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Not simply a grey issue: the worldwide introductions of *Callosciurus* squirrels and their consequences

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ABSTRACT

1. Rodents are traded as pet species, a practice that frequently results in new introduced populations. This is particularly true for tree squirrels where often only a few founders can establish viable colonies.
2. Here we review the worldwide introductions, ecology and impacts of two tree squirrel species, *Callosciurus erythraeus* and *C. finlaysonii*, and discuss the elements of a strategy to reduce squirrel introductions and settlements.
3. *C. erythraeus* has established viable populations in Argentina, France, Netherland, Hong Kong and Japan. An introduction to Belgium may have been stopped successfully. *C. finlaysonii* has been introduced to Italy, Singapore and Japan. After 1950, the mean number of introduction events was one every two years.
4. The most evident damage produced by these species relates to bark-stripping behavior that can be severe and significantly impact trees and timber plantations. Data on negative impacts to native species are reported but are not yet formally quantified. Both squirrel species carried with them parasites from the native range into the new habitats, causing new species introductions.
5. The ability of tree squirrels to establish successfully often with only a few founders combined with their human appeal make them high risk species and the pet trade should be considered as a high risk pathway for new introductions. A pro-active approach on preventing new introductions should therefore include trade restrictions and be combined with public education initiatives at the national and the European scale.
6. Tree squirrels represent an ‘alien species conundrum’. Experience from the UK and Italy have shown, that if action is delayed until introductions are recognised as a problem, it is generally too late to effectively control them due to logistic, legal, economic reasons or lack of public support. In case of new populations, a rapid response mechanism is therefore critical. Once established populations may become invasive and difficult or impossible to control.

Keywords: Alien species, Non-native, Pet trade, Trade regulation

Running head: Worldwide introductions of *Callosciurus* squirrels

Word count: 8,833

INTRODUCTION

The loss of biodiversity poses significant long-term threats to ecosystem functioning and human exploitation of biological resources. Next to habitat destruction, non-native invasive species comprise the second most important threat to loss of biodiversity (e.g. Vitousek et al. 1997, Lowe et al. 2000, Clavero et al. 2009). These effects occur through the ecological processes of competition, disease, predation, hybridization and, at higher levels, through ecosystem restructuring (Manchester & Bullock 1997, Macdonald & Burnham 2010). However, in contrast to tangible losses of habitat that can be quantified and illustrated by for example satellite imagery (Mayaux et al., 2005), the impacts of invasive species are often diffuse, may occur over relatively long time scales (e.g. decades as opposed to weeks or months) and are consequently often difficult to measure or demonstrate (Manchester & Bullock 1997, Strayer et al. 2006). Calls for early management action are therefore often ignored (e.g. Wauters et al. 1997) and by the time many invasive species have been publicly recognised as a problem, it is often too late for effective action due to logistic, economic or scale factors (Bertolino & Genovesi 2003).

Some spread of invasive species is inevitable but translocation to new environments is frequently a result of human activity such as shipping (e.g. Fernandez 2008) or in the case of many mammal species international trade (Genovesi et al. 2008). With respect to squirrel species often only a few founders and limited introduction events are needed to establish viable, expanding populations (Wood et al. 2007, Bertolino 2009). In many cases, these introductions are linked with impacts on native wildlife and or damage to crops or forests (e.g. Shorten 1954, Tamura & Ohara 2005, Nogales et al. 2006).

Among tree squirrel species, the North American grey squirrel (*Sciurus carolinensis*) has received widespread scientific and media attention and has been considered among the world's worst alien species by the IUCN (Lowe et al. 2000). It has been translocated beyond its natural range on the eastern seaboard, across the North American continent as far as Vancouver Island in Canada and California in the US. It was introduced to South Africa, Australia, UK, Ireland and Italy (Middleton 1930, Shorten 1954, Koprowski 1994, Peacock 2009, Bertolino 2008). This highly successful member of the tree squirrel family exemplifies our complex relationship with introduced non-native species that colonise not just remote woodlands and forests but often begin their 'invasion' from urban landscapes or parks as a result of human introductions. Grey squirrels compete with the native European red squirrel (*S. vulgaris*; e.g. Kenward & Holm 1993, Gurnell et al. 2004), are implicated in the decline of some woodland bird populations (Newson et al. 2010) and are a significant forest pest in Italy and the UK and subject to ongoing control in the latter (Kenward & Parish 1986, Currado et al. 1987, Mayle et al. 2007, Signorile & Evans 2007).

