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Distribution and management of non-native squirrels in Japan

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Three species of alien squirrels have been confirmed to have been introduced in Japan: *Tamias sibiricus, Callosciurus erythraeus* (including the species complex *C. finlaysonii*), and *Sciurus vulgaris*. Japan is home to endemic squirrel species *S. lis, Petaurista leucogenys*, and *Pteromys momonga*, as well as endemic subspecies *S. vulgaris orientis*, *T. sibiricus lineatus*, and *Pteromys volans orii.* It is important to address the issue of damage to ecosystems caused by alien species, including the conservation of endemic species. Chipmunks (*T. sibiricus*) have become established in at least 11 of 47 prefectures, but no measures have been taken because the damage is not yet apparent. Pallas's squirrels (*C. erythraeus*) that were reared in petting zoos for tourism purposes escaped and have become established in at least 17 localities in 13 prefectures. Because of the high population densities and significant damage caused by this species, removal measures have been implemented in at least 12 locations. The species is now eradicated or near eradication in four locations. Eurasian red squirrels (*S. vulgaris*) have become established at two sites in central Honshu and Kyushu. Due to possible hybridization with the Japanese squirrel (*S. lis*), trapping began in 2014 with the aim of eradication. This review summarizes the measures taken in Japan to conserve endemic species and emphasizes the importance of the involvement of researchers in early action.

KEYWORDS

***Callosciurus erythraeus*, endemic species, Japan, *Sciurus vulgaris*, management**

1. Introduction

Japan is located at the eastern end of the Asian continent and consists of about 6,800 islands that are home to a large number of endemic species. Excluding exotic species, there are 110 species of terrestrial mammals, of which 40% are endemic (Abe et al., 2008). Three Sciuridae species in Japan are endemic species, the Japanese squirrel (*Sciurus lis*), the Japanese giant flying squirrel (*Petaurista leucogenys*), and the Japanese flying squirrel (*Pteromys momonga*), distributed on Honshu, Shikoku, and Kyushu Islands. The Eurasian red squirrel (*S. vulgaris orientis*), the Siberian chipmunk (*Tamias sibiricus lineatus*), and the Siberian flying squirrel (*Pteromys volans orii*) are endemic subspecies distributed only on Hokkaido Island (Figure 1). The abundance and occupancy of these endemic species in Japan has reached a critically low level in some areas. The Japanese squirrel has not been observed in Kyushu for the past

100 years and is likely extinct (Figure 1A; Yasuda, 2007). In 14 prefectures, especially in western Honshu, the Japanese squirrel has only a small distribution area and even if it is present, its density is extremely low, so it is designated as a regionally endangered species (Figure 1A; Tamura et al., 2007). The Japanese flying squirrel is considered endangered in most of the prefectures in Japan (Figure 1B; Yasuda, 2007; Suzuki et al., 2011). The Japanese giant flying squirrel is also categorized as a regionally endangered species in Kyushu (Figure 1C; Yasuda, 2007).

Similar to previous reports from other countries (e.g., Bertolino and Genovesi, 2005; Palmer et al., 2007; Bertolino, 2009; Bertolino and Lurz, 2013; Guichón et al., 2020; Mazzamuto et al., 2021), alien squirrels are intentionally or accidentally released in Japan, causing various problems. However, as most reports are written in Japanese, the situation is not well known beyond Japan. This article summarizes the measures taken in Japan, where there is a need to conserve endemic species, with the aim of publicizing the Japanese situation to the world and obtaining solutions to this universal problem.

2. Background of alien squirrels in Japan

There are three species of non-native squirrels known to inhabit Japan (Ministry of the Environment, Government of Japan, 2021): Pallas's squirrel (*Callosciurus erythraeus*), Siberian chipmunk (*Tamias sibiricus*), and Eurasian red squirrel (*Sciurus vulgaris*). A fourth non-native squirrel species, the Finlayson's squirrel (*Callosciurus finlaysonii*) and hybrids with the Pallas's squirrel have also been identified in Japan (Oshida et al., 2007; Kuramoto et al., 2012). However, the Finlayson's squirrels are included in the Pallas's squirrels in this paper because recent genetic studies have shown that they are conspecifics, and part of the same species complex (Boonkhaw et al., 2017; Balakirev and Rozhnov, 2019). The distribution for each species as of 2022 are shown in Figure 2. We first address the initial establishment of these alien squirrel species in various parts of Japan and then we present the problems caused by each non-native squirrel species.

