

Spread and attempted eradication of the grey squirrel (*Sciurus carolinensis*) in Italy, and consequences for the red squirrel (*Sciurus vulgaris*) in Eurasia

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Abstract

In 1997, the National Wildlife Institute, in co-operation with the University of Turin, produced an action plan to eradicate the American grey squirrel from Italy, as this introduced species replaces the native red squirrel through competitive exclusion and damages trees through de-barking. The first step, a trial eradication of a small population of grey squirrels at Racconigi (Turin) to evaluate the efficiency of the removal techniques, started in May 1997. Preliminary results showed that eradication was feasible, but the project was opposed by radical animal rights groups which took the National Wildlife Institute to court in June 1997. This legal action caused a suspension of the project and led to a lengthy judicial enquiry that ended in July 2000 with the acquittal of the Institute. Nevertheless, the 3-year suspension of all actions led to a significant expansion of the grey squirrel's range and thus eradication is no longer considered practical. Therefore, in the medium to long term, grey squirrels are likely to expand through continental Eurasia. This constitutes a major threat to the survival of the red squirrel over a large portion of its distribution range and will have a significant impact on forests, with economic damage to timber crops. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Italy plays a key role in conservation of the red squirrel (*Sciurus vulgaris*), as the country contains the only populations of American grey squirrels (*Sciurus carolinensis*) in continental Europe (Mitchell-Jones et al., 1999). The red squirrel is considered threatened in Europe (Amori and Zima, 1994; Mitchell-Jones et al., 1999), owing to fragmentation of woodland habitats (Celada et al., 1994; Wauters, 1997) and competition with the introduced grey squirrel. In the British Isles, the grey squirrel has extensively replaced the native species, which is now restricted to some conifer forests in Scotland and a few areas in England and Wales (Gurnell and Pepper, 1993; Gurnell, 1996). A similar

replacement pattern is being recorded in Italy (Wauters et al., 1997a). Furthermore, in the UK, grey squirrels produce significant damage to forests and commercial tree plantations (Kenward, 1983; Rowe and Gill, 1985; Gurnell, 1996; Currado, 1998; Dagnall et al., 1998). Bark-stripping activity inflicts wounds that can facilitate the penetration of insects and fungi and severely degrade timber quality, especially for hardwood (Kenward, 1983, 1989; Rowe and Gill, 1985; Dagnall et al., 1998).

The threat posed to the red squirrel by the grey squirrel in Italy has been underlined by several national and international organisations (e.g. IUCN, the UK Forestry Commission, WWF) and has been stressed during international meetings (e.g. the resolution at the 1st European Workshop on Squirrel Ecology; The Conservation of Red Squirrels, Gurnell and Lurz, 1997). In 1995, with respect to the international obligations of Italy (Bern Convention, Convention on Biological Diversity), the NWI (National Wildlife Institute) informed

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the relevant authorities (Ministry of Environment, Ministry of Health, Regional administrations, Provincial administrations) about the potential risks of the presence of the grey squirrel in Italy and the urgent need to eradicate the species in the country.

In this paper, we discuss the competition between the two squirrel species, analyse the patterns of the grey squirrel's spread in Italy and describe the action undertaken by the NWI to eradicate the alien species. We then discuss the risk of future expansion and the related threat to conservation of the red squirrel in Eurasia.

2. Origin and spread of the grey squirrel in Italy, and consequences for conservation

2.1. Introduction and spread of the grey squirrel

In Italy, the American grey squirrel was first introduced into Piedmont (north-western Italy) in 1948, when two pairs were imported from Washington, DC (USA) and released at Stupinigi (province of Turin; Bertolino et al., 2000). In 1966, five animals imported from Norfolk (Virginia, USA) were released into the park of Villa Gropallo at Genoa Nervi. A third introduction occurred in 1994 at Trecate (province of Novara; see Fig. 1), when the municipality funded the release of three pairs of grey squirrels in an urban park; however, in response to pressure to eradicate this

nucleus, the animals were recaptured two years later (Bertolino et al., 2000).

The population at Genoa Nervi seems still to be confined to a 2–3 km² area close to the site of introduction in a residential district with several private gardens and parks (Spanò et al., 1999). The site is surrounded by the sea and by busy roads, and the very limited presence of wood cover in the surrounding area seems to make expansion of the population unlikely, at least in the short term.