However, the problems of non-native tree squirrel populations are not restricted to *S. carolinensis*. Bertolino (2009) listed 248 events of squirrel introductions, with 18 out of 20 species considered to be established. Squirrels have the potential to become a serious issue for biodiversity, conservation and crop damage and the problem is likely to grow. There is a need for clearly envisaged national and continental policy strategies. Here we present data on two other tree squirrel species, *Callosciurus erythraeus* and *C. finlaysonii*, introduced to Europe, South America and part of Asia outside their native range (Table 1). These two species are considered highly invasive, with the ability to establish viable populations from only few animals released (Bertolino 2009). Specifically we review their introductions, ecology and impacts in non-native habitats and discuss a strategy to reduce squirrel introductions and settlements.

THE GENUS *CALLOSCIURUS*

According to Wilson and Reeder (2005) there are 15 species in the genus *Callosciurus*: *C. adamsi*, *C. albescens*, *C. baluensis*, *C. caniceps*, *C. erythraeus*, *C. finlaysonii*, *C inornatus*, *C. melanogaster*, *C. nigrovittatus*, *C. notatus*, *C. orestes*, *C. phayrei*, *C. prevostii*, *C. pygerythrus*, *C. quinquestriatus*. They are all distributed in Southeast Asia, from central Nepal east to Kiangsu (China) and south to Java (Indonesia). Two of these species have been introduced outside their native range: *C. erythraeus* and *C. finlaysonii*.

C. erythraeus is native to much of central and southern China, Bangladesh, northeastern India, Myanmar, Thailand, Laos, Vietnam, eastern Cambodia, Peninsular Malaysia, and Taiwan (Moore & Tate 1965, Wilson & Reeder 2005, Duckworth et al. 2008a). Within this range, Wilson and Reeder

(2005) recognized 26 subspecies; recently Li and colleagues (2006) added a new subspecies (*C. e. zhaotongensis*).

C. finlaysonii is a species naturally present in central Myanmar, Thailand, Laos, Cambodia and Vietnam, where 16 subspecies are presently recognized (Moore & Tate 1965, Wilson & Reeder 2005, Duckworth et al. 2008b).

REVIEW OF INTRODUCTIONS

We recorded 28 events of *C. erythraeus*, 4 events of *C. finlaysonii* and 1 *Callosciurus* sp. introduction. These are listed in Table 1 with information on the date of introduction, animals introduced, population range and density; for 31 events, the date of introduction was available. The number of introduction events occurring every 10 years remained constant after 1950 (4.67 ± 0.89 events/10-years) and the cumulative number resulted in a straight line (Fig. 1, $R^2 = 0.99$, $F_{1,5} = 1049$, $P < 0.001$).

Callosciurus erythraeus

Japan

The first introduction of *C. erythraeus* occurred in 1935 in Izu-Oshima Island, Tokyo, when some animals escaped from the zoological garden (Miyamoto et al. 2004). The species has since been introduced and has become established in several sites and islands along the pacific Coast in the central and western Japan. Presently there are 13 populations in Japan at Izu-oshima Island (Tokyo), Eastern Kanagawa (Kanagawa Prefecture), Izu Peninsula and Hamamatsu City (Shizuoka Prefecture), Mt. Kinkazan (Gifu Prefecture), Osaka City (Osaka Prefecture), Wakayama City and Tomogashima Island (Wakayama Prefecture), Himeji City, (Hyogo Prefecture), Takashima Island (Oita Prefecture), Iki and Fukue Island (Nagasaki Prefecture) and Uto Peninsula (Kumamoto Prefecture) (Abe et al. 2005, Ikeda et al. 2011). At least on three occasions, the escaped squirrels did not manage to successfully establish as shown in Table 1.

A study of Oshida et al. (2007) with mitochondrial DNA control region sequences showed that *C. erythraeus* of five Japanese population are closely related to *C. erythraeus* from Taiwan; for another population the results suggest possible multiple introductions of *C. e. taiwanensis* from Taiwan or repeated translocations within Japan (Ikeda et al. 2011, Tamura et al. 1998).

The study of Oshida et al. (2007) also indicated that some individuals from Hamamatsu are closely related to *C. finlaysonii* and not to *C. erythraeus* (Oshida et al. 2007). This may indicate the introduction of both species at this site, or the presence of some hybrids. In the absence of further studies we listed both species for Hamamatsu.

