



Commentary

Ecology and protection of a flagship species, the Siberian flying squirrel

Vesa SELONEN^{1,*}, Sanna MÄKELÄINEN²

¹University of Turku, Department of Biology, Section of Ecology; FI-20014 Turku, Finland

²Metapopulation Research Centre, Department of Biosciences, P.O. Box 65 (Viikinkaari 1), FI-00014 University of Helsinki, Finland

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Abstract

Having clear ecological knowledge of protected species is essential for being able to successfully take actions towards conservation, but this knowledge is also crucial for managing and preventing conservation conflicts. For example, the Siberian flying squirrel, *Pteromys volans*, listed in the EU Habitats Directive and inhabiting mature forests that are also the target for logging, has had a major role in political discussions regarding conservation in Finland. This species has also been well-researched during recent decades, providing knowledge on the ecology and management of the animal. Herein, we review knowledge on habitats, demography, community interactions and spatial ecology of this flagship species. We compare the ecology of flying squirrels with that of other arboreal squirrels, and summarize conservation management and policy related to flying squirrels. Reviewed research on the Siberian flying squirrel shows that the species has many similarities in behaviour to other arboreal squirrels. For instance, arboreal squirrels deviate from the general pattern of male-biased sexual size dimorphism in mammals, which perhaps relates to the mating system of arboreal squirrels. Important differences are found in the response of Siberian flying squirrels to tree mast, i.e. pulsed food resource, compared to that of red squirrels, and in communal nesting behaviour compared to that of North American flying squirrels. The extensive knowledge on dispersal behaviour of the flying squirrel, well-studied habitat associations and the proved need for evidence-based conservation may guide researchers and managers working with other similar species. For conservation, the case of the Siberian flying squirrel demonstrates that habitat protection becomes both ineffective and uneconomical if ecological knowledge is not applied in the conservation planning process. The cost-effective conservation of the species requires both landscape-level conservation planning and flexible conservation options to increase the motivation of land owners for conservation.

Introduction

Protection of vulnerable species often creates conflicts between land use and conservation management. For example, in Europe the European Union (EU) Habitats Directive (92/43/EEC) lists species for which resting and nesting places are strictly protected, but implementation of the Directive has created conflicts in several countries (Haila et al., 2007). One problem for effective conservation is the difficulty to define what a protected habitat, its size and characteristics, should be for a particular species. To manage conflicts and promote actions towards successful conservation, accurate knowledge on the habitat use and ecology of any protected species is central. Ecological knowledge may provide justifications for practical actions and thus may help in resolving conflicts between land use and conservation.

One group of mammalian species with conservation interests across the world is arboreal squirrels, including tree squirrels and flying squirrels (Koprowski, 2005; Smith et al., 2005; Selonen et al., 2010a). These species may be showing a trend of declining in abundance because they are specialized to mature forest habitats, and these forests are often the target for logging. In addition, flying squirrels are typically on the “slow” end of the life-history spectrum of rodents, and feature traits such as low mortality, low metabolic rate, and few offspring per litter (Holmes and Austad, 1994; Fokidis et al., 2007). Declining populations have been observed for flying squirrels (Hanski, 2006; Smith, 2007; Selonen et al., 2010a), and sudden local extinctions for gliders,

the Australian analogue of flying squirrels (Lindenmayer et al., 2011), which suggests caution should be taken when planning actions that potentially affect the populations of gliding species.

The only flying squirrel occurring within the EU is the Siberian flying squirrel, *Pteromys volans*, hereafter the SFS. The species lives in northern boreal forests, and is limited to Finland and Estonia within the EU. The SFS is listed in the EU Habitats Directive, and due to conservation interests related to the species, it has received much research interest during recent decades in Finland. Consequently, much knowledge related to the ecology of this species and its practical conservation management have been gained, which may also guide researchers and managers interested in other arboreal squirrels (subfamily Sciurinae) that potentially have similar behaviours as SFSs. Here, we review current ecological knowledge of this flagship species and discuss the conservation policy of the SFS in Finland. We have two main aims with this paper. First (i), we strive to enhance ecological knowledge of arboreal squirrels in general by reviewing knowledge on habitat use, demography, community interactions and spatial ecology of the SFS and comparing some of these results with the ecology of other well-studied tree and flying squirrels (red squirrels: *Sciurus vulgaris*, from now on the EU red squirrel, and *Tamiasciurus hudsonicus*, from now on the NA red squirrel; and North American flying squirrels: the southern flying squirrel, *Glaucomys volans*, and the northern flying squirrel, *G. sabrinus*, from now on NA flying squirrels). Our second aim (ii) is to provide conclusions that might help when planning the management of other arboreal squirrels or species protected by the EU Habitats Directive; therefore, we summarize the conservation management and policy

*Corresponding author

Email address: vessel@utu.fi (Vesa SELONEN)

related to the SFS in Finland. For conservation, the case of the SFS demonstrates that habitat protection becomes both ineffective and uneconomical if ecological knowledge is not applied in the conservation planning process and a landscape-scale perspective is neglected.

General

The SFS is a nocturnal, arboreal rodent that nests in tree cavities, nest-boxes and dreys (twig nests) in boreal forests. It belongs to the Siberian fauna type, and its range spans Eurasia, from Finland and the Baltic countries, through Siberia, to Korea and Hokkaido Island, Japan (Wilson and Reeder, 2005). In Finland, the SFS is distributed roughly across half of the country, from south to north-eastern central Finland (Hanski, 2006). It is relatively rare in the Baltic counties, where the distribution is restricted to north-eastern and southern parts of Estonia and north-eastern Latvia (Timm and Kiristaja, 2002). In the latter region, no verified observations of the SFS have been made during the last few decades (Pilats, 2010). In Japan, the SFS occurs in forests from lowlands to montane regions (Abe et al., 2005).

Fossil records of the tribe *Pteromyini* show that flying squirrels existed in forests in southern and south-eastern Asia during the Quaternary period, where diversification also took place (Xuefei et al., 2013). Thus, the SFS survived through glacial periods in these scattered refuges, and developed rapidly after the cooling period. Phylogeographical studies based on mitochondrial DNA have found three different lineages: Hokkaido, Far East and north-eastern Eurasia (Oshida et al., 2005; Lee et al., 2008). According to Thorington et al. (2012), four sub-species differing in colouration have been identified; *P. v. volans* (from Finland to Russia) and *P. v. orii* (Hokkaido, Japan) look similar, whereas *P. v. athene* (Sakhalin island) is more brownish and *P. v. buechneri* (China and Korean peninsula) has a darker colour than the two aforementioned sub-species.

Other gliding squirrel species closely related to the SFS, or that have been well-studied, are the Japanese flying squirrel (*P. momonga*), a species larger than the SFS and endemic to three islands in Japan (Thorington et al., 2012); the northern flying squirrel (*G. sabrinus*) in North America—the only other boreal species in the *Pteromyinae*; and the southern flying squirrel (*G. volans*), which is distributed over the eastern part of North America, from Nova Scotia (Canada) southwards to Honduras (South America) (Thorington et al., 2012).

Habitat and food

In the European part of the distribution range, the SFS is clearly confined to mature spruce-dominated forests with a mixture of deciduous trees, such as birch (*Betula* spp.), alder (*Alnus* spp.) and aspen (*Populus tremula*) (Hanski, 1998; Reunanen et al., 2002a; Airapetyants and Fokin, 2003; Santangeli et al., 2013a). The species can also occupy urbanized areas (Mäkeläinen et al., 2015).

In Finland, species occurrence increases with the average forest age, the volume of spruce trees (*Picea abies*) and the occurrence of deciduous trees within the spruce forest (Hanski, 1998; Reunanen et al., 2002a; Santangeli et al., 2013a). On the landscape scale, the presence of agricultural fields has also been associated to the occurrence of the SFS (Santangeli et al., 2013a), as fields occur in regions with fertile soil (Remm et al., 2017). In addition, in Finnish forest-dominated landscapes, the coverage of fields does not extend above the level where it would affect SFS occupancy patterns (Remm et al., 2017). These studies are based on the extensive systematic survey of the SFS within an area that covers most of the distribution range of the species in Finland (177 600 km²; Hanski, 2006; Santangeli et al., 2013a; Haakana et al., 2017; Remm et al., 2017). Based on a mark-recapture study of two populations within a high-density area, the reproductive success of the SFS is not very sensitive to the cover of mature forests near nesting sites (Hoset et al., 2017). The preference for old growth forests may be more pronounced at the northern limits of the species' distribution range (Hurme et al., 2008a).

The preference for fertile soil and mixed forest structure in European boreal forests is explained by the food habits of the species: In Finland,

alder and birch are important food sources, but aspen, pine and spruce are also used as forage. During winter and early spring, birch and alder catkins are the main foods (Mäkelä, 1996; Hanski et al., 2000b; Selonen et al., 2016a). Birch catkins form the main part of the winter diet (80% of food consumed, based on diet analysis of faecal samples; Mäkelä, 1996), whereas alder catkins are preferred over birch (Sulkava and Sulkava, 1993; Mäkelä, 1996; Selonen and Wistbacka, 2016). In addition, the SFS stores alder catkins in cavities, nest-boxes and on tree branches (Sulkava and Sulkava, 1993; Mäkelä, 1996; Hanski et al., 2000b; Selonen and Wistbacka, 2016). Catkins develop in summer, and the SFS starts to consume them in autumn. Catkins remain on the trees, and individuals continue eating the catkins during the following winter and early spring when the catkins flower. After leaf-burst in the beginning of May, leaves form the main diet for the SFS in late spring and summer (Mäkelä, 1996). However, during pregnancy and parturition, females are still dependent on catkin production/storages and buds, because the mating season starts in mid-March and first litters are born in late April. Catkin production varies considerably between years (Selonen et al., 2016a), and mast of birch and alder before breeding is one determinant of reproduction in SFSs (Selonen and Wistbacka, 2016; Selonen et al., 2016a; Hoset et al., 2017). In contrast to some red squirrel studies (Boutin et al., 2006; Wauters et al., 2008), food abundance in upcoming autumn does not affect reproduction of SFSs (Selonen and Wistbacka, 2016). In Japan, similarly to Finland, the main food items during summer months are the leaves of different deciduous trees (e.g. *Salix* spp., *Populus* sp., *Ulmus* sp.), but buds and seeds (of both broadleaf trees and conifers) are also eaten. In early autumn, the SFS also forages on pine seeds (*Pinus koraiensis*) in Japan (Asari and Yanagawa, 2008).

In addition to food, the presence of nesting sites influences SFS habitat selection (Selonen and Hanski, 2004). In fact, the ability to locate a nest cavity heavily determines the dispersal patterns of the species (Selonen and Hanski, 2004, 2012) and affects adult spacing behaviour (Hanski et al., 2000a; Mäkeläinen et al., 2016). Since deciduous trees, such as aspen and alder, often occur at the edges of fields and forests, the occurrence of cavity trees and food sources may explain the observations that SFSs prefer edge sites (Desrochers et al., 2003).

Current studies on habitat associations are predominantly restricted to Finland. However, some knowledge on habitat associations is being gathered in other regions. Inhabited forests in the European part of Russia and Estonia are conifer-dominated mature forests with aspen, alder, birch and willow (Timm and Kiristaja, 2002; Airapetyants and Fokin, 2003), and are thus similar to those observed in Finnish studies (Hanski, 1998; Reunanen et al., 2002a; Santangeli et al., 2013a). In Japan, the SFS is found in mixed coniferous forests, but dominant tree species differ from in Europe; for example, subspecies *P. v. orii* in Hokkaido, Japan, inhabits forests dominated with Sakhalin fir (*Abies sakhalinensis*) (e.g. Suzuki et al., 2011) or coniferous trees belonging to genus *Pinus* sp. or *Picea* sp., and broadleaf trees belonging to various genera, such as *Betula*, *Quercus*, *Tilia*, or *Acer* (Yamamoto et al., 1995; Asari and Yanagawa, 2016).