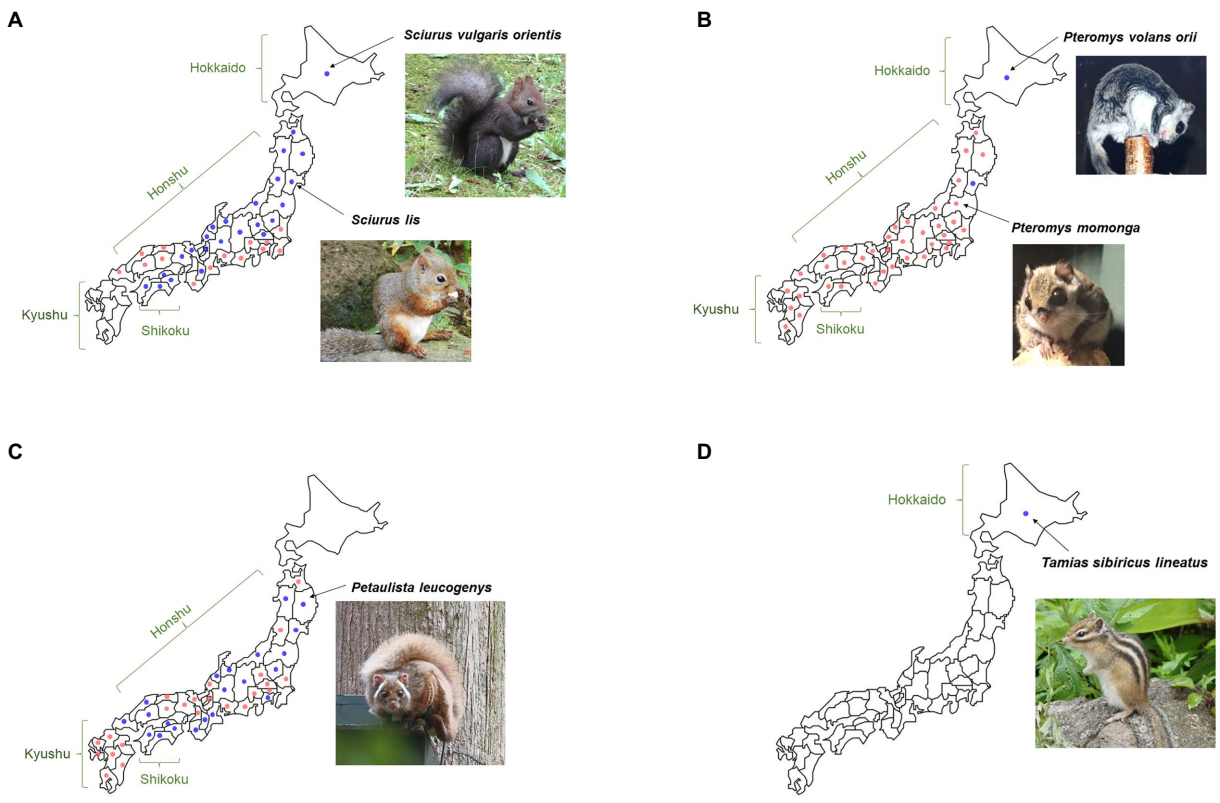

FIGURE 1
Distribution of the endemic species of squirrels in each prefecture. Blue circles indicate species that occur at normal densities in the prefecture, pink circles indicate those that are assessed as having low abundance and are listed on the Red List (Red List Data Search System, 2022). There are common criteria for the preparation of the Red List of mammals in each prefecture (Ministry of the Environment, Government of Japan, 2022). Information on the present status on each assessed species is collected from existing literature, documents, expert knowledge, and the results of field surveys. **(A)** Two species of arboreal tree squirrels, *Sciurus lis* and *S. vulgaris orientis*, **(B)** two species of flying squirrels, *Pteromys momonga* and *P. volans*, **(C)** the giant flying squirrel *Petaurista leucogenys*, and **(D)** the chipmunk, *Tamias sibiricus lineatus*.

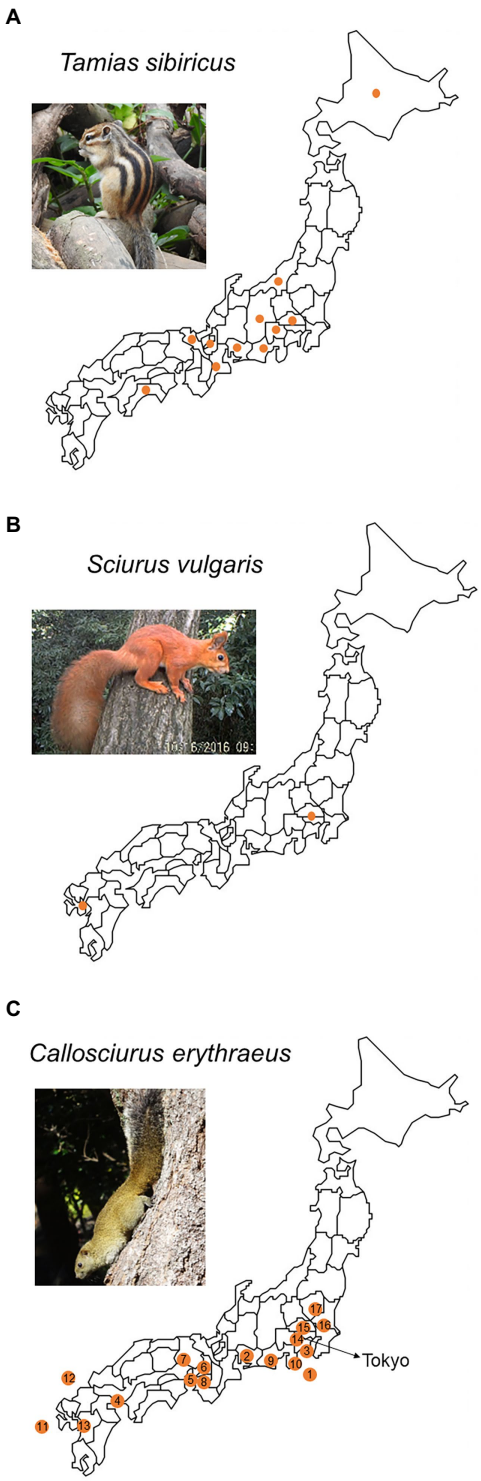

FIGURE 2
Distribution of nonindigenous squirrel species in Japan. Orange circles indicate that the species is present in the prefecture. **(A)** *Tamias sibiricus* is recorded in 7 prefectures including Hokkaido. **(B)** *Sciurus vulgaris* is recorded in Sayama Hills (border of Tokyo and Saitama Prefecture) and Nagasaki Prefecture. **(C)** *Callosciurus erythraeus* is recorded in 13 prefectures (the number corresponds to those in Table 1; Shikoku Institute of Natural History, 2002; Fukue, 2005; Mammal Society of Japan, 2017; Shiga Prefecture, 2019; Kyoto Prefecture, 2022).