Hong Kong

C. erythraeus was introduced into Hong Kong (South China) probably in the late 1960s or early 1970s. First records were on the Peak on Hong Kong Island, and then breeding populations were introduced on the mainland in the New Territories (Ho 1994). According to Ho (1994), animals in Hong Kong Island belong to the subspecies *C. e. thai*; populations now occupy all woody habitats and are very common around human habitations. In the New Territories there is also the subspecies *C. e. styani* which has a restricted distribution in the central area. This is probably due to the high fragmentation of woodland habitats.

France

The species was introduced in the late 1960s or before 1974 to Cap d'Antibes (Alpes-Maritimes) (Jouanin 1986, Dozières et al. 2010); animals belong to the subspecies *C. e. erythrogaster* (Gurnell & Wauters 1998). The animals remained for many years in the area of the Cap, in and around the botanical garden, probably limited in their expansion by the city of Antibes. A survey conducted in

2007-2008 showed however, that the squirrels are now present in a 10 km^2 area east to Antibes and the village of Vallauris (Gerriet 2009).

Belgium
In August 2005 a small nucleus of squirrels was reported in Flanders, in a 5 hectare suburban park in Dadizele, south of the province of West-Vlaanderen (Stuyck et al. 2009). Initially the animals were suspected to be Chinese rock squirrels, *Sciurotamias davidianus*, but genetic analysis confirmed the presence of *C. erythraeus*. Considering the damage due to bark stripping and cable gnawing and the risk of population expansion, a trapping campaign started in October 2005 and 45 squirrels were removed in three months (Stuyck et al. 2009). In successive years the number of animals removed increased to 244 and by 2011 the last known animal was removed (Stuyck et al. 2009; Jan Stuyck pers. comm.).

Netherland
In 1998 some squirrels escaped from an animal trader resulting in a population in the area south-east of Weert (Dijkstra et al. 2009). Presently the species is reported in and between the urban areas of Weert and Ell, with an estimated population of 50-110 animals over a 550 ha area (400 ha of forest and 150 ha of urban areas). The species may have also spread to three other localities clustered in the south-east of Netherland (Tungelroy and Leveroy) and in Belgium (Mariahof), but records still need to be confirmed (Dijkstra et al. 2009).

Argentina
The species is present in Argentina with 5 distinct populations. *C. erythraeus thai* was first introduced in 1970, when 10 squirrels were released in Luján, province of Buenos Aires (Aprile & Chicco 1999). The species adapted to local habitats and had spread to an area of 1,340 km^2 in 2010, with densities of 15-18 ind. ha^{-1} (Benitez et al. 2010). In 1995 some animals were captured and released at Escobar (Buenos Aires), where they are now present in an area of approximately 34 km^2 (Benitez et al. 2010). Another translocation of squirrels from Luján to La Cumbrecita, province of Cordoba, occurred in 2000. The population of Cañada de Gómez, province of Santa Fe, originated from 8 squirrels traded and released in 1999. A further population was discovered in an urban area of Buenos Aires in 2004 (Benitez et al. 2010).

Callosciurus finlaysonii
Italy
Two populations are present: one at Acqui Terme, in Piedmont region North-West of Italy, and another at Maratea, Basilicata region, South Italy; both seem to belong to the subspecies *C. f. bocourti* (Mazzoglio et al. 2007). The first population originated from two pairs released in 1981 in an urban park, where the population was estimated at 40-50 animals during a visual census in 1998 (Bertolino et al. 1999). The population of Maratea originated through the release of 3-4 pairs in the middle of the 1980s (Aloise & Bertolino 2005). At Maratea the species remained restricted to the urban area for some years, and then started to spread along the Tyrrhenian cost in both directions (South and North), colonising an area of 26 km^2 by 2004. At least in one case, some animals were captured and released some kilometers inland, beyond the previous range (Aloise & Bertolino 2005).

Japan
According to a recent genetic study, some of the animals present at Hamamatsu which previously were considered to be *C. erythraeus* in fact carry mtDNA of *C. finlaysonii* (Oshida et al. 2007). Although there is no evidence of the introduction of this species in Japan, *C. finlaysonii* was sold as a pet and may also have been released. Considering that cages of mixed species of squirrels were commonly visible at trading points, e.g. Chatuchak market in Bangkok (John Duckworth pers.

comm.), then hybrids, or mothers pregnant with hybrids, may have been brought into Japan. Further studies are necessary to clarify the origin of this population.