The Piedmont population has shown a rapid increase of its range in recent decades. From its introduction until 1970, the grey squirrel was only recorded close to the release site, occupying an area of about 25 km² (Fig. 2; Wauters et al., 1997a). Subsequently, the species started to spread into the surrounding area: in 1990, the species' range was 243 km² and in 1997 380 km². In 1996, 61 of the 125 identified woodlands and poplar plantations in the grey squirrel's range were monitored, and the species was found in 29 (48%) of them (Wauters et al., 1997a). Squirrels were more likely to occur in larger wood plots (plots <1 ha were avoided) with many species of large-seed-producing deciduous trees (Wauters et al., 1997a). After 1997, the range increased dramatically, and in the winter of 1999 the grey squirrel was present in an area of 880 km² (Table 1; Fig. 2). Although the methods used to assess the species' presence until 1997 (observation data) could have underestimated its range before 1999 (when presence was

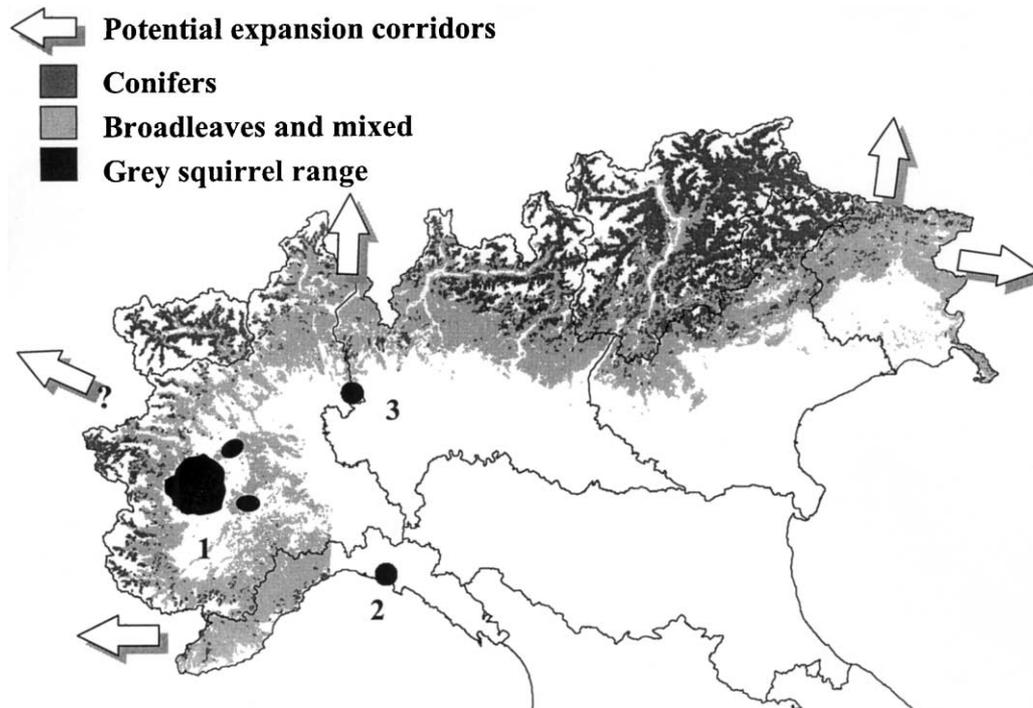


Fig. 1. Woodland cover in the Italian Alps, grey squirrel colonies and possible expansion corridors. 1: main colony (Piedmont); 2: Genoa Nervi; 3: Trecate (province of Novara).

assessed using hair tubes), an exponential growth of the grey squirrel distribution is evident (Fig. 3).

Over the whole 1948–2000 period, the grey squirrel has colonised at a mean rate of 17.2 km² per year (Table 1), similar to a value reported for Great Britain (18 km²/year, Okubo et al., 1989). However the colonisation of new areas has not been constant. In the first phase (1948–1970), when the spread outside the wooded area of Stupinigi was hindered by the presence of extended cultivated fields with very reduced and fragmented woods, it was only 1.1 km²/year. This increased to 10–20 km²/year once the species started spreading along rivers and recently increased to 250 km²/year when it reached the continuous broadleaf woods of the

hilly areas of eastern Piedmont and the Po River (Table 1).

The exponential range increase recorded in Piedmont (Fig. 3) is consistent with the pattern predicted by Elton (1927) for the establishment of a species. It is described by a sigmoid growth curve, characterised by a first phase of settlement, when the possibility of extinction is high, a phase of rapid increase, and finally a stabilisation phase. Accordingly, the spread of the grey squirrel in Italy can be described by a first phase of slow increase and a subsequent rapid population increase in the 1998–2000 period.

2.2. Effects on the red squirrel and forests

The spread of the grey squirrel in Great Britain and Ireland—where the species was introduced several times at the end of the 19th century and the beginning of the 20th century (Gurnell, 1987)—has caused the progressive disappearance of the native red squirrel from a large part of the two islands (Reynolds, 1985; Gurnell, 1987; Gurnell and Pepper, 1993). This pattern of replacement has also been observed in Italy: a distribution survey in the area where grey squirrels are present showed a 46% reduction of the red squirrel’s range from 1970 to 1990 and a further decrease of 55% from 1990 to 1996 (Wauters et al., 1997a).

The mechanisms by which the grey squirrel replaces the red squirrel are not yet clear but several hypotheses have been proposed (Skelcher, 1997). An interference competition hypothesis was recently tested by Wauters and Gurnell (1999) and rejected. Recent studies suggest that red squirrel juvenile recruitment is lower when grey squirrels are present (Wauters et al., 2000, 2001). A role of parapoxvirus in the replacement of reds by greys in the UK has also been hypothesised (Sainsbury et al., 1997, 2000; Rushton et al., 2000): the grey squirrel is believed to act as a reservoir host of this virus (Duff et al., 1996; Sainsbury et al., 1997, 2000).