Comparison with other squirrels

The food ecology of the SFS seems to be significantly similar to that of other arboreal squirrels (Tab. 1), because many arboreal squirrel species are dependent on tree mast at least to some degree. A major difference is that the reproduction of the SFS only depends on food conditions in the winter/spring before reproduction (Selonen and Wistbacka, 2016; Selonen et al., 2016a), whereas both EU and NA red squirrels may also reproduce in anticipation of the future food abundance of the following autumn (Boutin et al., 2006; Wauters et al., 2008). This has potential consequences on population fluctuations of these species. The food ecology of the northern flying squirrel also differs from that of the SFS, since the former is clearly dependent on truffle production of forests (Curah et al., 2000). This results in variations in behaviour (Smith, 2007) and also perhaps differences in habitat selection between the SFS and the northern flying squirrel.

Table 1 – Comparison of main characteristics of some arboreal squirrels. Deviation of a species from others is denoted with bold text.

	Siberian Flying Squirrel¹	Southern flying squirrel²	Northern flying squirrel³	NA red squirrel⁴	EU red squirrel⁵	Grey squirrel⁶
Main habitat	mixed coniferous forests, forest-field edge habitats	various deciduous forests, often with pine	coniferous forests, also other (mixed and deciduous)	coniferous forests, also other	coniferous forests, also other	deciduous and mixed forests
Main food	catkins , leaves, buds	tree mast, fungi and variety of items	fungi , lichens but also other	coniferous seeds, but varies	coniferous seeds, but varies	seeds, flowers, buds
Food caching	makes small alder catkin caches	scatter hoards tree mast	does not cache? Poorly documented	larder-hoarder , midden where cones stored	scatter hoards in deciduous forests, less in coniferous	scatter-hoarder
Main nest type	cavities, dreys	cavities	cavities, dreys	dreys, cavities	dreys, cavities	cavities, dreys
Mating system	polygynous-promiscuous, partly territorial female, possible intrasexual dominance hierarchies	polygynous-promiscuous, partly territorial female	polygynous-promiscuous, partly territorial female	polygynous-promiscuous, highly territorial females, intrasexual dominance hierarchies	polygynous-promiscuous, partly territorial female, intrasexual dominance hierarchies	polygynous-promiscuous, partly territorial female, intrasexual dominance hierarchies
Sexual size dimorphism	female-biased , on average ♀156 g ♂144 g	female-biased , 46.5 g–85 g, ♀few grams larger than ♂	no sex-bias reported, both sexes 110 g–230 g	no sex-bias, both sexes 200 g–250 g	no sex-bias, both sexes 250 g–340 g	no sex-bias, both sexes 300 g–710 g
Litter size	average 2.4, max 6, 1–2 litters per year	average 3–4, 1–2 litters per year	average 2.3–2.5, typically 1 litter per year	average 3.2–5.4, 1–2 litters per year	average 3–4, max 7, 1–2 litters per year	average 2.9, max 8, 1–2 litters per year
Factors affecting reproduction	catkin mast in winter before reproduction	unclear	truffle production affects e.g. density, but role in reproductive success unclear	seed mast before or after reproduction	seed mast before or after reproduction	seed mast before reproduction
Communal nesting in winter	solitary or adult male and female in the same nest	large aggregations , typically 3–10, but up to 50 unrelated or related individuals	communal nests common with 2–4 squirrels per nest	solitary, but communal nesting may occur between mother and daughters	solitary, but communal nesting may occur between partners	may nest in same-sex and mixed sex groups, usually mother and daughter in a group

¹ Hanski et al., 2000a,b; Santangeli et al., 2013a; Selonen et al., 2013, 2014, 2016a; Selonen and Wisbøcka, 2016
² Dolan and Carter, 1977; Taulman and Smith, 2004; Winterowd and Weigl, 2006; Winterowd et al., 2005; Thorington and Weigl, 2011; Garraway et al., 2013
³ Wells-Gosling and Heaney, 1984; Carey et al., 1997; Smith, 2007
⁴ Don, 1983; Steele, 1998; Boutin et al., 2006; Williams et al., 2013
⁵ Waiters and Diond, 1990; Lutz et al., 2005; Waiters et al., 2008; Selonen and Hanski, 2015
⁶ Nixon et al., 1975; Koprowski, 1994; Hayssen, 2016; Koprowski et al., 2016; Lawton et al., 2016



Figure 1—A typical flying squirrel nest box in Finland. Nest boxes are designed to resemble natural cavities. ©Toni Laaksonen.

Nest use

SFSs nest in cavities, dreys (twig nest) and nest boxes. In addition, nests occasionally are located in buildings in urban areas. SFSs typically have several nests (from 2 to 12), and there are possibly seasonal differences in the use of the various nest types (Hanski et al., 2000a; Hanski, Mäkeläinen, Selonen *unpublished data*). In Finland, cavities are the most common nest source, made by the great-spotted woodpecker (*Dendrocopus major*). These cavities are usually located in aspens and have an entrance-hole size (of ≈ 45 mm) that prevents most natural enemies, such as the Ural owl (*Strix uralensis*), from entering. This may be a reason why SFSs seldom abandon the cavity when disturbed (*pers. obs.*). The main tree species providing cavities varies regionally. In Korea (*P. volans*) and Japan (for Japanese flying squirrel *P. momonga*), most nests are located in coniferous trees (Suzuki et al., 2011; Lee et al., 2012). Male SFSs in general have more nest sites than females, and a greater proportion of their nests include dreys (Hanski et al., 2000a). Dreys are usually located in coniferous trees, in Finland mostly in spruces (Hanski et al., 2000a). Dreys resemble twig nests made by red squirrels, and in fact, the dreys used by SFSs may have been originally constructed by EU red squirrels. Mortality in cavities vs. dreys has not been studied, but dreys may serve as unsafe nests compared to cavities of SFSs. For example, pine martens (*Martes martes*) may kill individuals in dreys (Nyholm, 1970), but they cannot invade a cavity made by a great-spotted woodpecker. Indeed, it is uncertain whether SFS females give birth in dreys because all observations of new-born juveniles have come from cavities or nest boxes.

Nest boxes are widely used by the SFS (Fig. 1) and by NA flying squirrels (Fokidis and Risch, 2005). This has enhanced the research of these species on topics that require capturing and handling of individuals. In SFS studies, communal nesting patterns (Selonen et al., 2014) or reproductive success (similar litter sizes observed within the same year; V. Selonen, *unpublished data*) do not differ between nest boxes and natural cavities. In these studies, individuals have used boxes that have been made to resemble natural cavities (Fig. 1). Location of nests in different habitats, distance to edge or habitat connectivity between the nest sites do not seem to restrict habitat use of the species (Desrochers et al., 2003; Mäkeläinen et al., 2016). However, availability of nests affects space-use patterns, and individuals may have to search for suitable nests in a fragmented landscape, as SFSs with larger home-ranges also have more distinct nest sites (Mäkeläinen et al., 2016). Fine-scale factors, for example the height and diameter of a cavity and the condition of tree (live or snag), have affected nest use in Japan (Suzuki and Yanagawa, 2013). In general, SFSs were found to use cavities that were over one metre high, with entrances from three to five cm, which were in live trees (Suzuki and Yanagawa, 2013). The same study also found

that more nest boxes were used in forests with fewer cavities. However, since the reproductive success of the SFS may be similar in cavities and artificial nests (see above), nest boxes might provide an additional tool to improve habitat quality.

Comparison with other squirrels

Squirrel species that den in cavities usually prefer mature forests, like the SFS and the NA flying squirrel do (Menzel et al., 2004; Holloway and Malcolm, 2007; Pyare et al., 2010). Compared to flying squirrel species, both NA and EU red squirrels are more confined to use twig nests (Tab. 1), but prefer mature trees because of feeding habits (Wauters and Dhondt, 1990; Koprowski, 2005). In Finland, SFSs mainly nest in live trees (*pers. obs.*, but see Nakama and Yanagawa, 2009). However, for the northern flying squirrel, no preference has been observed regarding the use of live trees versus snags (Pyare et al., 2010), although it may also prefer cavities in certain regions (Smith, 2007). The main difference in nesting behaviour between the SFS and other arboreal squirrels seems to relate to communal nesting behaviour in winter (see section “Winter ecology” below).

Mating system

In Finland, the mating season of SFSs starts in mid-March (gestation period 41 days and lactation period 42–45 days). After the first litter, born in April, the female SFS can have a second litter in June. Females are territorial, living in separate home-ranges, but males live in overlapping home-ranges that encompass the home-ranges of several males and females (Fig. 2; Selonen et al., 2013). As with other arboreal squirrels (Tab. 1), the mating system of the SFS is polygynous-promiscuous with multiple paternity within one litter. Perhaps due to low population density, the level of multiple paternity within litters remains relatively low in SFSs (Selonen et al., 2013).

The SFS mating system may have elements of both scramble competition (Selonen et al., 2016b), in which the mating success for males depends on search effort to locate females (Koprowski, 2007; Lane et al., 2009), and female-defence system (Selonen et al., 2013, 2016b), where mating opportunities for males depend on an individual’s position in the male dominance hierarchy (Koprowski, 2007). Indeed, large body size has been observed to increase reproductive success both in female and male SFSs (Selonen et al., 2013; but see Hoset et al., 2017). In ad-

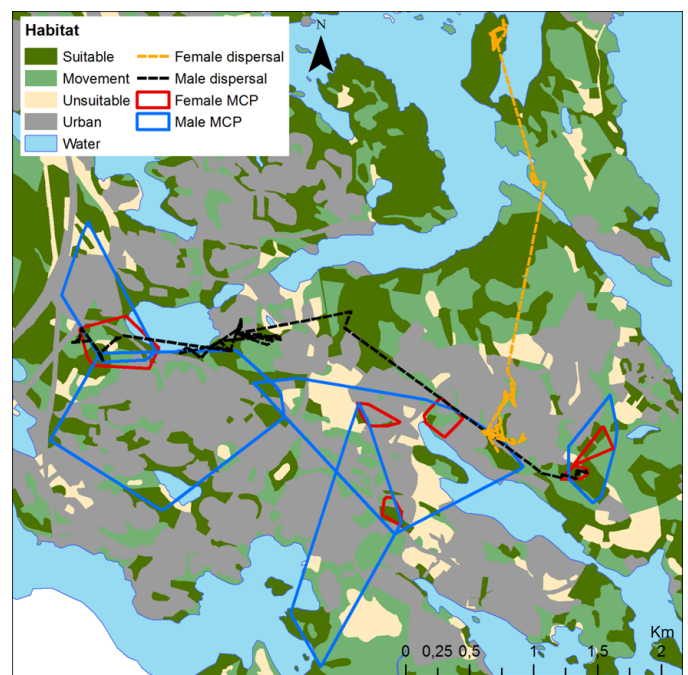


Figure 2 – An example of the locations of five male and six female home ranges, and dispersal paths of two juveniles in partially fragmented landscape near city of Kuopio, Finland ($62^{\circ}53'33''$ N, $27^{\circ}40'42''$ E). MCP: Minimum Convex Polygon home ranges.

dition, female SFSs are larger than males in the same species (Selonen et al., 2016b). This pattern may result from benefits of females being large, for example, to aid gliding when pregnant (Fokidis and Risch, 2008). Alternatively, males may benefit from being small and quick in scramble competition mating system. If low body mass facilitates fast gliding in SFS males, being small may benefit them in being able to locate several females during the short time period when females are in oestrus (Selonen et al., 2016b).

Comparison with other squirrels

There are major similarities between the mating system of SFSs and that of other tree and flying squirrels. At least during the breeding time, female arboreal squirrels are, to some extent, territorial, and the core areas of home-ranges are spatially separated (Tab. 1). Consequently, males need to actively move between territories of different females to increase their reproductive success. This may lead to a scramble competition mating system (Lane et al., 2009). However, both in EU and NA red squirrels and SFSs, larger males have higher reproductive success than smaller males, in line with the female-defence mating system (Wauters et al., 1990; Koprowski, 2007; Selonen et al., 2013). Indeed, the mating systems of many arboreal squirrels may have elements of both scramble competition and defence mating systems. It is also notable that arboreal squirrels usually deviate from the general mammalian pattern of males being larger than females (Tab. 1).