With the exception of Hokkaido, there are only a few areas in Japan where native squirrels can be observed. Consequently, squirrels are not familiar animals to the general public. From around 1960, many people in Japan traveled abroad and saw squirrels in parks, which may have led to a longing for Japanese parks inhabited by squirrels (Shigeoka, 1964). This may have been partly responsible for the introduction of nonindigenous squirrels into tourist sites in various regions in Japan (Abe, 1985).

Pallas's squirrels were first reared in Japan in the 1930s. A zoo was built as a tourist facility on Izu Oshima, a remote island near the capital city of Tokyo. Pallas's squirrels were introduced from Taiwan, but a typhoon in the 1930s destroyed the breeding cages, and squirrels became established throughout the island (Udagawa, 1954). In 1936, Pallas's squirrels escaped from an exposition in Gifu City, and the first 'squirrel village' in Japan was established in 1965 to use squirrels as a tourism resource (Gifu City, 2022). This was followed by an increasing number of 'petting zoos,' similar facilities where visitors can interact with animals and hand-feed them. In particular, Pallas's squirrels, which are easy to keep, were casually bred at tourist attractions in various regions (Table 1). Unlike official zoos, which are well-equipped and staffed with breeding and care specialists, squirrels frequently escaped from these tourist areas (e.g., Yasuda, 2010; Amano, 2015). Such tourist facilities often failed in business, and in many cases, squirrel breeding was abandoned (Table 1).

Japanese people began keeping squirrels as pets in their homes mainly after 1960 (Ishibashi, 2007), and the majority of these squirrels were Siberian chipmunks imported from Korea or China (Ohono, 2022). Chipmunks became established in at least 11 prefectures on Honshu and Hokkaido Islands (Figure 2A). Pallas's squirrels have also been kept by individuals since around the 1960s. Furthermore, a pet boom began in 1980, with various species of squirrels including Eurasian red squirrels being sold in pet shops (Yanagawa, 2000). Eurasian red squirrels of continental origin became established in at least two regions on Honshu and Kyushu Islands (Figure 2B). In 2005, the Ministry of the Environment of Japan established the Invasive Alien Species Act, designating the Pallas's squirrel, the Eurasian red squirrel, and the eastern gray squirrel (*Sciurus carolinensis*) as invasive alien species and prohibiting their import, trade, breeding and transportation (Ministry of the Environment, Government of Japan, 2021). The Siberian chipmunk was not designated as an invasive alien species, but was placed in the category of species for which priority measures are being taken due to its potential impact on the ecosystem (Ministry of the Environment, Government of Japan, 2021).

The ecological and agroforestry damage caused by the Siberian chipmunk is not yet reported in Japan. Human infection with the agent of *Lyme borreliosis* and competition with native squirrels and dormice has been speculated in other countries (Mori et al., 2018). On Honshu, where semi-arboreal chipmunks were originally absent, ecological impact can be expected in species with a similar ecological niche, such as the Japanese dormouse (*Glirulus japonicus*) and the small Japanese field mouse

TABLE 1 Locations where Pallas's squirrels *Callosciurus erythraeus* have established in Japan and the measures implemented until 2022.

Location	Year naturalized	Possible cause of introduction	Initial population size	Categories of measures divided by Mammal Society of Japan (2017)	Measures implemented	Present situation	References
Izu Oshima Island, Tokyo	1935	Escaped from the zoo	More than 100,000	1: Damage reduction	Pest control	High density	Udagawa (1954) and Tokyo Metropolitan Government (2021)
Kinkazan, Gifu Castle, Gifu	1936	Escaped from the expo cage	Unknown	4: Survey/ eradication	No	High density	Gifu City (personal communication)
Southeast Kanagawa	1948	Escaped from the zoo/the house pet	More than 100,000	2: Expansion control	Pest control	High density, expanding	Ono (2001) and Mammal Society of Japan (2019)
Takashima Island, Oita	1954	Released	*ca.* 1,000	3: Eradication	Eradication measure	Almost eradicated	Yasuda (2021)
Tomogashima Island, Wakayama	1954	Released	Unknown	1: Damage reduction	On survey	High density	Setoguchi (1984), Wakayama Prefecture (personal communication)
Osaka Castle, Osaka	1970s	Released	Unknown	4: Survey/ eradication	No	Unknown	Osaka City (personal communication)
Himeji Castle, Hyogo	1970	Released	Unknown	4: Survey/ eradication	No	Unknown	Iwasaka and Tanigawa (1981), Himeji City (personal communication)
Wakayama Castle, Wakayama	1970s	Escaped from the zoo	Unknown	4: Survey/ eradication	On survey	Unknown	Wakayama Prefecture (personal communication)
Hamamatsu Castle, Shizuoka	1970s	Escaped from the zoo	*ca.* 10,000	2: Expansion control	Eradication measure	High density, expanding	Suzuki and Torii (2016) and Hamamatsu City (2022)
Izu Peninsula, Shizuoka	1980	Escaped from the tourist facilities	Unknown	2: Expansion control	Pest control	Expanding	Ohba (2006)
Fukue Island, Nagasaki	1990s	Escaped from the tourist facilities	*ca.* 10,000	1: Damage reduction	Pest control	High density	Yasuda (2017)
Iki Island, Nagasaki	1990s	Escaped from the tourist facilities	*ca.* 50,000	1: Damage reduction	Pest control	High density	Yasuda (2017)
Uto Peninsula, Kumamoto	1990s	Escaped from the tourist facilities	*ca.* 5,000	3: Eradication	Eradication measure	Almost eradicated	Yasuda (2017)
Akiruno, Tokyo	2000	Unknown	15	3: Eradication	Eradication measure	Almost eradicated	Akiruno City (2014)
Iruma, Saitama	1990s	Released	70	3: Eradication	Eradication measure	Almost eradicated	Kasahi et al. (2014)
Bando, Ibaraki	1990s	Escaped from the tourist facilities	*ca.* 100	3: Eradication	Eradication measure	Expanding	Takeuchi et al. (2015) and Bando City (2022)
Mooka, Tochigi	2021	Escaped from the tourist facilities	Unknown	3: Eradication	Eradication measure	Unknown	Mooka City (personal communication)