The impact of the grey squirrel on the forest ecosystem and timber activity through de-barking is also a

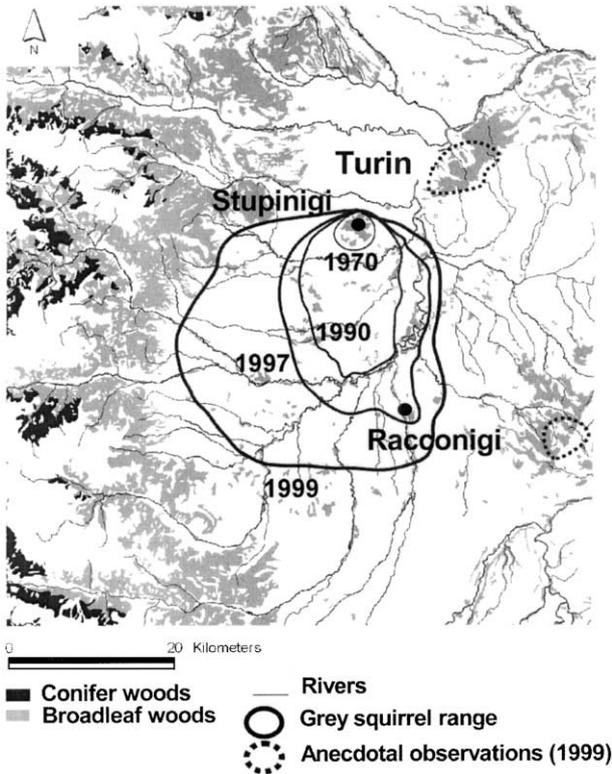


Fig. 2. Grey squirrel expansion in the 1970–1999 period. Distribution in 1970, 1990 and 1997 defined from data published in Wauters et al., 1997b (modified). Distribution in 1999 defined on the basis of hair-tube data.

Table 1
Area colonised by the grey squirrel in Piedmont, from its introduction until 1999

Period	Number of years	Range by the end of the period (km ²)	Range increase during the period (km ²)	Mean annual colonised area (km ² /year)
1948–1970	22	25	25	1.1
1971–1990	20	243	218	10.9
1991–1997	7	380	137	19.6
1998–1999	2	880	500	250
Total	51	880	880	17.2

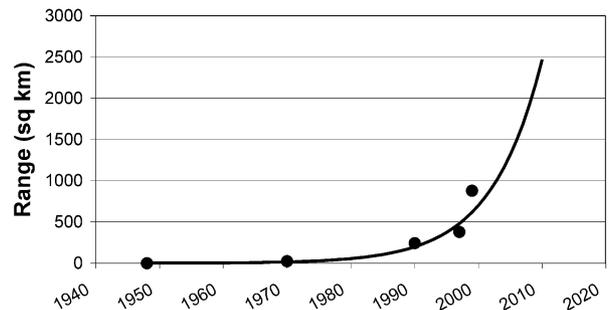


Fig. 3. An exponential growth model (from introduction until 2010) applied to grey squirrel range data (black dots). Model fitting: Range size = $e^{0.126 * \text{years from introduction}}$; regression analysis: Student’s *t* test, $t = 17.1$; $R^2 = 0.99$; $P = 0.0004$.

major concern. In this regard, it should be noted that sycamore (*Acer pseudoplatanus*) and beech (*Fagus sylvatica*), which are particularly vulnerable to de-barking in the UK (Rowe and Gill, 1985; Dagnall et al., 1998), are widely distributed in the Alps and represent the dominant species in some ecosystems (e.g. *Tilio-Acerion*, *Aceri-Fagetum*, *Abieti-Fagetum*; Pignatti, 1998).

3. Campaign for eradication of the Piedmont grey squirrel population

3.1. Piedmont population size

In Stupinigi (6.09 km² of woodland: 79.5% mixed deciduous woodland, 20.5% poplar plantation), where the species was first introduced, a drey count in 1996 led to an estimate of 0.5 squirrels ha⁻¹ (Wauters et al., 1997b). However, this estimate should be interpreted with caution, because in the particularly favourable climate of Italy, not all the squirrels build dreys.

In Racconigi, a density of about five individuals ha⁻¹ was estimated in a mark-recapture study in 1996, resulting in a total population of about 350 grey squirrels in the 70 ha of woodland (S. Bertolino, unpublished). When the data from Stupinigi and Racconigi were combined (see below), an average squirrel density of 1.27 individuals ha⁻¹ was obtained; considering the extension of the woodlands in the grey squirrel range, Wauters and co-authors (1997b) estimated the total grey squirrel population at about 2500.