Singapore
A small population of *C. finlaysonii* is present in Singapore (Benjamin Lee, pers. comm.), but there are no data available on its status. According to some photographs the animals seem to belong to the subspecies *C. f. bocourti*.

***Callosciurus* sp.**
Italy
A *Callosciurus* species has been recently discovered in Lombardy, in the province of Varese, close to the Lake Maggiore and a few kilometers from the Suisse border (A. Martinoli pers. comm.). The pelage color pattern was similar to *C. erythraeus* present at Dadizele in Belgium, with a brownish fur and a yellowish belly. Genetic analysis, however, did not confirm this attribution and the lack of DNA sequences for many *Callosciurus* species in GenBank made the species determination not yet possible.

CALLOSCIURUS AS INVADERS

Reasons for the successful establishment, subsequent spread and adaptation of these species to non-native and often urban habitat types relate both to their ecology as well as their innate appeal to humans (this attraction is for example reflected in the given name '*Callosciurus*' Beautiful squirrel). Whilst some are considered a significant pest species, squirrels are also often cherished as pets and appreciated for their ornamental value, and economic benefits as tourist attractions. The latter is an acknowledged factor in conservation efforts for the native red squirrel in the UK (e.g. Parrott et al. 2009) and has been listed as a factor in the perception of *C. erythraeus* in Argentina (Guichón et al. 2005).

Ecology
Tree squirrels are highly adaptive and opportunistic species and known diet ranges include tree seeds, plant materials such as flowers, buds, shoots, and fruit as well as fungi and insects. Populations introduced in urban areas benefit from human 'left-overs' and are often fed by the public (Bertolino et al. 2004, Jessen et al. 2010). This food supply may be important for squirrels to survive periods of natural food shortage (e.g. winter) and maintaining high population densities. Squirrels are also opportunistic predators of bird eggs and chicks and introduced species such as the grey squirrel in the UK have been implicated in the decline of some songbird species (Newson et al. 2010). Some species can also cause significant damage to trees trough bark stripping behavior, whilst not always known for the species' native range it is extensively reported for example for the grey squirrel in the UK and *C. erythraeus* in Japan and Argentina (e.g. Lurz et al. 2005, Tamura & Ohara 2005, Guichón et al. 2005, 2009, Gurnell et al. 2008).
Reported food habits of *C. erythraeus* in Vietnam include tree flowers and leaves as well as seeds, fruit and tree sap (e.g. Koyabu et al. 2009). Diet of the introduced populations in Japan varied seasonally with early feeding on tree flowers (e.g. *Camellia japonica*), followed by feeding on young leaves of several different species and as available different types of fruit (31 different species recorded). Other items included ants, cicadas and left-over food from tourists (Setoguchi 1990).
Available information on *C. finlaysonii* diet in native range is sparse and largely incidental in nature. The species is considered an important seed consumer and seed dispersal agent (Kitamura et al. 2004, Chanthorn et al. 2007, Suzuki et al. 2007) and also a frequent bird-nest predator. In Thailand, *C. finlaysonii* and *C. caniceps* were video recorded (5 out of 87 events) while taking eggs and nestlings from nests of trogons (Trogonidae) and Abbott's Babbler (*Malacocincla abbotti*)

(Andrew J. Pierce pers. comm.). Animals introduced in Italy fed mainly on seeds, fruits, buds, flowers, and occasionally on insects, switching from one resource to another according to seasonal availability (Bertolino et al. 2004).

Estimated population densities of *C. erythraeus* in conifer plantations on Taiwan is 2.5 squirrel ha^{-1} (Lin & Yo 1981); higher densities are recorded in Japan and Argentina (Table 1). Two distinct breeding peaks were observed in Taiwan (Jan-Mar and Jun-Aug) but studies on reproductive cycles indicated that *C. erythraeus* is capable of ovulation throughout the year (Tang & Alexander 1979). Observed population growth of the introduced *C. erythraeus* in Japan fits an exponential expansion curve (Tamura 2004). Rapid, 'explosive' expansion is also predicted for the introduced population of *C. erythraeus* in Argentina in the absence of systematic management and control measures (Guichón & Doncaster 2007) and the findings highlight the potential for spread of this species once populations have become firmly established. Data on densities and reproduction of *C. finlaysonii* are really scant. In Italy, three breeding periods were observed and females were associated with 1-2 weaned young, but sample size was small (Bertolino et al. 2004).