See text for the four management strategies classified by Mammal Society of Japan (2017).

(*Apodemus argenteus*) as reported in Europe (Fukue, 2005). Another concern is the hybridization with native subspecies, *Tamias sibiricus lineatus,* that inhabit Hokkaido (Oshida and Yanagawa, 2002).

The Eurasian red squirrel is also a concern for genetic introgression into the closely related Japanese squirrel, a close congener (Oshida et al., 1996, 2009). In addition, because a native subspecies of the Eurasian red squirrel lives in Hokkaido, their genetic endemism might be lost if they interbreed as was well documented in the United Kingdom (Hale et al., 2004). Hybridization between closely related species or subspecies is difficult to distinguish based on appearance; thus, study of the genetics of these populations is necessary. However, there has been no budgetary support by the government.

Although Pallas's squirrels have no genetic hybridization potential with native Japanese species, they cause considerable damage due to their high population densities. Agricultural and forestry damage has been reported for fruits (citrus, persimmons, grapes, loquats, camellia), field crops (radishes, cabbages, spinach, and onions), mushroom cultivation, and plantation trees in Japan (Fushimi, 1989; Torii, 1993; Ayukawa et al., 2005; Amano et al., 2010; Torii et al., 2010; Yasuda, 2010, 2013; Shigeta et al., 2014) and in other countries (reviewed by Bertolino and Lurz, 2013; Mazzamuto et al., 2021). The squirrels lick the sap for sugar, peel off the bark for nesting material, and scrape off the bark to feed on the insects (Okubo et al., 2005; Tamura and Ohara, 2005). This results in the loss of trees and associated landslides in natural forests, as well as the risk of falling dead branches gnawed by squirrels in urban parks (Hamamatsu City, 2022; Hayama Town, 2022). Bark stripping by the Pallas's squirrels has been reported in Taiwan, its original habitat (Chang, 1976; Kuo, 1982), as well as in other countries where the species has been introduced (Adriaens et al., 2015; Mori et al., 2016; Pedreira et al., 2020). In the city center, telephone lines and fiber optic cables were gnawed, causing damage that interrupted the telephone service in Japan (Fushimi, 1989; Ono, 2001), Argentina (Guichón et al., 2005) and Belgium (Adriaens et al., 2015). However, damage to ecosystems is not yet fully understood in Japan. Previous reports have indicated that the squirrels forage on bird eggs, which may affect bird populations (Azuma, 1998; Seki and Yasuda, 2018). In addition, their behavior of feeding on adult and larval wasps has raised concerns about their impact on insects (Asahi and Watanabe, 1967; Tamura et al., 1989; Shimizu and Nakamura, 2003). The direct impact of Pallas's squirrels on the endemic Japanese squirrels has not been investigated in Japan. On the Izu Peninsula in Shizuoka Prefecture, where the species are sympatric, the population of the Japanese squirrel has been too small to detect an impact of Pallas's squirrels. However, there is evidence of the ability of invasive Pallas's squirrels to compete with and negatively affect native squirrels as reported in Italy (Mazzamuto et al., 2017a,b).

3. Involvement of researchers

Even after 2005, when nonindigenous squirrels were designated as an invasive alien species by the Ministry of the Environment, the public was less aware of squirrels as an invasive alien species than raccoons (*Procyon lotor*) and mongooses (*Urva auropunctata*). In response, squirrel researchers explained to the governments the need to control non-native squirrels. In 2017, the Mammal Society of Japan submitted a written request to the relevant ministries advising them of the national control goal for Pallas's squirrels. Included was a list of the sites where Pallas's squirrels were established, the goals for each site, and the measures to achieve these goals (Table 1; Figure 2C; Mammal Society of Japan, 2017). Within the current budget, the number of individuals that can be captured annually by the local administration is around 2000 individuals (Mammal Society of Japan, 2017). Based on population studies, the number of individuals removed by such capture effort is of about 10,000 individuals (Tamura, 2004). Considering the number of Pallas's squirrels, the degree of impact on native ecosystems, and the feasibility, the management strategies were classified into four categories: (1) on small islands where there were no endemic species, the populations would be reduced for the purpose of damage reduction; (2) in areas where the population exceeded 10,000 and immediate eradication would not be possible, the expansion of distribution would be suppressed and invasion into natural forests prevented; (3) in areas where the number of animals was fewer than 10,000 and the ecological impact was significant, eradication should be targeted; and (4) in areas where the establishment status is unknown, surveys should be conducted as soon as possible to determine the distribution area and one of the previous strategies implemented dependent on population estimates.