Winter ecology

Belonging to boreal fauna type, the SFS seems to be well-adapted to cold climates; species survival is not lower in winter than during other seasons (Mäkeläinen, 2016). The activity period is, however, shorter, and distances moved decrease during the middle of winter, compared to other seasons (Hanski et al., 2000a). The same nest sites are used both in winter and summer (*own observation*). Catkins are important food in winter and SFSs cache catkins of alder (see above), but catkins can also be consumed directly from trees, where they remain throughout the winter. Nevertheless, caches may decrease the need to move long distances from the nest during the cold season. In low mast years, SFSs consume, e.g., coniferous buds, and it is unknown whether the lack of catkins affects winter survival.

In many rodent species, individuals may enhance thermoregulation and winter survival by communal nesting. However, Selonen et al. (2014) did not find that cold weather during winter increases communal nesting in SFSs, as individuals were observed to often nest alone, even on the coldest of nights. This observation further supports the notion that SFSs are well-adapted to cold climates. Interestingly, an increased amount of precipitation in winter is linked to a slight increase in reproductive success for the following spring and summer (Selonen et al., 2016a; Selonen and Wistbacka, 2016). It remains unclear what is behind this observed correlation, but the amount of precipitation in winter may be related to moisture conditions in spring, which is linked to growth of deciduous trees (food source of SFS).

Comparison with other squirrels

Similar to NA and EU red squirrels, the SFS depends on tree mast and cache food during winter. However, northern flying squirrels have a clearly different diet (Tab. 1) and another difference in winter ecology between the SFS and NA flying squirrels is related to communal nesting behaviour. For the SFS, communal nesting seems to be mainly related to mating behaviour (Selonen et al., 2014; Asari and Yanagawa, 2016), whereas in NA flying squirrels, communal nesting is explained by thermoregulation benefits of cold weather (Stapp et al., 1991; Layne and Raymond, 1994). The group structure observed in the communal nests of different arboreal squirrel species also shows other differences (Tab. 1); whether communal nests are same-sex or mixed-sex, or between kin or non-kin, may be related to variations in mating behaviour and dispersal patterns of offspring in different arboreal squirrel species.

Community interactions

Predators

In the European part of the distribution range, the main predators of SFSs are large owls, namely the Ural owl (*Strix uralensis*) and the eagle owl (*Bubo bubo*), but also the tawny owl (*Strix aluco*), goshawk (*Accipiter gentilis*) and pine marten (Hanski et al., 2000b; Selonen et al., 2010a). In urban areas, domestic cats are common predator (Mäkeläinen, 2016). The Ural owl is the main predator also in Japan (Yushin Asari, *pers. comm.*). SFSs appear less frequently than EU red squirrels in the diet of their main predators (Selonen et al., 2010a). The presence of a predator can obviously affect SFS occupancy patterns; SFSs are unlikely to exist near nests of the Ural owl, but apparently due to competition within the predator guild, they are positively associated with the goshawk, if both Ural owls and goshawks are present in the area (Byholm et al., 2012).

Parasites

Studies on the parasites of the SFS are limited, but seasonal variation was found in the abundance of two flea species; a specialist flea species on SFSs has been found to dominate during summer and autumn seasons, whereas a flea common for EU red squirrels was found to exist in more abundance during winter (Haukisalmi and Hanski, 2007). A new species of protozoa of genus *Trypanosoma* was also found in SFSs in China (Sato et al., 2007).

Competition with other species

We are unaware of studies on competition between the SFS and other species, but such interspecific competition is known to occur between the NA flying squirrels (Weigl, 1978; Smith, 2007). There is likely competition for cavities between the SFS and other cavity users, but it remains unknown whether some species might prevent SFSs from using nesting cavities. The pygmy owl (*Glaucidium passerinum*) is one potential cavity competitor, but is not a very common species in boreal forests. It also seems unlikely that SFSs would compete with EU red squirrels that have different nest and food requirements and are day active in contrast to nocturnal SFSs.

Working as a conservation surrogate

Due to the habitat association of the SFS, the species is suggested to be a potential umbrella species that can aid in the protection of other species with smaller area requirements but a similar dependence on mature forests (for example some beetles or polypores; Hurme et al., 2008b; Vierikko et al., 2010). However, this topic requires further study to verify the SFS's status of umbrella species in the various parts of its distribution range.

Comparison with other squirrels

In contrast to EU and NA red squirrels and NA flying squirrels (Carey et al., 1992; Studd et al., 2015), SFSs appear to only have a minor role in the food web of boreal forest communities (Hanski et al., 2000b; Selonen et al., 2010a), and they are not the main prey of any predator. EU and NA red squirrels are important in the diets of some predators, such as the goshawk (*Accipiter gentilis*), and also have a potential role in the reproductive ecology of spruce (Steele, 2008; Selonen et al., 2010a; Studd et al., 2015). Northern flying squirrels have a major role in the diet of northern spotted owls (*Strix occidentalis*) (Carey et al., 1992), and both species of NA flying squirrels are potential vectors for truffle dispersion (Lehmkuhl et al., 2004). For SFSs, we are unaware of any possible role in the dispersion of used food items. The likely reason for a negligible role by SFSs in food webs is their relatively low densities in forest landscapes.

Demography and densities

Mark-recapture studies of ear-tagged individuals and radio-telemetry studies have indicated yearly survival values of between 0.43 and 0.76 for adults (Lampila et al., 2009a; Brommer et al., 2017; Mäkeläinen, 2016). As for most other species, survival is generally lower among

juveniles, even though it is not affected by their dispersal distance (Mäkeläinen, 2016). In mark-recapture studies, survival estimates and population size are associated with habitat loss due to forest logging (Lampila et al., 2009a; Koskimäki et al., 2014). In addition, from a landscape perspective, an increase in unsuitable habitat (within a buffer of 500 m) seems to increase male mortality. There is also clear regional variation in survival probabilities (Mäkeläinen, 2016).

Survival of SFSs in relation to tree-species composition is not known, but a recent study from a high-density area indicates that amount of mature forest has a surprisingly low effect on lifetime reproductive success of females (Hoset et al., 2017). Instead, reproductive success is determined by mast abundance during the lifetime of a female (Hoset et al., 2017). Although mast affects reproductive success (Selonen and Wistbacka, 2016), there are no clear indications that population fluctuations follow food abundance (V. Selonen *unpublished*). For example, female survival shows only minor variation between years (Brommer et al., 2017). Reproduction is not only dependent on food conditions, but also on weather (Selonen and Wistbacka, 2016; Selonen et al., 2016a). Litter size usually varies from between two and four offspring for both the first and the second litter, but only a proportion (e.g. 15–30%) of females manage to produce two litters a year (Hanski et al., 2000b; Selonen and Wistbacka, 2016).

The density of SFSs clearly varies regionally (Kurhinen et al., 2011; Santangeli et al., 2013a; Remm et al., 2017), a phenomenon that can be linked to soil fertility and amount of preferred forest habitat in the landscape (Remm et al., 2017), and to spatial population dynamics (Hurme et al., 2008a; Brommer et al., 2017). In Hokkaido, much higher densities have been reported for *P. volans orii* (2 individuals/ha, Suzuki et al., 2011) than for SFSs in Finland (less than 0.1 individuals/ha in Finland; Hanski et al., 2000a).

SFSs are not of any major commercial use for humans, although they are hunted in some regions of East-Asia for the fur trade. This is not considered a major threat for SFSs (Nowak, 1991).

Comparison with other squirrels

Lampila et al. (2009a) stated that compared to other squirrel species, survival estimates for the SFS seem relatively low. In contrast, Mäkeläinen (2016) concluded that survival estimates are quite similar to other arboreal squirrel species. The highest densities of the northern flying squirrel have been found in old-growth forests, but its density is also strongly influenced by the availability of food and nest cavities (Smith, 2007, but see Wheatley et al., 2005). For the southern flying squirrel, density is not observed to be strongly affected by forest management, but its abundance has been associated with the density of mast trees (Holloway and Malcolm, 2007). In general, SFS densities appear clearly lower than NA flying squirrel densities in North America (Smith, 2007) and EU red squirrel densities (Lurz et al., 2005).

Movements

In Finland, SFSs occupy large home-ranges in relation to the average home-range sizes of rodents of the same weight; males move on average within a 60 hectare area (100% minimum convex polygon) and females within an 8 hectare area (Hanski et al., 2000a). Fragmentation of the forest landscape increases space utilization by males (Selonen et al., 2001). In a partially urban landscape, home-range sizes were similar to those in managed forests (Mäkeläinen et al., 2016). SFSs prefer using mature forests during their nightly movements, but are able to move through different and less suitable forested habitats (Selonen and Hanski, 2004). Both sexes show seasonal variation in distance moved and movement speed (Hanski et al., 2000a; Mäkeläinen et al., 2016).

The dispersal behaviour of SFSs has been intensively studied in Finland. Based on these studies, natal dispersal, i.e. the movement between the site of birth and site of first breeding, is the main process behind colonization, habitat selection and gene flow in SFSs (Hanski and Selonen, 2009; Selonen et al., 2010b; Selonen and Wistbacka, 2017). The natal dispersal period is during the first autumn after birth, and in general almost all females disperse, whereas only a minority of male offspring remain philopatric. Thus, natal dispersal is female-

biased in SFSs, a pattern that is atypical for a mammal, and may be related to competition for nesting sites between females in SFSs (Hanski and Selonen, 2009). In some cases, males may disperse in the spring before or during the first mating season or later (Hanski and Selonen, 2009; Selonen and Wistbacka, 2017). On average, movements of adults (potential breeding dispersal) do not increase the distance moved from the natal nest, and thus do not influence gene flow or population dispersion (Selonen and Wistbacka, 2017). In other words, on average, the spread of individual SFSs and their genes across the landscape does not continue after natal dispersal.

The average detected natal dispersal distances are 1.7 km and 2.5 km for males and females, respectively (maximum observed 9 km for both sexes, Hanski and Selonen, 2009; Selonen et al., 2010b). The final dispersal distance is determined by individual attributes (Selonen and Hanski, 2010a,b; Selonen et al., 2012), landscape structure at the natal site (Selonen et al., 2007), and that within dispersed landscape and at the settlement site (Selonen and Hanski, 2004). Interestingly, long-distance dispersal does not seem to have obvious survival effects, and probably is not selected against in the SFS (Selonen and Hanski, 2012; Selonen et al., 2012). In addition, parents do not force juveniles to abandon the natal site (Selonen and Hanski, 2010c). The dispersal data of the SFS also indicate that dispersal is a unique phase in the life of an individual that cannot be predicted from movement behaviour in non-dispersing life phases, such as adult movements within breeding home-ranges (van Dyck and Baguette, 2005; Selonen and Hanski, 2006). Using movement data only from non-dispersers may result in misleading conclusions on the species' response to fragmentation (Selonen and Hanski, 2004, 2006; van Dyck and Baguette, 2005). For example, dispersing SFSs more frequently use young forest stands and open areas for moving between forest fragments than adults use them (Selonen and Hanski, 2006).

Unlike the red squirrel or northern flying squirrel, the SFS hardly ever moves on the ground. Therefore, open areas (fields, clear cuts, lakes) wider than 100 metres may act as dispersal barriers, but can occasionally be crossed if single trees are found within the open area (Selonen and Hanski, 2004). Similar observations have also been made for NA flying squirrels (Wheatley, 2011; see also Taylor and Goldingay, 2012). In Finland, the lack of structural connectivity does not seem to have effect on the dispersal ability of SFSs (Selonen and Hanski, 2004, 2012), but the population seems to persist in a network of uncoupled subpopulations, where movement between sub-populations is of critical importance (Brommer et al., 2017). Thus, dispersal has a key role in population persistence (Brommer et al., 2017).

Comparison with other squirrels

Sex-specific patterns in home-range size are comparable between SFSs and other squirrel species (Tab. 2). NA flying squirrels respond to fragmentation similarly to SFSs, by increasing home-range sizes, but in general the home-ranges of SFSs are large (Hanski et al., 2000a), particularly for males (Tab. 2). In EU red squirrels, availability of food influences the home-range area and use (Wauters and Dhondt, 1992; Lurz et al., 2000), but similar observations are lacking for the SFS.