To take account of the different woodland habitats, we re-calculated the total population size for the entire range. We assumed that the lowest density (1.27 individuals ha⁻¹) could be applied to the less suitable habitat (poplar plantation, covering 1850 ha) and the highest density (five individuals ha⁻¹) could be applied to the most suitable habitat (deciduous woodlands, covering 808 ha). In this way, we obtained a much higher estimate (6390 animals) so in planning the eradication, we considered a population of 6400 individuals (worst case scenario).

3.2. Eradication proposal

In 1996, the grey squirrel was confined to the agricultural area of central Piedmont, characterised by a widespread distribution of small woods located in a small number of estates and villas. The species' distribution was thus very patchy, suggesting that an eradication of the population was still feasible. However, the grey squirrel's range was only ca. 7 km from the alpine wood belt and, on the basis of the recorded speed of dispersal (7 km²/year: Wauters et al., 1997b), the arrival of the species at the continuous woodlands of this area was predicted in 1–2 years.

On the basis of the presumed feasibility of an eradication and the urgency to start the control before further expansion, the NWI, in co-operation with the University of Turin, proposed a management action plan in late 1996. This consisted of three steps: (1) continuous monitoring of the grey squirrel's range using hair-tubes; (2) a trial eradication to assess the feasibility of total removal; (3) planning and implementation of the eradication of the entire Piedmont population, if feasible.

The trial eradication to assess the feasibility of total removal was prompted by the eradication of coypu (*Myocaster coypus*) from the UK (Gosling et al., 1988), one of the few eradications carried out in Europe. Indeed the methods used (live trapping and euthanasia) and the population size (2975 adult females: Gosling and Baker, 1987) were very similar to those of the proposed grey squirrel eradication in Italy.

3.3. Trial eradication

3.3.1. Background

The aims of the trial eradication were: (1) to evaluate the efficiency of live-trapping to remove grey squirrels, (2) to estimate the effort needed to eradicate the Piedmont population, (3) to assess the presence of parapoxvirus.

The trial was carried out in the Racconigi estate, a 170-ha park of which 70 ha are covered by mixed deciduous old growth woodland. Racconigi park was one of the largest woodland areas within the grey squirrel's range. It was surrounded by roads and not directly connected to other woodlands, so the grey squirrel population could be assumed to be closed.

In order to improve public acceptance, the programme was sent to the main national non-governmental organisations (NGOs), including animal rights groups, for their comments in early 1997. Several consultation meetings were also organised to discuss possible alternative techniques. Following the comments submitted by the NGOs, the guidelines reported in the "Panel of Euthanasia" (AVMA, 1993) were adopted. After a formal request of one NGO (Legambiente), it was decided to anaesthetise the squirrels with halothane (a tranquilliser that specifically reduces stress in rodents) and then euthanise them with an overdose of the same drug.

The trial eradication was officially presented to all the parties in April 1997; local authorities and most NGOs approved the project, and the operative phase started in May 1997.

3.3.2. Methods

In mid-April 1997, 162 traps (Long Meadow multi-capture live-traps) were placed in the park (ca. 2.3 traps/ha of wood), covered with black plastic sheets, and

baited with maize. After a pre-baiting session of 2 weeks, the traps were set and checked once a day. The trapping was to be continued until the total removal of the population was verified (expected time >2 months); regression analysis of the capture data could then provide an estimate of the effort needed to remove other populations. Captured animals were placed in a sealed box, treated with halothane, and monitored by a veterinarian to detect stress indicators and the time needed for unconsciousness. After euthanasia, a blood sample was taken and a post-mortem examination was carried out in the laboratory.

3.3.3. Results

The adopted euthanasia procedure was very effective in minimising stress in the animals. The squirrels reached unconsciousness in less than a minute (Scagliarini, unpublished) and were then euthanised in the field.

During the two trapping sessions (a total of eight trapping days), 188 animals (>50% of the estimated population) were trapped; no non-target species were captured.

3.3.4. Legal aspects

In June 1997, three radical animal rights groups took the co-ordinator of the trial eradication and the director of the NWI to court, under the charges of illegal hunting, damage to state property and cruelty to animals. The trial eradication was thus halted. Under Italian law, the NWI does not need any authorisation to carry out research involving the capture of animals, but it cannot directly carry out pest-control programmes. In the courts, it was thus debated whether a trial eradication involving the killing of 200 animals should be considered as research or a pest-control program (Genovesi and Bertolino, 2001a). The Ministry of Environment stated that the trial eradication was aimed at protecting state property, specifically the native red squirrel, and was consistent with the Bern Convention and the Convention on Biological Diversity adopted by Italy. The first level of the trial ended in December 1999. The judge ruled that the two officers were guilty of illegal hunting and cruelty to animals. They were acquitted of the charge of damage to state property. The sentence was appealed and in July 2000, 3 years after the initial charges, the two officers were acquitted by the Appeal Court (Genovesi and Bertolino, 2001a).

The legal case was reported by the media, including national television and all the main newspapers, with very different perspectives (Genovesi and Bertolino, 2001a). Several organisations, including the World Conservation Union (IUCN), the Italian Zoological Society and the Italian Mammal Society, supported the trial eradication, indicating that the project carried out by the NWI was scientifically and ethically correct.