Citizens and government officials cannot easily distinguish between non-native and native species and are unaware of the damage that squirrels cause to ecosystems, agriculture, and forestry. The efforts of squirrel and invasive species experts to connect to the government through the Science Council have been very effective to initiate measures against invasive squirrel species that otherwise would not have been taken. This paper presents four examples of cases where researchers were involved and appropriately moved toward eradication. The first case study is the eradication of the Pallas's squirrel on the Uto Peninsula, Kumamoto Prefecture, Kyushu, Japan (Mammal Society of Japan, 2010). This is the first involvement of researchers (the author Masatoshi Yasuda included) in the control of alien squirrels. The details are given below (see Section 4.1). The second case was on a small desert island, Takashima Island of Oita Prefecture, where no native mammals occur. In addition to the usual trapping methods, a new attempt using chemical control was successful (see Section 4.2). The third case of eradication was a small population of Pallas's squirrel in the suburbs of Tokyo. This case study shows that by including experts, small populations can be eradicated by volunteers with minimal cost (see Section 4.3).

The Mammal Society of Japan also submitted a request for early eradication measures for the Eurasian red squirrel to prevent gene introgression for Japanese squirrels (Mammal Society of Japan, 2013). This request was accepted by the Ministry of the Environment and became one of the few examples in Japan of a precautionary measure taken against invasive alien species before a problem arises (see Section 5).

4. Control projects for Pallas's squirrels

4.1. First attempt on Uto Peninsula, Kumamoto

Pallas's squirrels that established on the Uto Peninsula, Kumamoto, Kyushu had escaped from one of the tourist facilities that opened in 1993 (Yasuda, 2010; Amano, 2015). The invasion and dispersal routes of alien Pallas's squirrels in the Kyushu region were as follows: First, Pallas's squirrels increased in number on Izu Oshima Island, Tokyo, and in 1988, they were brought from Izu Oshima to the Unzen Squirrel Village, Kyushu to be used for tourism. When the facility was temporarily closed in 1992–1994 due to the eruption of Mount Unzen-Fugendake, the squirrels were transferred to several tourist facilities in Kyushu (Yasuda, 2010, 2017).

According to local residents, squirrels first appeared in 1998 and the first signs of them feeding on grapes and fruits were reported in 2004. Because fruit production is a major factor in this region, local governments (prefecture and two cities involved) started a population control action near agricultural lands under the Wildlife Protection and Proper Hunting Act in June 2009 and then launched an eradication program of the alien squirrels under the Invasive Alien Species Act in April 2010. One of the authors, Masatoshi Yasuda, has been involved in this eradication program as a scientific adviser. In March 2010, the number of feral alien squirrels occurring in the Uto Peninsula was estimated by one of the authors, Noriko Tamura, as *ca.* 5,000 individuals based on a confirmed distribution area of *ca.* 25 km^2, which accounted for 28% of the total area of the peninsula (Amano et al., 2010). Surprisingly this distribution survey was carried out by students and a teacher in a public high school as an extracurricular activity.

To capture the squirrels, cage traps were tightened on trees 1.5 m aboveground and baited with an attractant (Yasuda, 2010). Bait varies from region to region, but in Kyushu, chestnuts were used year-round. Captured animals were euthanized with an overdose of carbon dioxide according to guidelines of the Ministry of the Environment, Government of Japan (2021). On the fiscal year basis (April–March), the annual number of squirrels removed changed as shown in Supplementary Figure S1, suggesting squirrel density decreased successfully. In the first phase from 2010 to 2011, an incentive (800 yen per animal) strongly promoted trapping activity by local skilled hunters and farmers. The second phase started in autumn 2011, when the UKB (Uto-hanto Kurihararisu Busters), a government hunter team against alien squirrels, was established by local governments. The UKB, consisting of four persons, was expected to promote trapping activity in forests away from agricultural land, the population source of alien squirrel. The Uto Peninsula was divided by 1 km × 1 km grid design for trapping. One of the authors, Masatoshi Yasuda, calculated monthly catch-per-unit effort (CPUE) of each compartment based on the activity reports from UKB and discussed the eradication program with UKB and local government officers. This working group meeting was held monthly for the first 2.5 years of the second phase. The third phase started in 2018 and is still ongoing. We call it 'seek-and-trap' phase. As population density of Pallas's squirrel was getting lower and lower, UKB found detecting squirrels difficult. To solve this problem, we developed a new detection device that consists of two chestnuts (attractant bait) and two orange ping pong balls (inedible but visually attractive) tied to a standing tree with a wire (Supplementary Figure S2). Camelia oil was sprayed on the chestnuts (olfactory attractant). This attractant device was patrolled at regular intervals and once the food was eaten, a cage trap was set up. The 'seek-and-trap' method is effective to reduce remaining population of alien squirrels at low density (Yasuda, unpublished). This approach to the eradication has led to the removal of a medium-size population (up to 5,000 individuals) in a peninsular landscape in 15 years, for a cost of at least 100 million yens.