Information on the dispersal of arboreal squirrels other than SFSs has mainly been restricted to red squirrels (Larsen and Boutin, 1994; Berteaux and Boutin, 2000; Wauters et al., 2010; Fey et al., 2016). The major dissimilarity here to NA red squirrels is that natal dispersal distances of this species may be very short, partly due to the bequeathal of territories by mother NA red squirrels to their offspring (Boutin et al., 2000, but see Merrick and Koprowski, 2017). Conversely in SFSs, natal philopatry is linked to territory vacancy after the apparent death of a mother (Selonen and Wistbacka, 2017). Dispersal distances may partly be comparable between the SFS and northern flying squirrel (Smith et al., 2011b), and EU red squirrels (Wauters et al., 2010; Selonen and Hanski, 2015). Thus, behavioural dispersal studies of SFSs may give insight on dispersal behaviour in these squirrel species. Interestingly, in arboreal squirrels, dispersal is not, or is only weakly, male-biased (Tab. 2). One possible factor behind this pattern may be the mating system of arboreal squirrels, in which females are

Table 2 – Comparison of movement ability and responses to forest fragmentation of some arboreal squirrels. Deviation of a species from others is denoted with bold text.

	Siberian Flying Squirrel¹	Southern flying squirrel²	Northern flying squirrel³	NA red squirrel⁴	EU red squirrel⁵	Grey squirrel⁶
Adult movements	home range typically 8 ha–60 ha ; ♂ 5.6 times larger than ♀. No breeding dispersal observed. occasional long ♂ moves 4 km–5 km	home-range typically 1 ha–10 ha. ♂ 0–3 times larger than ♀. Breeding dispersal unknown. occasional long ♂ moves >2 km observed	home-range typically < 10 ha: ♂ 1.3 times larger than ♀. Breeding dispersal unknown. occasional long ♂ moves 4–5 km observed	home-range typically 1 ha–20 ha. ♂ 1.5 times larger than ♀. 100 m–200 m moves by ♀ to bequeath part of territory for offspring	home-range typically 5 ha–50 ha; ♂ 1.5 times larger than ♀. Breeding dispersal may occur when food scarce	home-range typically 1 ha–20 ha; ♂ 1.2 times larger than ♀. Poor data for breeding dispersal, but possible long migrations
Natal dispersal	female-biased. average 2 km , max 9 km	? but range expansion observations indicate high dispersal potential	? but observation for few kilometre natal moves	sex-unbiased, average 100 m or male-biased and average 680 m, max 4.5 km. Potential for higher vagility than reported	sex-unbiased, average around 1 km, max > 1.5 km	male-biased or sex-unbiased, no clear data, apparently high dispersal potential
Responses to forest fragment size	15 m buffers around nest site after cutting lead to unoccupancy. Minimum needed patch size unclear	often not in smallest fragments (e.g. < 4 ha)	mixed results, often not in smallest fragments, but can be seen as habitat generalist	mixed results, may not occur in smallest fragments. Increased density in small forest patches	long term occupancy of patches < 10 ha may depend on immigration	sometimes not in smallest patches (e.g. < 4 ha), but potentially occupy also very small forest fragments. Increased density in small forest patches
Responses to forest isolation	no isolation effects in Finnish forest-dominated landscapes, except in northern edge of distribution range	not clear	most studied have not found effects of isolation on occurrence	not clear, may not be very sensitive to forest isolation	indication for negative effects in agriculture-dominated landscapes when inter-fragment distances are ≥ 0.5–1 km	negative effect of forest isolation observed

¹ Hanski et al., 2000a; Hanski and Selonen, 2009; Selonen and Hanski, 2015; Selonen and Wisbacka, 2017; Kemm et al., 2017
² Dolan and Carter, 1977; Nupp and Swihart, 2000; Taulman and Smith, 2004; Bowman et al., 2005; Holloway and Malcoln, 2007
³ Wells-Gosling and Hearney, 1984; Nupp and Swihart, 2000; Wheatley et al., 2005; Smith, 2007; Paterson and Malcoln, 2010; Smith et al., 2011a,b
⁴ Larsen and Boutin, 1994, 1998; Nupp and Swihart, 2000; Paterson and Malcoln, 2010; Merrick and Koprowski, 2017
⁵ Lutz et al., 2005; Wauters et al., 2010, 2011; Selonen and Hanski, 2015
⁶ Koprowski, 1994; Nupp and Swihart, 2000; Koprowski, 2005; Lawton et al., 2016

to some extent territorial. Finally, in contrast to SFSs, red squirrels are reported to perform breeding dispersal, either related to recourse availability (EU red squirrels, Lurz et al., 1997) or as a form of parental investment (NA red squirrels, Boutin et al., 2000). However, the distances moved in these cases (at least in NA red squirrels) are usually comparable to movements within the home-range by the SFS (Tab. 2). Thus, the role of breeding dispersal in gene flow and population spread of red squirrels remains uncertain.

Habitat fragmentation

In forest-dominated Finnish landscapes the SFS is not very sensitive to habitat fragmentation (Selonen and Hanski, 2015; Remm et al., 2017), mainly because an individual's ability to move and disperse in fragmented landscapes is relatively good (Selonen and Hanski, 2004, 2012). In other words, the landscape is mainly functionally continuous, i.e. individuals can reach most habitat fragments in the landscape. Based on patterns in genetic differentiation between populations, Lampila et al. (2009b) claimed that the species suffers from habitat fragmentation. This conclusion was not supported by other studies observing comparable levels of genetic differentiation in areas where dispersal was not restricted by fragmentation (Selonen et al., 2005, 2010b). Koskimäki et al. (2014) argued that the observed population decline was larger than could be explained by habitat loss only in the study area in central Finland. However, in this study, fragmentation effects were not directly studied. Hoset et al. (2017) concluded that the area of mature forest near nest sites have little effect on the life-time reproductive success of female SFSs.

Although the above studies indicate no clear effect of fragmentation on SFSs, it is certain that wide open areas restrict the movements of arboreal squirrels (Selonen and Hanski, 2004). Heavy fragmentation by agriculture has been shown to affect EU red squirrel populations (Selonen and Hanski, 2015), and responses to fragmentation are likely density-dependent and region-specific (Remm et al., 2017). For example, the species may be more sensitive to fragmentation the near northern edge of its distribution range, where forests are more barren and densities lower than in the core distribution area (Mönkkönen et al., 1997; Reunanen et al., 2002b; Hurme et al., 2008a).

We are not able to predict when the effects of fragmentation start to aggravate the effects of habitat loss for SFS populations (Selonen and Hanski, 2015). There appears to be, however, an optimum value in the amount of preferred forest in the landscape in occupancy patterns; Reunanen et al. (2004) concluded that for the northern Finnish study areas, spruce-dominated forest habitat should make up 12–16% of the landscape (on a scale of 1 km²) to maintain SFSs. Based on occupancy data for almost the whole distribution area in Finland, Remm et al. (2017) concluded that the optimum level of preferred forests in the landscape is 10–15% (4 km landscape buffer). However, the abundance of SFSs was surprisingly observed to decline when the proportion of preferred habitat increased above the optimal level. In addition, the response varied in regions with high and low densities of SFSs (Remm et al., 2017).

Comparison with other squirrels

Densities of many tree squirrel species tend to increase with decreasing forest patch size, indicating a compaction response to fragmentation and thus increased densities in smaller forest fragments (Koprowski, 2005). In addition, many studies have observed that squirrels prefer large forest patches over smaller ones (Pyare et al., 2010; Selonen and Hanski, 2015), although SFSs may prefer edge habitats over large continuous forests (Remm et al., 2017; Hoset et al., 2017). Conclusions about the response of arboreal squirrels to fragmentation are difficult to make (Tab. 2), and there seems to be mixed views on the fragmentation-sensitivity of arboreal squirrels. Some argue arboreal squirrels are potentially sensitive to fragmentation (Koprowski, 2005; Smith et al., 2011b), while others do not (Wheatley et al., 2005; Mortelliti et al., 2011; Selonen and Hanski, 2015), and the same situation applies to SFSs (sensitive: Lampila et al., 2009b; Koskimäki et al., 2014; not sensitive: Selonen and Hanski, 2004; Remm et al., 2017). It can be

assumed that SFSs are more sensitive to fragmentation than EU red squirrels (Selonen and Hanski, 2015), but recent reviews on both species suggest that conservation management focusing on enhancing habitat quality should be more effective than management concentrating on enhancing landscape connectivity (Mortelliti et al., 2011; Selonen and Hanski, 2015). It is, however, clear that there are limits in patch area and distance between woodland patches, and when these limits are exceeded, both occupancy and movement of arboreal squirrels will be affected (Tab. 2). However, these limits are likely density-dependent and region-specific. In addition, variables describing the amount of forests on the landscape scale may be more effective than patch attributes in predicting occurrence of arboreal squirrels (Ritchie et al., 2009; Remm et al., 2017).

Decline and conservation status

The national population of the SFS in Finland is declining (Hokkanen et al., 1982; Hanski, 2006; Selonen et al., 2010a; Liukko et al., 2015). The species used to be classified as “vulnerable” in Finland, but in the most recent red-list assessment it was categorized as “nearly threatened”, because the decline was estimated to have been less severe during the last ten years (23% population decline, which is below the 30% benchmark listed by IUCN as an indication for severe decline of population size, Liukko et al., 2015) than it has been earlier (in the last half of the 20th century). This change in conservation status in Finland does not affect the protection of the SFS based on the EU Habitats Directive. Globally, the SFS is considered “least concern” based on IUCN status, but a declining population trend and possible threat of extinction because of habitat loss are generally observed throughout its distribution range (Shar et al., 2016a). For example, it has been classified as an endangered species in South Korea and Estonia, “vulnerable” in China and considered near extinct in Latvia (Won and Smith, 1999; Timm and Remm, 2011; Shar et al., 2016b).

Comparison with other squirrels

The case of the SFS supports the view that flying squirrels and gliders are a group of mammalian species warranting conservation concern around the world (Smith et al., 2005; Selonen et al., 2010a; Lindenmayer et al., 2011), even though, globally, all of the species are considered “least concern” (Tab. 3). For example, one subspecies of the northern flying squirrel (*G. s. coloratus*) is currently federally listed as endangered (U.S. Fish and Wildlife Service, 2013), and regional absence due to forest logging has been documented in the case of southern flying squirrel (Taulman et al., 1998). In addition to flying squirrels, some populations of tree squirrels have also been declining (e.g. Lurz et al., 2005; Koprowski, 2005; Selonen et al., 2010a), such as the EU red squirrel in the British Isles, whose population has drastically decreased due to the Squirrel Pox Virus spread by alien eastern grey squirrels, *Sciurus carolinensis* (Sainsbury et al., 2000).

Conservation and management

In general, boreal forests have a long history of forest management. The majority of the mature forests where SFSs live in Finland occur on managed privately or corporation-owned forest land. Within these areas, the protection of the SFS continuously conflicts with land use. The planning of forestry and other land use must consider the fact that conservation laws prohibit destroying SFS nesting sites. However, the overall land restrictions that result from these laws are minimal; according to earlier governmental guidelines, only an area with a 10 to 15 meter buffer must be left untouched around nest trees of SFS, resulting in a protected area of approximately 0.03 to 0.07 hectares (Anonymous, 2004). The predominant forest harvest method in Finland is clear cutting, and additional provisions are made to leave corridors or separate trees to ensure the connectivity of an area. In any case, the areas left around nest sites are excessively small, compared to the home-range size of SFSs (8 ha for females, Hanski et al., 2000a). Thus, it is not surprising that the management guidelines have been ineffective and have led to unoccupancy of protected sites (Santangeli et al., 2013b; Jokinen

et al., 2015). The low success of current conservation management in protecting SFSs implies poor cost-efficiency. For example, millions of euros were used to cause as little harm as possible to a SFS population when building a new motorway route between two major cities in Finland in 2002. However, in the end, the protection efforts were largely ineffective, i.e. they did not prevent the local population from declining, since sites protected from road construction were still exposed to normal forest management practices (Hanski, 2011).