Habitat use and the likelihood of woodlot occupancy of *C. erythraeus* in Japan have been linked to woodland area and composition. The latter was linked to the proportion of broad-leaved ever-green trees present within a woodland (Miyamoto et al. 2004, Tamura et al. 2004). Overall tree species diversity was also considered a factor in habitat selection and cedar plantations and shrubs were utilized in radio-tracking studies (Okubo et al. 2005a). Conifer plantations in suburban environments were an important habitat feature for the species with regard nesting sites and nest materials (Okubo et al. 2005b).

Populations of *C. finlaysonii* introduced in North Italy are still confined to urban areas and suburbs (Andrea Balduzzi pers. comm.), while in South Italy the species is spreading along the Tyrrhenian coast, colonizing small villages and coastal woods (Aloise & Bertolino 2005).

Human dimension

In many cases the initial populations of squirrels in non-native habitats are not the result of natural range expansions due to for example changing habitat conditions or rare dispersal events. They result from human trade in animals and founding populations are often released pets. The first recorded grey squirrels in the UK were not unwanted intruders digging up flower bulbs or damaging trees but 'captured guests' that were first introduced to Henbury Park in Cheshire in 1876 (Middleton 1930). The arrival of the grey squirrel in the British Isles was the result of human whim, a desire to perhaps show off a novelty that was subsequently released into local woodlands. This also appears characteristic for many *Callosciurus* releases; *C. erythraeus* in Japan, France, and Argentina was first introduced as a pet and subsequently naturalised (Aprile & Chicco 1999, Gerriet 2009, Okubo et al. 2005b), the same was for the two populations of *C. finlaysonii* in Italy (Bertolino et al. 1999, Aloise & Bertolino 2005).

Squirrels with their cute looks and endearing behavior are appealing to humans that often want to see them in urban and private parks. This may lead to further introductions, and once a species is introduced into a country it is common that it will be translocated to other parts. For instance, this happened with *C. erythraeus* in Argentina (Guichon et al. 2005) and Japan (Miyamoto et al. 2004), *C. finlaysonii* (Aloise & Bertolino 2005) and *S. carolinensis* (Martinoli et al. 2010) in Italy, and *S. stramineus* in Perù (Jessen et al. 2010). These translocations potentially create new propagules, help the species overcome ecological barriers and increase the spread rate.

IMPACTS

Within its native range significant impacts of *C. erythraeus* on commercial conifer plantations through bark-stripping behavior are reported from Taiwan, with particularly severe damage on species such as *Cryptomeria japonica*, *Cunninghamia lanceolata*, *Pinus luchuensis* and *P. elliottii* (Lin & Yo 1981, Kuo 1982, Tsui et al. 1982).

Documented impacts of introduced populations are reported from France, Japan and Argentina although most data collected are qualitative and quantitative data are still lacking. The most evident damage is bark-stripping that can if severe, cause the death of the tree or significant commercial damage to timber. Bark, leaves and branches are also used to in the construction of nests (dreys). *C. erythraeus* is reported to cause serious damage to trees in France (Jouanin 1986) and to conifer plantations and natural forests in Japan (Tamura & Ohara 2005). Investigations into the chemical composition of bark to explain the pattern of damage in different tree species in Japan was inconclusive. However, there was a suggestion that sugar content of phloem and concentrations of secondary compounds such as flavanols may influence bark stripping behavior (Tamura & Ohara 2005). Bark-stripping behaviour from *C. finlaysonii* has been observed in Italy (Bertolino et al. 2004, Aloise & Bertolino 2005). Here damage may be severe; especially in urban parks where dying trees have been cut to reduce the risk of injury for visitors (Authors unpublished observation).

Damage to forest plantations and fruit orchards and trees (e.g. citrus, pears, nuts) by *C. erythraeus* is also reported from the district of Luján, Argentina, in addition to consumption of cereals in storage silos, damage to electrical cabling such light, telephone and television cables and the consumption of eggs in bird-rearing farms (Guichón et al. 2005, 2009). There is also the potential of negative impacts on the native fauna in Argentina, in particular on bird populations. However, at the moment there are only some occasional observations of squirrels preying on eggs (Pereira et al. 2003) and an anecdotal report from Japan of *C. erythraeus* predating a nest of the Japanese White-eye, *Zosterops japonica* (Azuma 1998).