Yasuda (2017) lists several factors that contributed to the successful eradication of Pallas's squirrels. The first is the importance of academic engagement in the initial response. In December 2008, the presence of Pallas's squirrels was first publicly confirmed by the members of a high school biology club in Kumamoto Prefecture (Amano, 2015). This information was shared with a local group of naturalists and led to subsequent surveys. Second, the establishment of a council involving government agencies and researchers to promote measures in early 2010 was important. Subsequently, a control system was organized and implemented, and the plan was reviewed from a scientific viewpoint based on the results of captures (Yasuda and Amano, 2011). The researchers proposed changes to the trapping regime based on the calculation of capture efficiency adapting from an incentive scheme to a government hunter scheme (Yasuda, 2014). Third, the academic society pushed the administration for continued efforts. The Mammal Society of Japan submitted requests for management efforts in 2010, 2013, 2016, and 2019, specifying the necessary actions. Last but not least was public awareness. Through newspapers and lectures, a better understanding of the impact of alien squirrels was fostered, which helped minimize the negative reactions to the control project.

In nearly 14 years since the population of Pallas's squirrels was officially confirmed at the end of 2008, 6,115 animals were captured and the population is nearly eradicated (Wildlife Statistics provided by Kumamoto Prefecture). Among the captured animals, 3,112 were caught in 2010 just after the council

was initiated and the incentive scheme was started. The experience of controlling Pallas's squirrels on the Uto Peninsula included learning many methods and systems that can be applied to similar challenges in other areas. Monitoring must continue before a declaration of eradication can be issued, and efforts are still underway to make this one of the few successful cases of eradication of a population that had grown to over 5,000 animals.

4.2. Trial of new eradication methods on a remote island 'Takashima'

The Pallas's squirrel was introduced as a tourist attraction in Takashima Island, a 1 km^2 island in Oita Prefecture, by local government in 1954 just after the island became uninhabited (Yasuda and Morita, 2021). Since then, no control actions had been performed in Takashima Island, though peoples recognized the alien squirrel population increased in density and squirrels started to severely damage trees. Seki and Yasuda (2018) clearly showed that the Pallas's squirrel was an effective predator of bird eggs by an artificial nest experiment on Takashima Island. This study highlighted that the eradication of the alien squirrel population was essential to restore the natural ecosystem of Takashima Island, a part of the Setonaikai National Park. In 2018, one of the authors, Masatoshi Yasuda, started a research project of Pallas's squirrel eradication on Takashima Island under the Invasive Alien Species Act and the Wildlife Protection and Proper Hunting Act. The project was financially supported by Japan Government and was greatly helped by local naturalists and government officers. To shorten the expected period to the eradication, we employed two different types of population control methods: trapping and chemical control. Ordinary cage-traps were mainly used from spring to autumn, and humane kill-traps with automatic recovery system (A18, goodnature, New Zealand) were mainly used in winter. The number of trap sites was 48 in the first trapping session of autumn 2018 and later increased to 118 in spring 2022. The total number of trapped squirrels was *ca.* 1,600 in 5 years.

Chemical control was performed after the density of alien squirrel population became low, with permissions from the Ministry of the Environment and Oita Prefecture, in consecutive years. Pellets containing 0.005% diphenadione (a US-EPA registered first-generation rodenticide) were used. A total of 116 nest-box-type bait stations containing 500 g of diphenadione pellets were installed on tree trunk in winter 2021/2022. With the use of chemical control, the catch-per-unit effort (CPUE) of Pallas's squirrel per 100 trap-days dropped from 14 in autumn 2021 to 0.45 in spring 2022 (Yasuda, unpublished). We considered that chemical control in winter is effective because it is a season of lowest food availability for squirrels. Now we can say that it is possible to eradicate a small population of Pallas's squirrel (*ca.* 1,000 individuals) on an island, but it will take five years and more and cost 10 million yens under certain circumstances. This case was a first trial run of intensive population control of alien squirrels using diphenadione in Japan, though diphenadione has been applicable to rats and mice as agriculture and forestry pests since 1976. In remote islands where there are not native mammals that could be affected, a combination of trapping and chemical control is recommended.

4.3. Eradication of small populations by volunteers in the suburbs of Tokyo

In March 2011, a Pallas's squirrel was confirmed at a golf course in Iruma City, Saitama Prefecture (Kasahi et al., 2014). This was the first confirmation of this species in Saitama Prefecture. It was believed to have originated from free-ranging Pallas's squirrels on the university campus adjacent to the golf course in the 1990s. In July 2011, squirrel researchers (including the author Noriko Tamura), staff of private wildlife research company, and government officials formed the Iruma-Mizuho Squirrel Control Group and conducted a voluntary distribution survey and capture of squirrels. First, the distribution was assessed by means of distinctive field tracks, interviews with residents, and direct observation. In addition, a new method was developed that attracted squirrels by playing back their distinctive vocalizations (Tamura et al., 2013). This sound playback method was used effectively to determine the distribution in Hamamatsu, Shizuoka Prefecture (Suzuki and Torii, 2016), and the method became widely used for distribution surveys of this species conducted by the government in Kanagawa, Ibaraki, Tochigi, Tokyo, and elsewhere.