The early end of the programme did not permit the regression analysis to estimate the effort needed to remove the entire Piedmont population (Fig. 4).

4. Discussion

Biotic invasions are responsible for global environmental changes (Vitousek et al., 1996; Mack et al., 2000) and are considered a major threat to biodiversity (IUCN, 2000). Furthermore, the biotic homogenisation caused by the introduction of alien species is expected to increase rapidly in the near future, as a consequence of the increasing level of transport, trade and tourism related to economic globalisation (Mooney and Hobbs, 2000).

To face this threat, priority should be given to the prevention of unauthorised introductions. However, it is evident that even the most efficient framework of quarantine measures and regulation of species movements cannot prevent all new accidental or intentional introductions of invasive alien species (Wittemberg and Cock, 2001). Once prevention has failed and a new invasive (or potentially invasive) alien species has arrived in a new environment, the best option is its rapid and complete eradication. Indeed, only this measure will prevent future impact on biodiversity and human activities (Myers et al., 2000; Wittemberg and Cock, 2001). Moreover, it is a better alternative than permanent control because the latter strategy cannot definitively resolve the problem, is generally more expensive and, in the long term, requires the killing of larger numbers of animals (Lodge, 1993; OTA, 1993; Genovesi, 1999, 2000; Pimentel et al., 2000). Therefore,

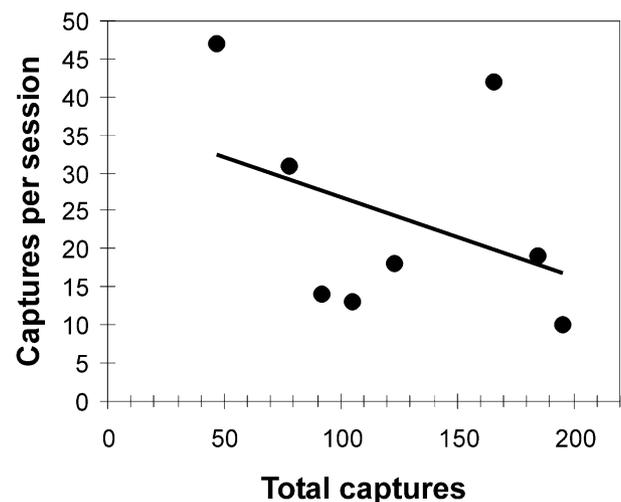


Fig. 4. Captures of grey squirrels at Racconigi during the eight days of the trial eradication. Removal method of estimating population size: $n = 354$ ($y = -0.1053x + 37.29$); regression analysis: $R^2 = 0.1603$; $F = 1.145$; $P = 0.326$.

eradication of alien invasive species is explicitly recommended by the IUCN Guidelines for the Prevention of Biodiversity Loss Caused by Alien Invasive Species (IUCN, 2000) and by the Convention on Biological Diversity (1992).

Eradications for conservation purposes started around 1950 and have become a widespread conservation tool in recent decades (Pascal, 1999; Myers et al., 2000; Simberloff, in press; Aitkinson, in press; see Veitch and Clout, in press for a review of eradications on islands). In Europe, there have been successful eradications of the muskrat (*Ondatra zibethicus*) and coypu from the UK (Gosling and Baker, 1987; Gosling, 1989; Gosling and Baker, 1989), the brown rat (*Rattus norvegicus*) from several islands around Corsica (France; Thibault, 1992) and from 10 islands in Brittany (France; Pascal, 1999), and the rabbit (*Oryctolagus cuniculus*) and goat from the Deserta Grande reserve (Portugal; Oliveira, 1999, also see Genovesi, 2000).

4.1. Feasibility of a grey squirrel eradication in Italy

The results of the trial eradication indicated that the adopted removal techniques are highly selective and humane and that, at least at a high-medium density, the rate of removal greatly exceeds the rate of population increase. However, the dramatic change in the grey squirrel's range, as a consequence of the 3-year suspension of the eradication programme, has strongly affected the feasibility of total removal. While the range of the grey squirrel was still very limited in 1997, a distribution survey carried out in winter 1999, using transects of hair-tubes (Gurnell et al., 2001), showed that grey squirrels had reached the edge of the Alps, the hilly area of Turin and the eastern part of Piedmont, characterised by a hilly landscape with continuous broadleaf woods and hazelnut plantations (Genovesi and Bertolino, 2001b).

The expansion of the grey squirrel to the continuous optimal habitats of the Alps and eastern Piedmont and its observed ability to establish populations from just a few pairs of individuals limits the practicability of eradication. This would now require the simultaneous implementation of removal techniques over the entire range of the species, with methods maintaining a high level of efficiency even at very low densities. Given our limited ability to predict the time needed to remove the population, substantial resources (personnel, traps, funds) would also be needed over the long term. Furthermore, as the species is now present in many residential parks, where any control program would require a complex authorisation process, it would be necessary to provide the relevant bodies with the authority to carry out the trapping activity in all areas, including private property.

