2009)
Ehime	1983 to 1985	1100 to 1325	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	-	Direct observation	broad leaved trees	Yano (2009)
Ehime	1999	400 to 500	Direct observation	-	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	1030	Nest box	Fc, Qac, Sm, Acer sp.	Furukawa and Miyamoto (2010)
Ehime	2009 to 2010	650	Nest box and camera trapping	Crj, Co, Zs, Qs, Acer sp., Pr	Yano (2009)
Tokushima	1996	1100	Direct observation	-	Kawamichi (2009)
Tokushima	2007	730	Direct observation	-	Kawamichi (2009)
Kochi	2007	600 to 840	Direct observation	-	Kawamichi 2009)

Table 1. Environments of habitat of Japanese flying squirrel (continued)

Prefecture	Year	Elevation (m)	Method	Tree species	References
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	1000 to 1607	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	900	Camera trapping	Pd, broad leaved trees	Yasuda and Kurihara (2009)

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*; 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 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*

Table 2. Measurements of Japanese flying squirrels in norther and central areas of Japan

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

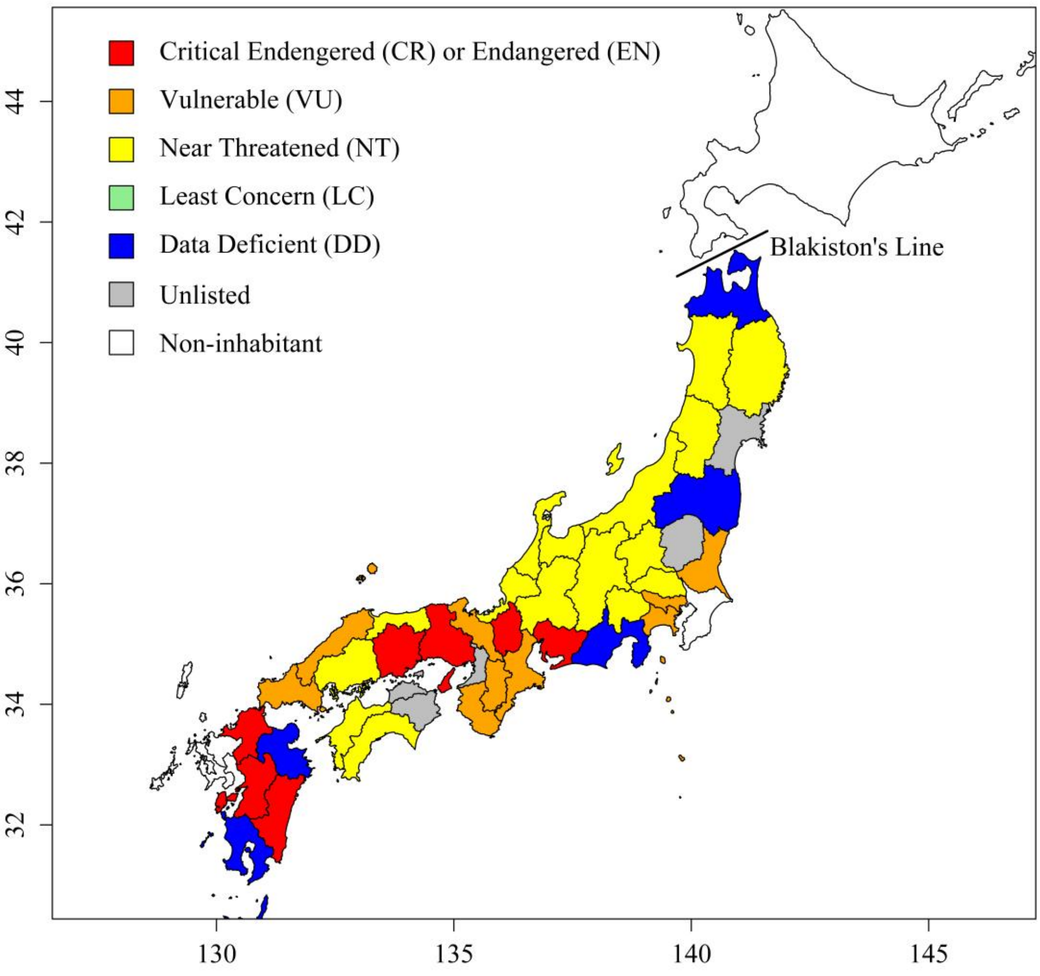

Fig. 1. Prefectural red list rank of Japanese flying squirrel (JFS) in Japan. Since some prefectures do not distinguish between Critical Endangered and Endangered, the color of both ranks is unified here. There is no prefecture that ranked JFS as Least Concern.

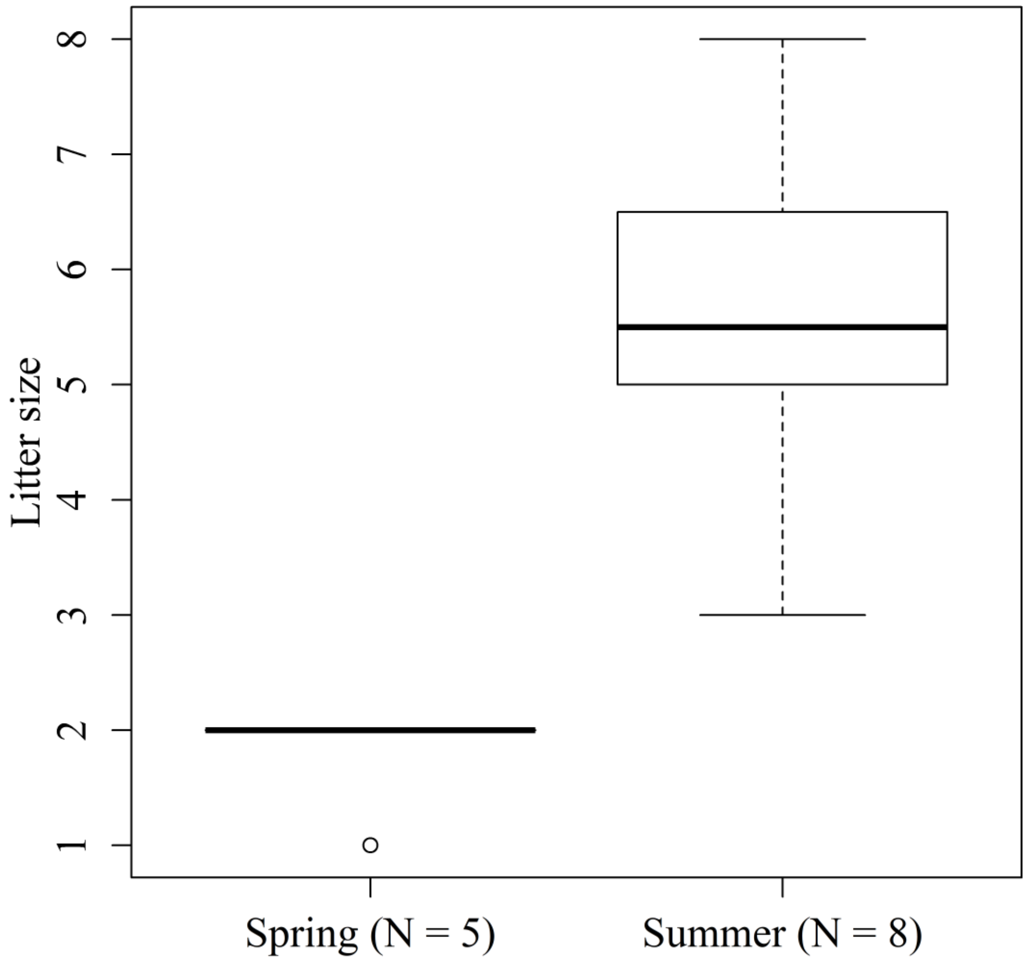

Fig. 2. Boxplot showing seasonal changes in litter size of Japanese flying squirrel.