The results of the survey showed that the squirrels were not confined to the golf course, but also inhabited five surrounding woodlands. The trapping campaign, using cage traps and peanuts as bait, began in December 2011 and a total of 71 squirrels (51 in the golf course and 20 in the surrounding woodland) were capture over 6 years. Attempts have been made to confirm their presence using camera traps and sound playback surveys up to 2022, but the species has not been documented since 2017. However, eradication has not yet been declared, following one sighting by a citizen in 2021. Squirrels are small and difficult to identify; detection is a challenge in evergreen woodland where visibility is poor. We believe that further surveys are necessary to prove that eradication has been achieved. Fecundity has been measured from the data of 71 captured individuals. Placental scars showed that 26% of the females were pregnant and the average litter size was 1.3 (Yamasaki et al., 2013), comparable to or lower than in the original habitat (T'sui et al., 1982) and other introduced sites (e.g., Tamura, 1999; Santicchia et al., 2015). These values can be used to calculate the rate of population increase if there are remaining individuals and researchers continue to monitor the forests for squirrels to evaluate the likelihood of eradication based on that estimate.

This initiative is one of the few examples of voluntary work conducted by researchers and volunteers with expertise on squirrels. The cost of the measures was covered by local private

funds and a small budget from the local administration. In addition to the research group members, free help came from university students and landowners. The key reasons for success of this case study were (1) experts lived in the area, thus eliminating transport costs for the measures, and (2) the process from discovery to capture was expedited by the intervention of experts. The distribution survey and trapping techniques developed in this project can be easily conducted by local citizens. In the future, the techniques developed in this project should be shared so that the measures can be implemented at a low cost by volunteers in each region.

5. Control projects for Eurasian red squirrels

In 2000, the Eurasian red squirrel (*Sciurus vulgaris*) was reported in the isolated woods of Sayama Hills (~35 km^2), on the border between Tokyo and Saitama Prefectures, central Honshu. Although present in the surrounding mountains 5 km distant (Kasahi, 2011), no reliable record of the Japanese squirrel (*S. lis*) from Sayama Hills exists. Sightings of squirrels increased from the 1980s to the 1990s in Sayama Hills (Shigeta et al., 2000; Nakazawa, 2001), and DNA analysis revealed that it was the Eurasian red squirrel (Shigeta et al., 2000). One of the authors, Noriko Tamura, submitted a report to the Mammal Society of Japan on the 'Problem of Eurasian red squirrels in the Sayama Hills' and requested that immediate action to be taken. In November 2013, the request was submitted by the president of the Mammal Society of Japan to the Minister of the Environment, Japan. In May 2014, the Ministry of the Environment launched the 'Sayama Hills Red Squirrel Control Model Project for the Promotion of the Control of Specified Invasive Alien Species.'

The surveys included three methods: searching of their feeding signs, collecting information on sightings by citizens, and monitoring with wildlife cameras. Cage traps were placed at sites where the surveys indicated that squirrels were likely to be present and baited with walnuts. By conducting 17 trapping operations over a total of 54 days during a period of 3 years, 32 squirrels were captured at 12 sites (Tamura et al., 2017). After 4 years of capture, no trace or information has been found since 2018, and no photographs have been taken by the cameras. However, a sighting by a citizen in 2022, despite the lack of formal evidence, prohibits declaration of eradication.

Based on data on the population dynamics of red squirrels in deciduous woodland in north Belgium (Wauters and Dhondt, 1995), future population increase was estimated assuming that one pregnant female remained. Based on this projection, in 10 years, following an exponential growth of the population without control, the population could return to its original density (Tamura et al., 2017). We assume that this population size would be enough for park visitors to witness the species. Conversely, if there are no sightings by the public after 10 years, it can be assumed that eradication has been achieved. Therefore, monitoring should continue for 10 years; information gathering and regular surveys are ongoing as of 2022.

Previous molecular phylogenetic analyses of *Sciurus* species suggest that *S. vulgaris* and *S. lis* are closely related but are significantly differentiated (Oshida and Masuda, 2000; Tamura and Hayashi, 2007; Grill et al., 2009; Oshida et al., 2009; Liu et al., 2014; Koh et al., 2015; Boukhdoud et al., 2021; İbiş et al., 2022). In Japan, *S. vulgaris* is distributed only in Hokkaido and the distribution area of *S. lis* is separated from it by a deep strait. However, hybridization may occur if these two species lived sympatrically. To identify the squirrel species and examine the population genetic structure between *S. vulgaris* and *S. lis* in and near Sayama Hills, genetic analysis was conducted (Wildlife Management Office Inc., 2017). The genetic analysis of mitochondrial D-loop region suggested that two species are completely separated as two distinct species (Supplementary Figure S3). One male in Sayama Hills (haplotype Sl-6) was identified as *S. lis*, but all other 32 individuals were the same single haplotype (Sv-4) of *S. vulgaris*, which is close to the conspecific haplotype in Russian Far East, northeast China and Japanese Hokkaido. Genetic analysis based on a nuclear gene reveled that *S. lis* is homogenous but *S. vulgaris* is heterogenous in RAG1. At present, interspecific hybridization is unlikely in and near Sayama Hills (Supplementary Figure S4; Wildlife Management Office Inc., 2017), although further analysis based on more samples and for a longer period is needed to rule out the introgression of genes from *S. vulgaris* to *S. lis* in this area.