In conclusion, although biologically feasible, complete eradication of the grey squirrel from Piedmont appears to be impracticable, requiring extraordinary legal instruments, the definition of a clear line of authority and very substantial resources. However, this task could be reconsidered in the future if an adequate political commitment at the highest State levels was ensured.

4.2. Risks of further expansion

The expansion rates recorded in the 1998–1999 period and the habitat of the alpine region (Fig. 1) make colonisation of the Alps in the short term very probable. This prediction is also supported by a model developed by Lurz et al. (2001): it indicates that the spread of the grey squirrel is likely to speed up in the pre-alpine forest because of the more continuous woodland and that the species will cross the Alps and reach France in 30–50 years. The data collected in the UK and Italy consistently support the conclusion that the species could rapidly and successfully colonise a wide area of continental Eurasia (potentially including the entire global distribution range of the red squirrel) in the medium-long term.

4.3. A strategy for the future

If eradication of grey squirrels is now impracticable, an alternative is needed to ensure the long-term survival of the red squirrel in Italy and to delay, as much as possible, further expansion of the grey squirrel toward the Alps and Apennines. A scheme has been presented by the NWI to the Ministry of Environment which has endorsed it (Genovesi and Bertolino, 2001b). The strategy requires the creation of an ad hoc technical group to define key areas for conservation of the red squirrel and corridors of potential expansion of the grey squirrel in which local eradication or control of the alien species are recommended. Re-introduction of red squirrels to areas where the species has disappeared, after successful removal of grey squirrels (if this can be achieved), is also suggested.

5. Conclusions

There have been numerous successful eradications carried out in the past century, including hundreds of small-scale programs (see reviews in Pascal, 1999; Veitch and Clout, in press) but also some large-scale cases, such as the extirpation of smallpox from the Earth and of *Anopheles gambiae* from over 30,000 km² of north-eastern Brazil (Davis and Garcia, 1989; Myers et al., 2000; Simberloff, in press). However, the main limits to the wider application of this critical management tool in conservation seem to be the pessimistic view that eradication is usually an impossible goal (e.g. Bomford

and O'Brian, 1995) and the opposition by a part of society, concerned with the costs and/or the undesired effects of the removal techniques.

The case of the grey squirrel is emblematic of this general picture: the impact of the species on the native red squirrel is confirmed by the observations collected in the UK and Italy; the possible expansion of the alien species on a continental scale could have a severe impact on the woodland ecosystems of Eurasia and on timber production; the biology of the grey squirrel and the data collected in the trial eradication carried out in Italy confirm that the species is vulnerable to trapping, allowing the use of a very humane removal technique. Thus, although it would require substantial resources, eradication of the species appears to be a possible alternative which could prevent huge economic losses and ecological disaster. Nevertheless, the limited political commitment and the opposition of a few animal rights groups, which caused the failure of the trial, make eradication an impracticable option. As far as the general issue of biotic invasions is concerned, the grey squirrel eradication failure indicates that to reduce the threat posed by invasive alien species, it is essential to: (1) disseminate more information on the issue to the competent authorities and to the general public; (2) revise the legal framework dealing with wildlife management and animal trade (see Shine et al., 2000 for a review); (3) define a clear line of authority at a national level; and (4) create rapid alert mechanisms and task forces for the eradication of newly established populations of alien species.

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References

Aitkinson, I.A.E. Introduced mammals and models for restoration. *Biological Conservation* (in press).