Ecological studies have provided knowledge on how to perform cost-effective conservation management of the SFS on the landscape scale (Kurttila and Pukkala, 2003; Haila et al., 2007; Hurme et al., 2007; Selonen and Hanski, 2012; Santangeli et al., 2013b; Remm et al., 2017), but ultimately, these studies have not influenced management practices (Haila et al., 2007; Jokinen et al., 2015). Studies comparing different forest harvesting methods have concluded that with alternative methods, such as continuous-cover silviculture, protected sites can still be subjected to commercial forest use (Hurme et al., 2007; Jokinen et al., 2015), without forest owners necessarily losing money from the process of protecting the animals (Kurttila and Pukkala, 2003; Hurme et al., 2007). Haila et al. (2007) suggested conducting dynamic spatial conservation, which takes into account that not all habitats are of equal quality for SFSs and not all suitable habitats are occupied at the same time. For example, the protection of occupied, yet low-quality, sites may be less important than the protection of unoccupied high-quality sites. This view is quite different from current management practice, which ineffectively protects all known sites, creating a situation where motivation for conservation is low. Currently, around 90% of sites occupied by the species are estimated to remain without any protection, because it is not known or it is unreported that the sites are occupied by SFSs (Jokinen et al., 2015).

Current ecological knowledge has not influenced the conservation of the SFS for several reasons, including land owners fearing the loss of money (strict rules for protection result in a situation where only the minimum actions required are performed), ambiguity between institutions planning SFS conservation, and a lack of co-operation between people involved in the management process (Haila et al., 2007). It has also been suggested that the people (ecologists) who contribute knowledge to conservation planning should also play a central role in explaining the consequences and possibilities of alternative management options to other participants in the management process (Haila et al., 2007; see also Santangeli and Sutherland, 2016).

One key point for consideration in avoiding conservation conflict is that land owners must trust that the management process is fair. This means that some sort of compensation of money loss for land owners may be needed (Haila et al., 2007). For a species still quite common, like the SFS in Finland (population size around 300000 individuals; Hanski, 2006), it is clear that all sites occupied by the species cannot be protected with the money currently available for conservation. An important aspect for optimal conservation planning is to take into account possible differences in motivation for land use, for example, motives linked to the type of forest ownership. When forests are under private ownership, conservation programs that are appealing and convenient to the owner may be more likely to lead to conservation success (Santangeli et al., 2016). In principle, increasing forest owner “buy-in” should decrease the level of expected monetary compensation and thus increase the cost-efficiency of conservation (Horne et al., 2009). For example, one voluntary-based conservation option in Finland available for private forest owners is the Forest Biodiversity Programme for Southern Finland (METSO) (Government of Finland, 2014). Alternatively, habitat offsetting, i.e. a process where local nature losses can be compensated by habitat restoration or by protecting equivalently valuable habitat elsewhere, can be a valid means of conservation regarding land owned by the government and forest companies. How and when biodiversity offsetting should be applied in conservation management has received attention in recent years (e.g. Kiesecker et al., 2009). Biodiversity offsetting needs careful case-by-case planning, and can lead to economic interests superseding conservation actions (Coralie et al., 2015). In any case, biodiversity offsetting could benefit the

Table 3 – Comparison of threats and conservation management of arboreal squirrels. Deviation of a species from others is denoted with bold text.

	Siberian Flying Squirrel¹	Southern flying squirrel²	Northern flying squirrel³	NA red squirrel⁴	EU red squirrel⁵	Grey squirrel⁶
Threats	habitat destruction by forest logging	habitat destruction	possible interspecific competition with Southern FS, forest logging	habitat loss, forest fires, insect outbreaks, competition with Abert's squirrel	interspecific competition with invasive squirrel species, habitat destruction	no threats listed
Global IUCN category, regional status if applicable	Least concern, NT in EU	Least concern	Least concern, federally EN ssp. in USA	Least concern, federally EN ssp. in USA	Least concern, NT in Ireland and listed in UK priority species	Least concern
Management and conservation practice	habitat protection (protection of breeding and resting places by EU Habitats Directive), forest management guidelines in Finland	no conservation management plans found	regional practices such as monitoring at potential sites and preserving and maintaining the most important resources	forest management guidelines that prevent forest damages, restricted use of primary habitats by humans, the management of competitor species	habitat protection and forest management guidelines, removal of the grey squirrel, local reintroduction programs	no conservation management found (management as an invasive species in Europe)

¹ Anonymous, 2004; Jokinen et al., 2015; Liukko et al., 2015; Santangeli et al., 2013b; Shar et al., 2016a
² Cassola, 2016a; Taulman et al., 1998
³ Cassola, 2016b; Lehmkuhl et al., 2006; Smith, 2007; U.S. Fish and Wildlife Service, 2013; Weigl, 2007
⁴ Edelman et al., 2009; Gwinn and Koprowski, 2017; Koprowski et al., 2005, 2006; U.S. Fish and Wildlife Service, 2011
⁵ Biodiversity Reporting and Information Group (BRIG), 2007; Gurnell and Pepper, 1993; Gurnell et al., 2004; Lutz et al., 1998; Marnell et al., 2009; Pepper and Patterson, 1998; Shar et al., 2016b
⁶ Cassola, 2016c; Bertolino and Genovesi, 2003

cost-effective management of relatively common species that are protected by the Habitats Directive, such as the SFS, but also for the moor frog, *Rana arvalis*, or bats (*O. Chiroptera*) in Finland, for example, and help in dealing with tight conflict situations (Nygren, 2015). Moreover, biodiversity offsetting does not necessarily contradict with the Habitats Directive if planned to improve the current conservation practices (Anonymous, 2007). However, in the case of the SFS, habitat restoration as a mitigation tool (van Teeffelen et al., 2014) is not practical because the growth of a mature forest habitat takes long time. Still, the “no net loss” principle might be achieved by compensating habitat loss with protection of equivalent suitable forest habitats elsewhere. Biodiversity offsetting in the case of the SFS could include a landscape-level forest management plan and a condition to grow suitable forest for species.

According to recent observations, SFSs are capable of persisting in urban forests (Mäkeläinen et al., 2015, 2016). This might be the case because near cities, there is less-intensive forest harvesting and fewer natural predators. Therefore, protection of this species can also be implemented in urban areas, where forest harvesting does not generate a significant profit. However, zoning processes in urban areas are particularly sensitive when it comes to conservation conflicts; even the protection of small areas around nest trees may have large ramifications, such as the prevention of house or road construction.

Comparison with other squirrels

The conservation of all arboreal squirrels potentially conflicts with the interests of forestry (Tab. 3), a situation that may create challenges for squirrel population management. For example, with the protection of the EU red squirrel in UK, the main strategy is preserving and managing suitable forest habitats. Spatially explicit population modelling has been used to revise forest management plans of important protection sites to maintain sites where strong populations of red squirrels could persist for the long-term (Lurz et al., 1998, 2003). Recommendations for forest management have included preserving large enough woodland patches, with a tree species composition that provides sufficient food resources (Lurz et al., 1998). Broadleaf trees are favoured by the invasive grey squirrel, and forest management favouring conifers benefit the EU red squirrel (Pepper and Patterson, 1998). Indeed, in the UK and Italy, the conservation of the EU red squirrel is strongly related to the management of the grey squirrel population (Gurnell et al., 2004; Bertolino et al., 2014). Conservation measures have included grey squirrel removal and trials to prevent its range expansion, as well as red squirrel reintroductions (Gurnell and Pepper, 1993; Bertolino and Genovesi, 2003).

Management guidelines for the NA red squirrel (for the endemic and isolated red squirrel *T. h. grahamensis* in Arizona) have included aims to increase the area of suitable mature forest habitats and prevent damage caused by crown fires or insect outbreaks (Koprowski et al., 2005, 2006). However, the conservation of this subspecies is complicated by the presence of the exotic Abert's squirrel (*Sciurus aberti*), which is both a possible competitor of resources, and less sensitive to altered fire regimes (Edelman et al., 2009; Gwinn and Koprowski, 2017). It is also suggested that middens built by NA red squirrels could serve as indicators of diversity in forests, and that midden protection with some forest buffer around them would benefit forest conservation in general (Posthumus et al., 2015). For the northern flying squirrel, protection of old growth forest is the recommended conservation tool (Smith, 2007), but the species is very much a forest generalist, occupying both young and old forests. Thus, providing clear management guidelines for the species is complicated (Weigl, 2007). As a general guideline for forest management that supports northern flying squirrels, fine-scale harvesting and retention of large trees have been suggested (Lehmkuhl et al., 2006). However, the evidence of effectiveness of these conservation measures is often limited in arboreal squirrels, and more evidence should be provided for evaluating how arboreal squirrels respond to management.

Conclusion

Research on the SFS draws a picture of an arboreal squirrel with behaviour and mating systems similar to many other arboreal squirrels. There are also some clear differences, such as the species' response to mast abundance compared to the response of red squirrels (Boutin et al., 2006; Selonen and Wistbacka, 2016), and differences in communal nesting behaviour compared to that of NA flying squirrels (Layne and Raymond, 1994; Selonen et al., 2014). The extensive research that has been carried out on the dispersal behaviour of SFSs is one factor that may help to manage and protect other arboreal squirrels. The SFS dispersal studies indicate the central role of dispersal in the population dynamics of the species (Brommer et al., 2017). Thus, dispersal behaviour must be understood if one wants to understand population dynamics and the response of arboreal squirrel populations to landscape changes. Indeed, for research on arboreal squirrels other than the SFS, we suggest increasing knowledge on dispersal behaviour of the species. Further guidance for knowledge gaps in ecology of arboreal squirrels can be found in Tab. 1 and 2. In general, many important questions in squirrel research require more attention in the future, including how squirrels and their food sources (masting of trees) respond to climate change (Bisi et al., 2016). It remains unclear how to predict when the effects of habitat fragmentation start to aggravate the effects of habitat loss for arboreal squirrel populations (Selonen and Hanski, 2015). In addition, more focus is needed on relative roles of resources, habitat (type/loss/fragmentation), predators, and dispersal on population size. These studies require multispecies data on large spatial and temporal scales, which, although laborious to collect, will provide a way to better understand squirrel populations in the changing world.

The case of the SFS demonstrates how money can be lost through inefficient management if ecological knowledge is not applied in a meaningful manner. Until now, considerable effort by environmental authorities in Finland has been made to protect a small number of the overall area occupied by the species, with actions that in most cases have still led to protection failure (Jokinen et al., 2015). It is probably clear to many politicians and management practitioners in Finland that the current management strategy for this species is cost-inefficient, and management conflicts have likely decreased the will to improve current practices (Nygren, 2015). The SFS can survive in fragmented forest landscapes (Selonen and Hanski, 2012; Hoset et al., 2017; Remm et al., 2017), leading one to believe that even slightly more planning on a landscape scale, using ecological knowledge, would result in more cost-efficient practices. For protected species that are declining but still relatively abundant and widely distributed, the case of the SFS suggests that the best-practise conservation plans should include landscape-level management of high-quality habitats, combined with carefully planned habitat offsetting and methods aiming to increase the motivation of land owners for conservation. ☞

References

- Abe H., Ishii N., Ito T., Kaneko Y., Maeda K., Miura S., Yoneda M., 2005. A Guide to the Mammals of Japan. Tokai University Press, Kanagawa, Japan.
- Airapetyants A.E., Fokin I.M., 2003. Biology of European flying squirrel *Pteromys volans* L. (Rodentia: Pteromyidae) in the North-West of Russia. *Russ. J. Theriol.* 2: 105–113.
- Anonymous, 2004. Liito-oravan lisääntymis- ja levähdyspaikkojen määrittäminen ja turvaaminen metsien käytössä (MMM Dnro 3713/430/2003, YM Dnro YM4/501/2003). A Guideline for Determining and Maintaining Breeding and Resting Sites of the Flying Squirrel in the Forest Use. Ministry of Agriculture and Forestry, and Ministry of the Environment. [in Finnish]
- Anonymous, 2007. Guidance document on the strict protection of animal species of Community interest under the Habitats Directive 92/43/EEC. Environment Directorate General of the European Commission. available at http://ec.europa.eu/environment/nature/conservation/species/guidance/index_en.htm
- Asari Y., Yanagawa H., 2008. Field observations on the food items of the Siberian flying squirrel, *Pteromys volans orii*. *J. Jpn. Wildl. Res. Soc.* 33: 7–11. [in Japanese with English abstract]
- Asari Y., Yanagawa H., 2016. A Preliminary Study of Communal Nesting of Siberian Flying Squirrels *Pteromys volans* in Japan. *Mammal Study* 41: 97–100.
- Berteaux D., Boutin S., 2000. Breeding dispersal in female North American red squirrels. *Ecology* 81: 1311–1326.
- Bertolino S., Genovesi P., 2003. Spread and attempted eradication of the grey squirrel (*Sciurus carolinensis*) in Italy, and consequences for the red squirrel (*Sciurus vulgaris*) in Eurasia. *Biol. Cons.* 109: 352–359.
- Bertolino S., Cordero di Montezemolo N., Preatoni D.G., Wauters L.A., Martinoli A., 2014. A grey future for Europe: *Sciurus carolinensis* is replacing native red squirrels in Italy. *Biol. Inv.* 16: 53–62.