The release of Eurasian red squirrels may also occur in other regions. The Unzen Squirrel Village tourist facility in Nagasaki Prefecture, Kyushu Island closed in 2004. In 2007, a female Eurasian red squirrel was found dead on the road about 5.5 km from the facility (Yasuda and Matsuo, 2012). This species has not been observed again in the vicinity and further surveys have not been conducted in the area since the endemic Japanese squirrel is absent from Kyushu Island.

As a rule of the Invasive Alien Species Act in Japan, facilities with a breeding permission may keep new individuals (including those bred on the premises) within the permitted number of animals. In Honshu, where the Japanese squirrel is distributed, tourist facilities still exist, so there is still a high risk for Eurasian red squirrels to escape from the facility. Management of the facilities to prevent escape and surveys of their distribution in the surrounding area are urgently required.

6. Discussion

Table 1 summarizes the status of measures taken for the control of Pallas's squirrels in various regions to date. Small populations in the early stages of establishment, such as in Iruma and Akiruno, have been successfully reduced (or nearly eradicated). Eradication was also feasible on Takashima Island

with >1,000 individuals and on the Uto Peninsula with *ca.* 5,000 individuals. The eradication of the Eurasian red squirrel, which is in danger of genetic introgression, was also almost successful.

As we have speculated, the applicable methods and stakeholders involved differ depending on the environment, such as peninsulas, remote islands, and urban areas. However, five main factors can be pointed out as key elements common to all of these successful examples: (1) the project was initiated in the early stages of establishment or when the population was <10,000 individuals, and more individuals were captured in the early stages; (2) the active involvement of researchers in the project, testing new strategies and methodologies (playback, chemical control, kill traps) to improve capture success rates and monitoring efficiency, and educating the public; (3) the Mammal Society of Japan in the conversations with the Ministry to transform science-based suggestions from researchers in actions supported by law; (4) Upon the request of the Mammal Society of Japan, government agencies immediately initiated plans to capture the non-native squirrels; (5) the creation of networks and working groups made of different figures that allow the increase of resources in the field.

However, the cases that have not been eradicated show the challenges that need to be considered. The most challenging problem is how to take action in areas where the population has already increased to the point where eradication is unlikely. For example, in Kanagawa Prefecture, the Pallas's squirrel has been established since the 1950s and its distribution had already expanded over a wide area of 300 km^2 in 2001 (Tamura, 2004). The population is estimated to be around 100,000 individuals, which is currently impossible to eradicate. Capturing must continue on the frontline of the distribution in perpetuity to prevent the spread into natural forests inhabited by endemic species. Therefore, under the lead of the author, Noriko Tamura, universities, high schools, museums, local nature conservation NPOs and the government have set up a volunteer network to collect information on squirrels and initiated trapping at the frontline of the known distribution (Kanagawa Pallas's squirrel Information Network, 2022). Through these activities, we are in the process of trying to build a system to control and locally eradicate non-native squirrels as economically and sustainably as possible. Many areas require a low-cost system that can be handled by the local community. Our experience in the field so far has shown that distribution surveys and trapping can be done more efficiently by local citizens. All that remains is to build a system that works well for stakeholders (e.g., researchers, government, local nature conservation volunteers, educational institutions, and citizens) using each other's resources.

Another problem is that sporadic escape of alien squirrels with subsequent establishment still occurs, albeit in small populations. For example, three Pallas's squirrels were captured in Hibiya Park, midtown Tokyo City in 2020 (Tamura, unpublished). More recently, a new habitat of the Pallas's squirrel was discovered in Beppu City, Oita Prefecture, Kyushu in 2022 (Yasuda et al., 2023). Even though the Invasive Alien Species Act has been into force and great costs have been paid to eradicate non-native squirrel species, the same challenges continue to emerge. The greatest challenges are that Japanese people have few opportunities to encounter endemic squirrels in the field and are not aware that endemic species in Japan are globally valuable. This is also true, surprisingly, for many involved in environmental administration in local governments. Among a number of issues regarding alien and native mammals, activities related to the protection of endemic squirrel species and measures against alien squirrel species are low in priority. Researchers must continue to work directly with governments and citizens to promote and undertake conservation activities. What is most needed is an understanding of the ecology and status of endemic squirrel species in Japan to inform decision making and educate as many people as possible on the importance of alien squirrels as a community problem.

Invasive species control in Japan began in earnest after the Invasive Alien Species Act came into force in 2005, lagging behind Europe, Australia, New Zealand and other countries (Yamada et al., 2011). Examples of successful or unsuccessful measures in other countries served as a reference for measures in Japan, which started belatedly (Murakami et al., 2006; Yamada et al., 2009). In the case of squirrels, the difficulties of attempting to protect native Eurasian red squirrels from non-native gray squirrels in the United Kingdom and Italy were already known by the 1990s (e.g., JNCC, 1996; Currado, 1998; Bertolino and Genovesi, 2003; Parrott et al., 2009). Knowledge of the negative impacts by non-native squirrels on native squirrels in Europe and other countries has led to the initiation of precautionary trapping in Japan. Researchers have learned that early action is of the utmost importance in the control of invasive alien species (Mazzamuto et al., 2021). Although public awareness, stakeholders and budgets, differ from country to country or even region to region within the same country, measures can be shared in particular if the invasive alien squirrel is the same species. In this sense, we hope that this review will be of assistance in the management measures for invasive alien squirrels in other parts of the world.

Author contributions

NT and MY gathered the data and references. NT made the draft of the review and MY revised it. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articless/10.3389/fevo.2022.1061115/full#supplementary-material

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