PARASITES, DISEASES AND ZOONONSIS

Introduced species may carry parasites into new habitats that could switch to native host species (Barton 1997; Bertolino et al. 2010); in turn invading animals have to adapt to new communities of parasite species (Torchin and Mitchell 2004). The sum of these two phenomena may change the composition of the parasite community and the host-parasite interactions (Esch et al. 1990). Furthermore, the introduction of new diseases carried by introduced species has the potential to significantly affect native populations and competitive interactions. Disease-mediated competition has extensively been described in the interaction between the threatened native European red and the introduced North American grey squirrel in the UK and is one of the main factors in red squirrel decline in the UK (e.g. Rushton et al. 2006, Sainsbury et al. 2008).

C. erythraeus introduced into Japan carried 6 macroparasite species: a hard tick, *Haemaphysalis flava*; two sucking lice, *Enderleinellus kumadai* and *Neohaematopinus callosciuri*; a flea, *Ceratophyllus* (*Monopsyllus*) *anisus*; and three nematodes, *Brevistriata callosciuri*, *Strongyloides callosciureus* and *Gongylonema neoplasticum* (Kaneko 1954, Shinozaki et al. 2004a, b, Asakawa 2005, Sato et al. 2007). *Ceratophyllus anisus* and *H. flava* are fairly common on other hosts in Japan (Shinozaki et al. 2004a), thus they may be considered native to this country, while the other species were probably introduced with *Callosciurus* squirrels.

Dozières et al. (2010) analysed the macroparasite fauna of *C. erythraeus* from two populations introduced into urbanised areas in France and Belgium. They found a sucking louse *Enderleinellus kumadai* and a flea *Nosopsyllus fasciatus* in the French population; *E. kumadai* and another sucking louse *Hoplopleura erismata* in the Belgian population. Internal parasites were immature *Hymenolepis* sp. cestodes in France and immature *Mastophorus* sp. nematodes in Belgium. The scarcity of newly acquired parasites is probably due to the low number of mammalian species present in the urban areas where *C. erythraeus* was introduced (Dozières et al. 2010).

The mite *Androlaelaps fahrenhhozi* and the flea *Polygenis rimatus*, both from the American continent, and larvae of the flies *Cuterebinae* have been reported in *C. erythraeus* introduced to Argentina (Benitez et al. 2010).

Little is currently known about diseases with regard to *Callosciurus,* however, the potential risk of introducing disease is not just confined to native wildlife but may also in some cases pose a severe risk to human health. For example, monkeypox virus a disease known to potentially be carried by squirrels (e.g. *Funisciurus anerythrus* in Zaire, Khodakevich et al. 1986) as well as other rodents was introduced to the US in a shipment of 800 small mammals from Ghana. Traceback investigations identified a common distributor in Illinois where prairie dogs (*Cynomys* sp. ground squirrel) were housed together with imported Gambian giant rats (*Cricetomys* sp.). The incident led in 2003 to a multi-state outbreak of monkeypox virus in humans; 51 out of 53 patients reported close contact with prairie dogs (Center for Disease Control and Prevention 2003).

MANAGING INVADING SQUIRRELS

Game management activities and fur farming are recognized historically as pathways for squirrel introduction, while nowadays, the importation of pets either as a deliberate introduction or as an escape from captivity has become the main source of new populations (Bertolino 2009, this study). Animal trade has increased during the last few decades and it has become an important source of species introductions (Westphal et al. 2008). Squirrels are still being traded and sold as pets and further introductions may be expected. Thus, there is an urgent need that recommendation and restrictions on trade should be part of a global strategy on introduced species.

Europe still lacks a pro-active approach on invasive alien species. Releasing non-native animals is prohibited in many countries; however most of the squirrel introductions come from illegal releases or escapes from captivity. Single countries have occasionally prohibited importing, keeping and releasing species that were recognized as invasive, but usually after their successful establishment (e.g. *S. carolinensis* in England, *C. erythraeus* and other squirrels in France and Belgium). It is legitimate for European Union Member States to impose trade bans to protect their environment, as long as these regulations are based on scientific evidence which justifies their need. The same principle is true at the global level, where countries that are signatories of the World Trade Organization can impose trade regulations to protect their environment, as long as these regulations comply with the Sanitary and Phytosanitary Measures Agreement (SPS). An additional possibility to prohibit importing and keeping non-indigenous species within the European Union is to list them into the Annex B of EC Regulation No. 338/97 (The European Union Wildlife Trade Regulation that enforces CITES within the European Union). Four species are currently listed (*Trachemys scripta elegans*, *Rana catesbeiana*, *Chrysemys picta*, *Oxyura jamaicensis*) because they constitute an ecological threat to native species (Shine 2006); *Sciurus carolinensis*, *Sciurus niger* (the fox squirrel) and *C. erythrerus*, have recently been listed in the same annex, and a decision by the European Parliament on the inclusion of these three species is expected for the end of 2011. However, this is a re-active approach, species are proposed to be included in this list by single countries when they are already established and damage is relevant. An alternative option is to encourage a voluntary ban of the trade of these high risk species and the Bern Convention is working at a Code of Conduct of Companion Animals (Davenport & Collins, 2009).