- Biodiversity Reporting and Information Group (BRIG), 2007. Report on the species and habitat review. UK Biodiversity Action Plan. Available at: http://jncc.defra.gov.uk/PDF/UKBAP_Species-HabitatsReview-2007.pdf (Accessed 10 April 2017)
- Bisi F., von Hardenberg J., Bertolino S., Wauters L.A., Imperio S., Preatoni D.G., Provenzale A., Mazzamuto M.V., Martinoli A., 2016. Current and future conifer seed production in the Alps: testing weather factors as cues behind masting. *Eur. J. Forest. Res.* 135: 743.
- Boutin S., Larsen K.W., Berteaux D., 2000. Anticipatory parental care: acquiring resources for offspring prior to conception. *Proc. R. Soc. B.* 267: 2081–2085.
- Boutin S., Wauters L.A., McAdam A.G., Humphries M.M., Tosi G., Dhondt A.A., 2006. Anticipatory reproduction and population growth in seed predators. *Science* 314: 1928–1930.
- Bowman J., Holloway G.L., Malcolm J.R., Middel K.R., Wilson P.J., 2005. Northern range boundary dynamics of southern flying squirrels: evidence of an energetic bottleneck. *Can. J. Zool.* 83: 1486–1494.
- Brommer J.E., Wistbacka R., Selonen V., 2017. Immigration ensures population survival in the Siberian flying squirrel. *Ecol. & Evol.* 7: 1858–1868.
- Byholm P., Burgas D., Virtanen T., 2012. Competitive exclusion within the predator community influences the distribution of a threatened prey species. *Ecology* 93: 1802–1808.
- Carey A.B., Horton S.P., Biswell B.L., 1992. Northern spotted owls: influence of prey base and landscape character. *Ecol. Monogr.* 62: 223–250.
- Carey A.B., Wilson T.M., Maguire C.C., Biswell B.L., 1997. Dens of northern flying squirrels in the Pacific Northwest. *J. Wildl. Manage.* 61: 684–699.
- Cassola F., 2016a. *Glaucomys volans*. The IUCN Red List of Threatened Species 2016: e.T9240A22257175. (Downloaded on 10 April 2017)
- Cassola F., 2016b. *Glaucomys sabrinus*. The IUCN Red List of Threatened Species 2016: e.T39553A22256914. (Downloaded on 10 April 2017)
- Cassola F., 2016c. *Sciurus carolinensis*. The IUCN Red List of Threatened Species 2016: e.T42462A22245728. (Downloaded on 10 April 2017)
- Coralie C., Guillaume O., Claude N., 2015. Tracking the origins and development of biodiversity offsetting in academic research and its implications for conservation: A review. *Biol. Cons.* 192: 492–503.
- Curah R.S., Smrecl E.A., Lehesvirta T., Niemi M., Larsen K.W., 2000. Fungi in the diets of northern flying squirrels and red squirrels in the boreal mixedwood forests of north-eastern Alberta. *Can. J. Botany* 78: 1514–1520.
- Desrochers A., Hanski I.K., Selonen V., 2003. Siberian flying squirrel responses to high- and low-contrast forest edges. *Lands. Ecol.* 18: 543–552.
- Dolan P.G., Carter D.C., 1977. *Glaucomys volans*. *Mammalian Species* 78: 1–6.
- Don B.A.C., 1983. Home range characteristics and correlates in tree squirrels. *Mammal. Rev.* 13: 123–132.
- Edelman A.J., Koprowski J.L., Bertelsen S.R., 2009. Potential for nest site competition between native and non-native tree squirrels. *J. Mamm.* 90: 167–174.
- Fey K., Hämäläinen S., Selonen V., 2016. Roads are no barrier for dispersing red squirrels in an urban environment. *Beh. Ecol.* 27: 741–747.
- Fokidis H.B., Risch T.S., 2005. The Use of Nest Boxes to Sample Arboreal Vertebrates. *Southeastern Naturalist* 4: 447–458.
- Fokidis H.B., Risch, T.S., 2008. Does gliding when pregnant select for larger females? *J. Zool.* 275: 237–244.
- Fokidis H.B., Risch T.S., Glenn T.C., 2007. Reproductive and resource benefits to large female body size in a mammal exhibiting female-biased sexual size dimorphism. *Anim. Behav.* 73: 479–488.
- Garrow C.J., Bowman J., Wilson P.J., 2013. Complex social structure of southern flying squirrels is related to spatial proximity but not kinship. *Behav. Ecol. Sociobiol.* 67: 113–122.
- Government of Finland, 2014. Government Resolution on continuation of the Forest Biodiversity Programme for Southern Finland 2014–2025 (METSO). Available at: http://ym.mti.fi/multiedition.fi/fi/METSO/METSO_periaateptsuomi.pdf (Accessed January 2017) [in Finnish]
- Gurnell J., Pepper H., 1993. A critical look at conserving the British red squirrel *Sciurus vulgaris*. *Mammal. Rev.* 23: 127–137.
- Gurnell J., Wauters L.A., Lurz P.W.W., Tosi G., 2004. Alien species and interspecific competition: effects of introduced eastern grey squirrels on red squirrel population dynamics. *J. Anim. Ecol.* 73: 26–35.
- Gwinn R.N., Koprowski J.L., 2017. Differential response to fire by an introduced and an endemic species complicates endangered species conservation. *Hystrix*, 27(2): 181–187. doi:10.4404/hystrix-27-2-11447
- Haakana H., Hirvelä H., Hanski I.K., Packalen T., 2017. Comparing regional forest policy scenarios in terms of predicted suitable habitats for the Siberian flying squirrel (*Pteromys volans*). *Scand. J. For. Res.* 32: 185–195.
- Haila Y., Kousis M., Jokinen A., Nygren N., Psarikiidou K., 2007. Building trust through public participation: Learning from conflicts over the implementation of the Habitats Directive. Participatory Governance and Institutional Innovation (PAGANINI). Work package 4.
- Hanski I.K., 1998. Home ranges and habitat use in the declining flying squirrel *Pteromys volans* in managed forests. *Wildl. Biol.* 4: 33–46.
- Hanski I.K., 2006. Liito-oravan *Pteromys volans* Suomen kannan koon arviointi. Raport. Ministry of Environment. [in Finnish]
- Hanski I.K., 2011. Liito-orava ja valtatie 1. In: Niemelä J., Furman E., Halkka A., Hallanaro E-L., Sorvari S. (Eds.) Ihminen ja ympäristö. Gaudeamus, Helsinki. [in Finnish]
- Hanski I.K., Mönkkönen M., Reunanen P., Stevens P., 2000b. Ecology of the Eurasian flying squirrel (*Pteromys volans*) in Finland. In: Goldingay R., Scheibe J. (Eds.) Biology of gliding mammals. Filander Verlag, Fürth. 67–86.
- Hanski I.K., Selonen V., 2009. Female-biased natal dispersal in the Siberian flying squirrel, *Pteromys volans*. *Beh. Ecol.* 20: 60–67.
- Hanski I.K., Stevens P.C., Ihalempää P., Selonen V., 2000a. Home-range size, movements, and nest-size use in the Siberian flying squirrel, *Pteromys volans*. *J. Mamm.* 81: 798–809.
- Hauksalmi V., Hanski I.K., 2007. Contrasting seasonal dynamics in fleas of the Siberian flying squirrel (*Pteromys volans*) in Finland. *Ecol. Entomol.* 32: 333–337.
- Hayssen V., 2016. Reproduction in grey squirrels: from anatomy to conservation. In: Shuttleworth C., Lurz P., Gurnell J. (Eds.) The Grey Squirrel: Ecology & Management of an Invasive Species in Europe. European Squirrel Initiative, Stoneleigh Park, Warwickshire CV8 2LG UK. 115–180
- Hokkanen H., Törmälä T., Vuorinen H., 1982. Decline of the flying squirrel *Pteromys volans* L. populations in Finland. *Biol. Cons.* 23: 273–284.
- Holloway G.L., Malcolm J.R., 2007. Northern and southern flying squirrel use of space within home ranges in central Ontario. *For. Ecol. Manage.* 242: 747–755.
- Holmes D.J., Austad S.N., 1994. Life-history correlates of gliding and flying mammals. *J. Mamm.* 75: 224–226.
- Horne P., Koskela T., Ovaskainen V., Horne T., 2009. Safeguarding forest biodiversity in Finland: Citizens' and non-industrial private forest owners' views. Working Papers of the Finnish Forest Research Institute 119. Available at <http://www.metla.fi/julkaisut/workingpapers/2009/mwpl19.htm>
- Hoset K., Villers A., Wistbacka R., Selonen V., 2017. Pulsed food resources, but not forest cover, determine lifetime reproductive success in a forest-dwelling rodent. *J. Anim. Ecol.* 86: 1235–1245. doi:10.1111/1365-2656.12715
- Hurme E., Kurttila M., Mönkkönen M., Heinonen T., Pukkala T., 2007. Maintenance of flying squirrel habitat and timber harvest: a site-specific spatial model in forest planning calculations. *Lands. Ecol.* 22: 243–256.
- Hurme E., Mönkkönen M., Reunanen P., Nikula A., Nivala V., 2008a. Temporal patch occupancy dynamics of the Siberian flying squirrel in a boreal forest landscape. *Ecography* 31: 469–476.
- Hurme E., Mönkkönen M., Sippola A.-L., Ylinen H., Penttinen M., 2008b. Role of the Siberian flying squirrel as an umbrella species for biodiversity in northern boreal forests. *Ecol. Indi.* 8: 246–255.
- Jokinen M., Mäkeläinen S., Ovaskainen O., 2015. “Strict”, yet ineffective: legal protection of breeding sites and resting places fails with the Siberian flying squirrel. *Anim. Cons.* 18: 167–175.
- Kiesecker J.M., Copeland H., Poczewicz A., McKenney B., 2009. Development by design: blending landscape-level planning with the mitigation hierarchy. *Frontiers Ecol. Env.* 8: 261–266.
- Koprowski J.L., 1994. *Sciurus carolinensis*. *Mammalian Species*. 480: 1–9.
- Koprowski J.L., 2005. The response of tree squirrels to fragmentation: a review and synthesis. *Anim. Cons.* 8: 369–376.
- Koprowski J.L., 2007. Alternative reproductive tactics and strategies of tree squirrels. In: Wolff J.O., Sherman P.W. (Eds) *Rodent Societies: an Ecological and Evolutionary Perspective*. University of Chicago Press, Chicago, USA. 86–95
- Koprowski J., Munroe K., Edelman A., 2016. Gray not Grey: Ecology of *Sciurus carolinensis* in native range in North America. In: Shuttleworth C., Lurz P., Gurnell J. (Eds.) *The Grey Squirrel: Ecology & Management of an Invasive Species in Europe*. European Squirrel Initiative, Stoneleigh Park, Warwickshire CV8 2LG UK. 1–17.
- Koprowski J.L., Leonard K.M., Zugmeyer C.A., Lolley J.A., 2005. Direct effects of fire on endangered Mount Graham red squirrels. *The Southern Naturalist* 51: 59–63.
- Koprowski J.L., Alanen M.I., Lynch A.M., 2006. Nowhere to run and nowhere to hide: Response of endemic Mt. Graham red squirrels to catastrophic forest damage. *Biol. Conserv.* 124: 491–498.
- Koskimäki J., Huitu O., Kotiaho J.S., Lampila S., Mäkelä A., Sulkava R., Mönkkönen M., 2014. Are habitat loss, predation risk and climate related to the drastic decline in a Siberian flying squirrel population? A 15-year study. *Popul. Ecol.* 56: 341–348.
- Kurhinen J., Kulebyakina E., Zadiraka E., Mamontov V., Muravskaya E., Hanski I.K., 2011. Distribution of the Siberian flying squirrel (*Pteromys volans* L.) in taiga isthmuses between Baltic and White sea regions. *Acta Zool. Lit.* 21: 306–310.
- Kurttila M., Pukkala T., 2003. Combining holding-level economic goals with spatial landscape-level goals in the planning of multiple ownership forestry. *Lands. Ecol.* 18: 529–541.
- Lampila S., Wistbacka R., Mäkelä A., Orell M., 2009a. Survival and population growth rate of the threatened Siberian flying squirrel (*Pteromys volans*) in a fragmented forest landscape. *Ecoscience* 16: 66–74.
- Lampila S., Kvist L., Wistbacka R., Orell M., 2009b. Genetic diversity and population differentiation in the endangered Siberian flying squirrel (*Pteromys volans*) in a fragmented landscape. *Europ. J. Wildl. Res.* 55: 397–406.
- Lane J.E., Boutin S., Gunn M.R., Coltman D.W., 2009. Sexually-selected behaviour: red squirrel males search for reproductive success. *J. Anim. Ecol.* 78: 296–304.
- Larsen K.W., Boutin S., 1994. Movements, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. *Ecology* 75: 214–223.
- Larsen K.W., Boutin S., 1998. Sex-unbiased philopatry in the North American red squirrel (*Tamiasciurus hudsonicus*). In: Steele M., Merritt J., Zegers D. (Eds) *Ecology and evolutionary biology of tree squirrels*. Special Publication, Virginia Museum of Natural History, Martinsville, Virginia, USA. 21–32.
- Layne J.N., Raymond M.A.V., 1994. Communal nesting of southern flying squirrels in Florida. *J. Mamm.* 75: 110–120.
- Lawton C., Shuttleworth C., Kenward R.E., 2016. Ranging Behaviour, Density And Social Structure In Grey Squirrels. In: Shuttleworth C., Lurz P., Gurnell J. (Eds.) *The Grey Squirrel: Ecology & Management of an Invasive Species in Europe*. European Squirrel Initiative, Stoneleigh Park, Warwickshire CV8 2LG UK. 133–150.
- Lee M.-Y., Park S.-K., Hong Y.-J., Kim Y., Voloshina I., Myslenkov A., Saveljev A.P., Choi T.-Y., Piao R.-Z., An J.-U., Lee M.-H., Lee H., Min M.-S., 2008. Mitochondrial genetic diversity and phylogenetic relationships of Siberian flying squirrel (*Pteromys volans*) populations. *Animal Cells and Systems* 12: 269–277.
- Lee J.-W., Cho H.-J., Kim D.-H., Kang T.-H., Kim I.-K., 2012. Basic Research on the Habitat Characteristics of Endangered Species *Pteromys Volans*. *Korean J. Environ. Ecol.* 27: 544–549.
- Lehmkuhl J.F., Gould L.E., Cazares E., Hosford D.R., 2004. Truffle abundance and mycophagy by northern flying squirrels in eastern Washington forests. *For. Ecol. Manage.* 200: 49–65.
- Lehmkuhl J.F., Kistler K.D., Begley J.S., Boulanger J., 2006. Demography of the northern flying squirrels informs ecosystem management of western interior forests. *Ecol. Appl.* 16: 584–600.
- Lindenmayer D., Wood J., McBurney L., MacGregor C., Youngentob K., Bank S.C., 2011. How to make a common species rare: A case against conservation complacency. *Biol. Conserv.* 144: 1663–1672.
- Liukko U.-M., Henttonen H., Hanski I.K., Kauhala K., Kojala I., Kyheröinen E.-M., Pitkänen J., 2015. The 2015 red list of Finnish mammal species. Ministry of Environment & Finnish Environment Institute.
- Lurz P.W.W., Garson P.J., Wauters L., 1997. Effect of temporal and spatial variation in habitat quality on red squirrel, *Sciurus vulgaris*, dispersal behaviour. *Anim. Behav.* 54: 427–435.