- Amori, G., Zima, J., 1994. Threatened rodents in Europe: species status and some suggestions for conservation strategies. *Folia Zoologica* 43 (1), 1–9.
- AVMA (American Veterinary Medical Association), 1993. Panel of Euthanasia. *Journal of the American Veterinary Medical Association* 202 (2), 229–249.
- Bertolino, S., Currado, I., Mazzoglio, P.J., Amori, G., 2000. Native and alien squirrels in Italy. *Hystrix Italian Journal of Mammalogy* (n.s.) 11 (2), 49–58.
- Bomford, M., O'Brien, P., 1995. Eradication or control for vertebrate pests? *Wildlife Society Bulletin* 23 (2), 249–255.
- Celada, C., Bogliani, G., Gariboldi, A., Maracci, A., 1994. Occupancy of isolated woodlots by the red squirrel *Sciurus vulgaris* L. in Italy. *Biological Conservation* 69, 77–183.
- Currado, I., 1998. The gray squirrel (*Sciurus carolinensis* Gmelin) in Italy: a potential problem for the entire European continent. In: Steele, M.A., Merritt, J.F., Zegers, D.A. (Eds), *Ecology and Evolutionary Biology of Tree Squirrels*. Virginia Museum of Natural History, Special Publication, no. 6, pp. 263–266.
- Dagnall, J., Gurnell, J., Pepper, H., 1998. Bark-stripping by gray squirrels in state forests of the United Kingdom: a review. In: Steele, M.A., Merritt, J.F., Zegers, D.A. (Eds), *Ecology and Evolutionary Biology of Tree Squirrels*. Virginia Museum of Natural History, Special Publication, no. 6, pp. 249–261.
- Davis, J.R., Garcia, R., 1989. Malaria mosquito in Brazil. In: Dahlsten, D.L., Garcia, R. (Eds.), *Eradication of Exotic Pests*. Yale University Press, New Haven and London, pp. 274–283.
- Duff, J.P., Scott, A., Keymer, I.F., 1996. Parapox virus infection of the grey squirrel. *Mammal News*, The Quarterly Newsletter of the Mammal Society, 10.
- Elton, C.S., 1927. *Animal Ecology*. Sidgwick & Jackson, London.
- Genovesi, P., 1999. Activities of the World Conservation Union (IUCN). In: Report of the Workshop on the Control and Eradication of Non-native Terrestrial Vertebrates, Malta, 3–5 June 1999, organised by the Council of Europe in co-operation with the Ministry of the Environment of Malta, pp. 107–108.
- Genovesi, P., 2000. Guidelines for Eradication of Terrestrial Vertebrates: a European Contribution to the Invasive Alien Species Issue. Council of Europe, tpvs65e-2000, 61 pp.
- Genovesi, P., Bertolino, S., 2001a. Human dimension aspects in invasive alien species issues: the case of the failure of the grey squirrel eradication project in Italy. In: McNeely, J.A. (Ed.), *The Great Reshuffling: Human Dimensions of Invasive Alien Species*. IUCN, Gland Switzerland and Cambridge, UK, pp. 113–119.
- Genovesi, P., Bertolino, S., 2001b. Guide lines for the control of the American grey squirrel (*Sciurus carolinensis*). *Quaderni Conservazione Natura*. Min. Environment—National Wildlife Institute, no. 4, pp. 51 (in Italian, English executive summary).
- Gosling, L.M., 1989. Extinction to order. *New Scientist* 44–49.
- Gosling, L.M., Baker, S.J., 1987. Planning and monitoring an attempt to eradicate coypus from Britain. *Symposia of the Zoological Society of London* 58, 99–113.
- Gosling, L.M., Baker, S.J., 1989. The eradication of muskrats and coypus from Britain. *Biological Journal of the Linnean Society* 38, 39–51.
- Gosling, L.M., Baker, S.J., Clarke, C.N., 1988. An attempt to remove coypus (*Myocastor coypus*) from a wetland habitat in east Anglia. *Journal of Applied Ecology* 25, 49–62.
- Gurnell, J., 1987. *The Natural History of Squirrels*. Christopher Helm, London.
- Gurnell, J., 1996. The effects of food availability and winter weather on the dynamics of a grey squirrel population in southern England. *Journal of Applied Ecology* 33, 325–338.
- Gurnell, J., Lurz, P., 1997. *The Conservation of Red Squirrels, Sciurus vulgaris* L. People Trust for Endangered Species.
- Gurnell, J., Lurz, P.W.W., Pepper, H., 2001. Practical Techniques for Surveying and Monitoring Squirrels. *Forestry Commission Practical Notes*, no. 11, 12 pp.