A more pro-active approach for species that enter states through animal trade needs to consider their potential invasiveness before importation. A similar strategy has been established by some leading countries that have based their strategy on prevention of new introductions. Japan has built a system with three lists: species that are proved to be highly invasive in Japan or elsewhere are banned from the country (e.g. *C. erythraeus* already established in the country and *S. carolinensis* not present but invasive elsewhere), closely related species are subject to a risk-assessment procedure before importation (e.g. all species of the genus *Callosciurus* and *Sciurus*), while many others species simply need a certificate attached during their importation in order to verify the species (any member of the family Sciuridae not included in the other lists). Australia and New Zealand have established even more strict regulations, based on the so called approach "guilty until proven innocent" (Ruesink et al. 1995). Species that are permitted to be imported into these countries are included in a white list, while all other species are banned and cannot be imported before the risk they may pose is assessed and a permit is obtained.

Failing prevention, alternative management options are prompt eradication or spatial containment and/or a population control program (Wittenberg & Cock 2001). Eradication may be appropriate for isolated and newly colonized areas. For already established populations that are impacting significantly on ecosystems or human activities a permanent targeted control campaign may be the only alternative to inaction and accepting the damage (Barr et al. 2002, Peacock 2009, Stuyck et al. 2009). However, with squirrels and other similarly appealing species the human dimension is a crucial aspect to take into consideration (Genovesi & Bertolino 2001). The development of approaches that aim to involve the wider public and build up consensus on non-native species strategies, should thus constitute a priority. Consensus on actions should be based on rational judgments as well as ethical and legal considerations regarding the possibility that the released species will spread and may cause significant economic and ecosystem impacts.

CONCLUSION

This review attempted to highlight the risk posed by recent tree squirrel introductions. Whilst attention has largely been focused on the invasive American grey squirrel, this review has shown that other species, such as the two *Callosciurus* species considered here, potentially pose equal risks to native species, some agricultural crops and economic forestry operations. The history of tree squirrel introduction in many parts of the world has shown that successful establishment with only few founders, is often linked subsequently with a rapid exponential range expansion (e.g. Koprowski 1994, Tamura 1994, Lurz et al. 2001, Wood et al. 2007, Tattoni et al. 2006). This is often significantly extended by further translocations (Benitez et al. 2010, Martinoli et al. 2010). This is not only a heritage of the past but a major and increasing problem due to the number of recent and potential future introductions.

Tree squirrels in effect represent a ‘non-native species conundrum’. Public perceptions of invasive species are often based on emotional responses, expecially in urban populations, and understanding of non-native/native species interactions and their potential for detrimental impacts tend to be limited. The issue is made more complex because successful solutions to invasive species should ideally be instigated early on and experience from grey squirrels in the UK and Italy have shown, that if action is delayed until introductions are publicly recognised as a problem, it is generally too late for effective action due to logistic, legal or economic reasons or lack of public support (Sheail 1999, Bertolino 2008, Bertolino & Genovesi 2003). We therefore propose that, whilst assessments of ecosystem impacts as well as impacts on wildlife and the potential for economic damage should inform and guide non-native invasive species strategies (e.g. Lundberg 2010), for tree squirrels prevention through trade restrictions, prohibition of keeping and releasing animals, public education and early intervention should be considered a priority. Restrictions in trade could follow a number of examples and could be complete (e.g. Australia and New Zealand) or partial (Japan). Considering the trappability of many squirrels species, small populations could easily be removed if action is taken in time.

Once established, populations may become invasive and difficult or impossible to control. In case of new populations, a rapid response mechanism is therefore critical and could involve the setting up of a contingency fund and protocols for required actions on a national or supranational level. Furthermore, as soon as a problem is detected, the difficult process of informing the public, achieving a consensus and getting public support must be initiated.