- Lurz P.W.W., Garson P.J., Ogilvie J.F., 1998. Conifer species mixtures, cone crops and red squirrel conservation. *Forestry* 71: 67–71.
- Lurz P.W.W., Geddes N., Lloyd A.J., Shirley M.D.F., Rushton S.P., Burlton B., 2003. Planning a red squirrel conservation area: using a spatially explicit population dynamics model to predict the impact of felling and forest design plans. *Forestry* 76: 95–108.
- Lurz P.W.W., Garson P.J., Wauters L.A., 2000. Effects of temporal and spatial variations in food supply on the space and habitat use of red squirrels, *Sciurus vulgaris* L. *J. Zool.* 251: 167–178.
- Lurz P.W.W., Gurnell J., Magris L., 2005. *Sciurus vulgaris*. *Mamm. Species* 769: 1–10.
- Marnell F., Kingston N., Looney D., 2009. Ireland Red List No. 3: Terrestrial mammals. National Parks and Wildlife Service, Department of the Environment, Heritage and Local Government, Dublin, Ireland.
- Menzel J.M., Ford W.M., Edwards J.W., Menzel M.A., 2004. Nest Tree Use by the Endangered Virginia Northern Flying Squirrel in the Central Appalachian Mountains. *Am. Midl. Nat.* 151: 355–368.
- Merrick M.J., Koprowski J.L., 2017. Altered natal dispersal at the range periphery: The role of behavior, resources, and maternal condition. *Ecol. & Evol.* 7: 58–72.
- Mortelliti A., Amori G., Capizzi D., Cervone C., Fagiani S., Pollini B., Boitani L., 2011. Independent effects of habitat loss, habitat fragmentation and structural connectivity on the distribution of two arboreal rodents. *J. Appl. Ecol.* 48: 163–172.
- Mäkelä A., 1996. Liito-oravan (*Pteromys volans* L.) ravintokohteet eri vuodenaikoina ulosteanalyysin perusteella (diet of flying squirrel). WWF Finland Reports 8: 54–58. [in Finnish]
- Mäkeläinen S., 2016. Occurrence, habitat use and movements of the flying squirrel in human-modified forest landscapes. PhD thesis, University of Helsinki.
- Mäkeläinen S., Schrader M., Hanski I.K., 2015. The factors explaining the occurrence of the Siberian flying squirrel in urban forest landscape. *Urban Ecosyst.* 18: 223–238.
- Mäkeläinen S., de Kegt H.J., Ovaskainen O., Hanski I.K., 2016. Home-range use patterns and movements of the Siberian flying squirrel in urban forests: Effects of habitat composition and connectivity. *Movem. Ecol.* 4: 5.
- Mönkkönen M., Reunanen P., Nikula A., Forsman J., Inkeröinen J., 1997. Landscape characteristics associated with the occurrence of the flying squirrel *Pteromys volans* L. in old-growth forests of northern Finland. *Ecography* 20: 634–642.
- Nakama S., Yanagawa H., 2009. Characteristics of tree cavities used by *Pteromys volans orii* in winter. *Mammal Study* 34: 161–164.
- Nature Conservation Act, 1996. Nature conservation Act 20.12.1996/1096 and 15.4.2016/195. Available at <http://www.finlex.fi/en/> (Accessed December 2016)
- Nixon C.M., Worley D.M., Donohoe R.W., 1975. Effects of hunting and mast crops on a squirrel population. *J. Wildl. Manage.* 39: 1–25.
- Nowak R.M., 1991. Walker's Mammals of the World, vol. 1, 5th Ed. Johns Hopkins University Press, Baltimore.
- Nupp T.E., Swihart R.K., 2000. Landscape-level correlates of small mammal assemblages in forest fragments of farmland. *J. Mammal.* 81: 512–526.
- Nygren N., 2015. Biodiversity offsetting — a solution for conflicts over biodiversity values in land use planning? *The Finnish Journal of Urban Studies* 53: 3. [in Finnish]
- Nyholm E.S., 1970. Näädän elintavoista, saalistuksesta ja ravinnosta. *Suomen Riista* 22: 105–118. [in Finnish]
- Oshida T., Abramov A., Yanagawa H., Masuda R., 2005. Phylogeography of the Russian flying squirrel (*Pteromys volans*): implication of refugia theory in arboreal small mammal of Eurasia. *Mol. Ecol.* 14: 1191–1196.
- Patterson J.E.H., Malcolm J.R., 2010. Landscape structure and local habitat characteristics as correlates of *Glaucomys sabrinus* and *Tamiasciurus hudsonicus* occurrence. *J. Mammal.* 91: 642–653.
- Pepper H., Patterson G., 1998. Red squirrel conservation. Practice note issued by forestry practice. Forestry Commission, Edinburgh. Available at [https://www.forestry.gov.uk/PDF/fcpn5.pdf/\\$FILE/fcpn5.pdf](https://www.forestry.gov.uk/PDF/fcpn5.pdf/$FILE/fcpn5.pdf) (Accessed March 2017)
- Pilats V., 2010. Results of flying squirrel survey in Latvia. In: *Wildlife census methods: reliability and application. Workshop proceedings. International scientific practical workshop.* Kaunas. 28–30.
- Posthumus E.E., Koprowski J.L., Steidl R.J., 2015. Red Squirrel Middens Influence Abundance but Not Diversity of Other Vertebrates. *PLoS ONE* 10: e0123633.
- Pyare S., Smith W.P., Shanley C.S., 2010. Den use and selection by northern flying squirrels in fragmented landscapes. *J. Mammal.* 91: 886–896.
- Remm J., Hanski I., Tuominen S., Selonen V., 2017. Multilevel landscape utilization of the Siberian flying squirrel: Scale effects on species habitat use. *Ecology and Evolution* 7(20): 8303–8315.
- Reunanen P., Mönkkönen M., Nikula A., 2002a. Habitat requirements of the Siberian flying squirrel in northern Finland: comparing field survey and remote sensing data. *Ann. Zool. Fenn.* 39: 7–20.
- Reunanen P., Nikula A., Mönkkönen M., Hurme E., 2002b. Predicting the occupancy of the Siberian flying squirrel in old-growth forest patches in northern Finland. *Ecol. Appl.* 12: 1188–1198.
- Reunanen P., Mönkkönen M., Nikula A., Hurme E., Nivala V., 2004. Assessing landscape thresholds for the Siberian flying squirrel. *Ecol. Bulletin* 51: 277–286.
- Ritchie L.E., Betts M.G., Forbes G., Vernes K., 2009. Effects of landscape composition and configuration on northern flying squirrels in a forest mosaic. *For. Ecol. Manage.* 257: 1920–1929.
- Sainsbury A.W., Nettleton P., Gilray J., Gurnell J., 2000. Grey squirrels have high seroprevalence to a parapoxvirus associated with deaths in red squirrels. *Anim. Cons.* 3: 229–233.
- Santangeli A., Sutherland W.J., 2016. The financial return from measuring impact. *Cons. Lett.* 10(3): 354–360.
- Santangeli A., Hanski I.K., Mäkelä H., 2013a. Integrating multi-source forest inventory and animal survey data to assess nationwide distribution and habitat correlates of the Siberian flying squirrel. *Biol. Conserv.* 157: 31–38.
- Santangeli A., Wistbacka R., Hanski I.K., Laaksonen T., 2013b. Ineffective enforced legislation for nature conservation: A case study with Siberian flying squirrel and forestry in a boreal landscape. *Biol. Conserv.* 157: 237–244.
- Santangeli A., Arroyo B., Dicks L.V., Herzon I., Kukkala A.S., Sutherland W.J., Moilanen A., 2016. Voluntary non-monetary approaches for implementing conservation. *Biol. Conserv.* 197: 209–214.
- Sato H., Al-Adhami B.H., Une Y., Kamiya H., 2007. *Trypanosoma (Herpetosoma) kuseli* sp. n. (Protozoa: Kinetoplastida) in Siberian flying squirrels (*Pteromys volans*). *Parasitol. Res.* 101: 453–461.
- Selonen V., Hanski I.K., 2004. Young flying squirrels (*Pteromys volans*) dispersing in fragmented forests. *Beh. Ecol.* 15: 564–571.
- Selonen V., Hanski I.K., 2006. Habitat exploration and use in dispersing juvenile flying squirrels. *J. Anim. Ecol.* 75: 1440–1449.
- Selonen V., Hanski I.K., 2010a. Decision making in dispersing Siberian flying squirrels. *Beh. Ecol.* 21: 219–225.
- Selonen V., Hanski I.K., 2010b. Condition-dependent, phenotype-dependent and genetic-dependent factors in the natal dispersal of a solitary rodent. *J. Anim. Ecol.* 79: 1093–1100.
- Selonen V., Hanski I.K., 2010c. Movements of dispersing flying squirrels in relation to siblings and parents. *Beh. Ecol. Socio.* 64: 1019–1027.
- Selonen V., Hanski I.K., 2012. Dispersing Siberian flying squirrels (*Pteromys volans*) locate preferred habitats in fragmented landscapes. *Can. J. Zool.* 90: 885–892.
- Selonen V., Hanski I.K., 2015. Occurrence and dispersal of the red squirrel and the Siberian flying squirrel in fragmented landscapes. In: *Shuttleworth C.M., Lurz P.W.W., Hayward M.W. (Eds.) Red Squirrels: Ecology, Conservation & Management in Europe.* European Squirrel Initiative, Woodbridge, Suffolk, UK. 67–82.
- Selonen V., Wistbacka R., 2016. Siberian flying squirrels do not anticipate future resource abundance. *BMC Ecol.* 16: 51.
- Selonen V., Wistbacka R., 2017. Role of breeding and natal movements in lifetime dispersal of a forest-dwelling rodent. *Ecol. & Evol.* 7: 2204–2213.
- Selonen V., Hanski I.K., Stevens P.C., 2001. Space use of the Siberian flying squirrel *Pteromys volans* in fragmented forest landscapes. *Ecography* 24: 588–600.
- Selonen V., Painter J.N., Hanski I.K., 2005. Microsatellite variation in the Siberian flying squirrel in Finland. *Ann. Zool. Fenn.* 42: 505–511.
- Selonen V., Hanski I.K., Desrochers A., 2007. Natal habitat-biased dispersal in the Siberian flying squirrel. *Proc. R. Soc. B* 274: 2063–2068.
- Selonen V., Sulkava P., Sulkava R., Sulkava S., Korpimäki E., 2010a. Decline of flying and red squirrels in boreal forests revealed by long-term diet analyses of avian predators. *Anim. Cons.* 13: 579–585.
- Selonen V., Hanski I.K., Painter J.N., 2010b. Gene flow and natal dispersal in the Siberian flying squirrel based on direct and indirect data. *Cons. Genet.* 11: 1257–1264.
- Selonen V., Hanski I.K., Mäkeläinen S., 2012. Predictors of long-distance dispersal in the Siberian flying squirrel. *Evol. Ecol.* 26: 1361–1369.
- Selonen V., Painter J.N., Rantala S., Hanski I.K., 2013. Mating system and reproductive success in the Siberian flying squirrel. *J. Mamm.* 94: 1266–1273.
- Selonen V., Hanski I.K., Wistbacka R., 2014. Communal nesting is explained by subsequent mating rather than kinship or thermoregulation in the Siberian flying squirrel. *Beh. Ecol. Socio.* 68: 971–980.
- Selonen V., Wistbacka R., Korpimäki E., 2016a. Food abundance and weather modify reproduction of two arboreal squirrel species. *J. Mamm.* 97: 1376–1384.
- Selonen V., Wistbacka R., Santangeli A., 2016b. Sex-specific patterns in body mass and mating system in the Siberian flying squirrel. *BMC Zool.* 1: 9.
- Shar S., Lkhagvasuren D., Henttonen H., Maran T., Hanski I.K., 2016a. *Pteromys volans*. The IUCN Red List of Threatened Species 2016. e.T18702A22270935. (Accessed on 16 December 2016)
- Shar S., Lkhagvasuren D., Bertolino S., Henttonen H., Kryštufek B., Meinig H., 2016b. *Sciurus vulgaris*. The IUCN Red List of Threatened Species 2016: e.T20025A22245887. (Accessed on 10 April 2017)
- Smith W.P., Gende S.M., Nichols J.V., 2005. The northern flying squirrel as an indicator species of temperate rain forests: test of an hypothesis. *Ecol. Appl.* 15: 689–700.
- Smith W.P., 2007. Ecology of *Glaucomys sabrinus*: habitat, demography, and community relations. *J. Mamm.* 88: 862–881.
- Smith J.R., van Vuren D.H., Kelt D.A., Johnson M.L., 2011a. Spatial organization of northern flying squirrels *Glaucomys sabrinus*: territoriality in females? *Western North American Naturalist* 71: 44–48.
- Smith W.P., Person D.K., Pyare S., 2011b. Source-sinks, metapopulations, and forest reserves: conserving northern flying squirrels in the temperate rainforests of Southeast Alaska. In: *Liu J., Hull V., Morzillo A.T., Wiens J., (Eds) Sources, sinks, and sustainability across landscapes.* Cambridge University Press, Cambridge, United Kingdom.
- Stapp P., Pekins P.J., Mautz W.M., 1991. Winter energy expenditure and the distribution of southern flying squirrels. *Can. J. Zool.* 69: 2548–2555.
- Steele M., 1998. *Tamiasciurus hudsonicus*. *Mammalian Species*. 586: 1–9.
- Steele M.A., 2008. Evolutionary interactions between tree squirrels and trees: A review and synthesis. *Current Science* 95: 871–876.
- Studd E.K., Boutin S., McAdam A.G., Krebs C.J., Humphries M.M., 2015. Predators, energetics and fitness drive neonatal reproductive failure in red squirrels. *J. Anim. Ecol.* 84: 249–259.
- Sulkava P., Sulkava R., 1993. Liito-oravan ravinnosta ja ruokailutavoista Keski-Suomessa (feeding habits of flying squirrel. Luonnon tutkija 97: 136–138. [in Finnish]
- Suzuki M., Kato A., Matsui M., Okahira T., Iguchi K., Hayashi Y., Oshida T., 2011. Preliminary Estimation of Population Density of the Siberian Flying Squirrel (*Pteromys volans orii*) in Natural Forest of Hokkaido, Japan. *Mammal Study* 36: 155–158.
- Suzuki K., Yanagawa H., 2013. Efficient placement of nest boxes for Siberian flying squirrels *Pteromys volans*: effects of cavity density and nest box installation height. *Wildl. Biol.* 19: 217–221.
- Taulman J.F., Smith K.G., 2004. Home range and habitat selection of southern flying squirrels in fragmented forests. *Mamm. Biol.* 69: 11–27.
- Taulman J.F., Smith K.G., Thill R.E., 1998. Demographic and behavioral responses of Southern flying squirrel on experimental logging in Arkansas. *Ecol. Appl.* 8: 1144–1155.
- Taylor B.D., Goldingay R.L., 2012. Restoring connectivity in landscapes fragmented by major roads: a case study using wooden poles as “stepping stones”. *Restor. Ecol.* 20: 671–678.
- Thorington R.W., Koprowski J.L., Steele M.A., Whatton J.F., (Eds.) 2012. *Squirrels of the world.* Johns Hopkins University Press, Baltimore, USA.
- Thorington K.K., Weigl P.D., 2011. Role of kinship in the formation of southern flying squirrel winter aggregations. *J. Mammal.* 92: 179–189.
- Timm U., Kiristaja P., 2002. The Siberian flying squirrel (*Pteromys volans* L.) in Estonia. *Acta. Zool. Lit.* 12: 433–436.
- Timm U., Remm J., 2011. Lendorava lugu. *Eesti Loodus* 62: 90–92. [in Finnish]
- U.S. Fish and Wildlife Service, 2013. Carolina Northern flying squirrel (*Glaucomys sabrinus coloratus*). 5-year review: summary and evaluation. Southeast Region, Asheville