Considering their innate appeal to humans and the fact that tree squirrels are readily found in pet shops in many countries (e.g. in Italy or Denmark; Sandro Bertolino and Karl Larsen pers. comm.), the pet trade must be considered a high risk pathway for new introductions with concomitant threats and impacts on native species, agriculture and forestry. In addition, there is also the risk of potential, linked introductions of diseases or parasites that can contribute to declines of native species (disease mediated competition) or result in disease outbreaks in humans (zoonosis). National and coordinated (e.g. European level) preventive actions should therefore also focus on public education and on a legal framework with regard to import and trade restrictions for tree squirrel species.

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Table 1. List of worldwide *Callosciurus* introductions.

Country	Locality	Year of introductio n	Animals released	Result	Area in km^2 (year)	Density in ind./ha (year)	Source
Callosciurus erythraeus							
Argentina	Luján	1970	10	Established	1340 (2006-2009)	15-18 (2006-2009)	1
Argentina	Escobar	1995		Established	34 (2006-2009)	3 (2006-2009)	1
Argentina	Cañada de Gómez	1999	8	Established	33 (2006-2009)	10 (2006-2009)	1
Argentina	La Cumbrecita	2000	30	Established	0.6 (2006-2009)	0.5 (2006-2009)	1
Argentina	Buenos Aires	2004		Established			1
Japan	Izu-oshima Island, Tokyo	1935	30 in 1935; 10 in 1927	Established	0.11 (all island)		4, 5, 6
Japan	Eastern Kanagawa	1951	50	Established	304 km^2 (2002)	3.9-4.0 (1983-1988)	4, 5, 7, 8
Japan	Nogeyama, Kanagawa	1967		Removed			4, 5
Japan	Tomogashima Is., Wakayama	1954	100	Established	1.4 (all island)		4, 5, 9
Japan	Mt. Kinkazan, Gifu	1955	< 10	Established			4, 5
Japan	Takasima Is., Oita	1955	4-6	Established			4, 5
Japan	Himeji City, Hyogo	1970	10	Rare*			4, 5
Japan	Osaka City, Osaka	1970s		Rare*			4, 5
Japan	Hamamatsu, Shizuoka	1970	10	Established			4, 5, 10
Japan	Wakayama City, Wakayama	1970s		Established			4, 5
Japan	Izu Peninsula, Shizuoka	1980		Established	145 km^2 (2007)		4, 5,
Japan	Nishiarai, Tokyo	1980s		Unsuccesfull			4, 5
Japan	Nippori, Tokyo	1980s		Unsuccesfull			4, 5

Japan	Meguro, Tokyo	1980s		Unsuccesfull		4, 5
Japan	Fukue Is., Nagasaki	1986	15	Established		4, 5
Japan	Renkouji, Tokyo	1995?		Unsuccesfull		4, 5
Japan	Iki Island, Nagasaki	1999?	< 20	Established		4, 5
Japan	Uto Peninsula, Kumamoto	2008		Established	25 km^2 (2010)	11
France	Antibes, Vallauris	1960s-1974	2	Established	10 (2009)	12
Netherland	Weert	1998		Established	0.055 (2009)	2
Belgium	Dadizele	< 2005		Eradicated?		3
China	Hong Kong	1960-1970s		Established		13
China	Hong Kong	1960-1970s		Established		13
Callosciurus finlaysonii						
Italy	Acqui Terme	1982	4	Established	Urban area (2010)	14, 15
Italy	Maratea	1980s	6-8	Established	26 (2004)	16
Singapore	Singapore			Established		17
Japan	Hamamatsu, Shizuoka	1970	10	Established		10
Callosciurus sp.						
Italy	Varese			Established		18

* Once established, but decreased without control and rare in 2011

1: Benitez et al. 2010; 2: Dijkstra et al. 2009; 3: Stuyck et al. 2009; 4: National Institute for Environmental Studies 2010; 5: Abe et al. 2005; 6: Udagawa 1954; 7: Tamura 2004; 8: Tamura et al. 1989; 9: Setoguchi 1990; 10: Oshida et al. 2007; 11: Ikeda et al. 2011; 12: Gerriet 2009; 13: Ho 1994; 14: Bertolino et al. 1999; 15: Andrea Balduzzi pers. comm.; 16: Aloise & Bertolino 2005; 17: Benjamin Lee, pers comm.; 18: Adriano Martinoli pers. comm.

Fig. 1. Number of world-wide *Callosciurus* introductions (n = 31 cases) every ten years (grey bars) and cumulative (black dors).