- Ecological Services Field Office, North Carolina. Available at https://ecos.fws.gov/docs/five_year_review/doc4177.pdf (Accessed 22 December 2016)
- U.S. Fish and Wildlife Service, 2011. Draft recovery plan for the Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*), 1st revision. Southwest Region, Albuquerque, New Mexico.
- van Dyck H., Baguette M., 2005. Dispersal behaviour in fragmented landscapes: routine or special movements? *Basic. Appl. Ecol.* 6: 535–545.
- van Teeffelen A.J., Opdam P., Wätzold F., Hartig F., Johst K., Drechsler M., Vos C.C., Wisser S., Quétier F., 2014. Ecological and economic conditions and associated institutional challenges for conservation banking in dynamic landscapes. *Landsc. Urban. Plann.* 130: 67–72.
- Vierikko K., Pellikka J., Hanski I.K., Myllyviita T., Niemelä J., Vehkamäki S., Lindén H., 2010. Indicators of sustainable forestry: The association between wildlife species and forest structure in Finland. *Ecol. Indi.* 10: 361–369.
- Wauters L.A., Dhondt A.A., 1990. Nest-use by red squirrels (*Sciurus vulgaris* Linnaeus, 1758). *Mammalia* 54: 377–389.
- Wauters L., De Vos R., Dhondt A.A., 1990. Factors affecting male mating success in red squirrels (*Sciurus vulgaris*). *Ethol. Ecol. Evol.* 2: 195–204.
- Wauters L., Dhondt A., 1992. Spacing behaviour of red squirrels, *Sciurus vulgaris*: variation between habitats and the sexes. *Anim. Behav.* 43: 297–311.
- Wauters L.A., Githiru M., Bertolino S., Molinari A., Tosi G., Lens L., 2008. Demography of alpine red squirrel populations in relation to fluctuations in seed crop size. *Ecography* 31: 104–114.
- Wauters L.A., Preatoni D., Martinoli A., Verbeylen G., Matthysen E. 2011. No sex bias in natal dispersal of Eurasian red squirrels. *Mammalian Biol.* 76: 369–372.
- Wauters L.A., Verbeylen G., Preatoni D., Martinoli A., Matthysen E., 2010. Dispersal and habitat cuing of Eurasian red squirrels in fragmented habitats. *Popul. Ecol.* 52: 527–536.
- Weigl P.D., 1978. Resource overlap, interspecific interactions, and the distribution of the flying squirrels *Glaucomys volans* and *G. sabrinus*. *Am. Midl. Nat.* 100: 83–96.
- Weigl P.D., 2007. The northern flying squirrel (*Glaucomys sabrinus*): A conservation challenge. *J. Mammal.* 88: 897–907.
- Wells-Gosling N., Heaney L.R., 1984. *Glaucomys sabrinus*. *Mammalian Species* 229: 1–8.
- Wheatley M.T., 2011. Ecological scale and species-habitat modelling: studies on the northern flying squirrel. PhD thesis, University of Victoria, Canada.
- Wheatley M., Fisher J.T., Larsen K., Litke J., Boutin S., 2005. Using GIS to relate small mammal abundance and landscape structure at multiple spatial extents: the northern flying squirrel in Alberta, Canada. *J. Appl. Ecol.* 42: 577–586.
- Williams C.T., Gorrell J.C., Lane J.E., McAdam A.G., Humphries M.M., Boutin S., 2013. Communal nesting in an “asocial” mammal: social thermoregulation among spatially dispersed kin. *Behav. Ecol. Socio.* 67: 757–763.
- Wilson D.E., Reeder D.M., (Eds). 2005. *Mammal Species of the World. A Taxonomic and Geographic Reference (3rd Ed.)*. Johns Hopkins University Press.
- Winterrowd M.F., Weigl P.D., 2006. Mechanisms of cache retrieval in the group nesting southern flying squirrel (*Glaucomys volans*). *Ethology* 112: 1136–1144.
- Winterrowd M.F., Gergits W.F., Laves K.S., Weigl P.D., 2005. Relatedness within nest groups of the southern flying squirrel using microsatellite and discriminant function analysis. *J. Mammal.* 86: 841–846.
- Won C., Smith K.G., 1999. History and current status of mammals of the Korean Peninsula. *Mammal Rev.* 29: 3–33.
- Xuefei L., Deyan G., Lin X., Zhaoqun Z., Song L., Qisen Y., 2013. The Evolution and Paleobiogeography of Flying Squirrels (Sciuridae, Pteromyini) in Response to Global Environmental Change. *Evol. Biol.* 40: 117–132.
- Yamamoto H., Nitami T., Kisanuki H., 1995. Stand structure of mixed-species stands (I) Relation of species composition and topographic factors. *Journal of the Japanese Forestry Society* 77: 47–54 [in Japanese with English abstract]

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