- Gurnell, J., Pepper, H., 1993. A critical look at conserving the British red squirrel *Sciurus vulgaris*. *Mammal Review* 23, 125–136.
- IUCN, 2000. Guidelines for the Prevention of Biodiversity Loss caused by Alien Invasive Species. IUCN, Gland, Switzerland, February 2000, 14 pp.
- Kenward, R.E., 1983. The causes of damage by Red and Grey squirrel. *Mammal Review* 13 (2–4), 159–166.
- Kenward, R.E., 1989. Bark-stripping by grey squirrels in Britain and North America: why does the damage differ? In: Putman, R.J. (Ed.), *Mammals as Pests*. Chapman and Hall, pp. 144–154.
- Lodge, D.M., 1993. Biological invasions: lessons for Ecology. *Trends in Ecology and Evolution* 8 (4), 133–137.
- Lurz, P.W.W., Rushton, S.P., Wauters, L.A., Bertolino, S., Currado, I., Mazzoglio, P.J., Shirley, M.D.F., 2001. Predicting grey squirrel expansion in North Italy: a spatially explicit modelling approach. *Landscape Ecology* 16, 407–420.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., Bazzaz, F.A., 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10, 689–710.
- Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Kryštufek, B., Reijnders, P.J.H., Spitzenberger, F., Stubbe, M., Thissen, J.B.M., Vohralik, V., Zima, J., 1999. *The Atlas of European Mammals*. Academic Press, London.
- Mooney, H.A., Hobbs, R.J., 2000. Global change and invasive species: where do we go from here? In: Mooney, H.A., Hobbs, R.J. (Eds.), *Invasive Species in a Changing World*. Island Press, Washington, pp. 425–434.
- Myers, J.H., Simberloff, D., Kuris, A.M., Carey, J.R., 2000. Eradication revisited: dealing with exotic species. *Trends in Ecology and Evolution* 16 (8), 316–320.
- Okubo, A., Maini, P.K., Williamson, M.H., Murray, J.D., 1989. On the spatial spread of the grey squirrel in Britain. *Proceedings of the Royal Society of London B* 238, 113–125.
- Oliveira, P.J., 1999. Habitat restoration on Deserta Grande, Madeira (Portugal—eradication of non-native mammals). In: *Workshop on the Control and Eradication of Non-native Terrestrial Vertebrates*. Council of Europe, Environmental Encounters, No. 41, pp. 49.
- OTA (Office of Technology Assessment), 1993. *Harmful Non-Indigenous Species in the United States* (OTA F-565). US Government Printing Office, Washington, DC.
- Pascal, M., 1999. Eradication of mammals introduced in the islands. In: *Proceedings of the Workshop on the Control and Eradication of Non-native Terrestrial Vertebrates*. Council of Europe, Environmental Encounters, No. 41, pp. 31–42.
- Pignatti, S., 1998. *Italian Woodlands: Ecology and Biodiversity*. UTET, Torino (in Italian).
- Pimentel, D., Lach, L., Zuniga, R., Morrison, D., 2000. Environmental and economic costs of nonindigenous species in the United States. *BioScience* 50 (1), 53–65.
- Reynolds, J.C., 1985. Details of the geographic replacement of the red squirrel (*Sciurus vulgaris*) by the grey squirrel (*Sciurus carolinensis*) in eastern England. *Journal of Animal Ecology* 54, 149–162.
- Rowe, J.J., Gill, M.A., 1985. The susceptibility of tree species to bark-stripping damage by grey squirrels (*Sciurus carolinensis*) in England and Wales. *Quarterly Journal of Forestry* 79, 183–190.
- Rushton, S.P., Lurz, P.W.W., Gurnell, J., Fuller, R., 2000. Modelling the spatial dynamics of parapoxvirus disease in red and grey squirrels: a possible cause of the decline in the red squirrel in the UK? *Journal of Applied Ecology* 37 (6), 997–1012.
- Sainsbury, A.W., Nettleton, P., Gurnell, J., 1997. Recent developments in the study of parapoxvirus in red and grey squirrels. In: Gurnell, J., Lurz, P. (Eds.), *The Conservation of Red Squirrels, Sciurus vulgaris L.* People Trust for Endangered Species, pp. 105–108.
- Sainsbury, A.W., Nettleton, P., Gilray, J., Gurnell, J., 2000. Grey squirrels have high seroprevalence to a parapoxvirus associated with deaths in red squirrels. *Animal Conservation* 3, 229–233.
- Shine, C., Williams, N., Gündling, L., 2000. A guide to designing legal frameworks on alien invasive species. IUCN Environmental Policy and Law paper no. 40, 138 pp.
- Simberloff, D. From today Taragiri tomorrow the world!—are we aiming too low in invasives control? In: Veitch, C.R., Clout, M.N. (Eds.), *Turning the Tide: the Eradication of Invasive Species*. Invasive Species Specialist Group of IUCN, Auckland (in press).
- Skelcher, G., 1997. The ecological replacement of red by grey squirrels. In: Gurnell, J., Lurz, P. (Eds.), *The Conservation of Red Squirrels, Sciurus vulgaris L.* People Trust for Endangered Species, pp. 67–78.
- Spanò, S., Oliva, E., Marsan, A., 1999. Lo Scoiattolo grigio (*Sciurus carolinensis* Gmelin, 1788) in Liguria. *Regione Liguria*, 30 pp.
- Thibault, J.-C., 1992. Eradication of the Brown rat from Toro islets (Corsica): remarks about an unwanted colonizer. *Avocetta* 16, 114–117.
- Veitch, C.R., Clout, M.N. (Eds.). *Turning the Tide: the Eradication of Invasive Species*. Invasive Species Specialist Group of IUCN, Auckland (in press).
- Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Westbrooks, R., 1996. Biological invasions as global environmental change. *American Scientist* 84, 468–478.
- Wauters, L.A., 1997. The ecology of red squirrel (*Sciurus vulgaris*) in fragmented habitats: a review. In: Gurnell, J., Lurz, P. (Eds.), *The Conservation of Red Squirrels, Sciurus vulgaris L.* People Trust for Endangered Species, pp. 5–12.
- Wauters, L.A., Currado, I., Mazzoglio, P.J., Gurnell, J., 1997a. Replacement of red squirrels by introduced grey squirrels in Italy. In: Gurnell, J., Lurz, P. (Eds.), *The Conservation of Red Squirrels, Sciurus vulgaris L.* People Trust for Endangered Species, pp. 79–88.
- Wauters, L., Gurnell, J., 1999. The mechanism of replacement of red squirrels by grey squirrels: a test of the interference competition hypothesis. *Ethology* 105, 1053–1071.
- Wauters, L.A., Gurnell, J., Currado, I., Mazzoglio, P.J., 1997b. Grey squirrel management in Italy—squirrel distribution in a highly fragmented landscape. *Wildlife Biology* 3 (2), 117–124.
- Wauters, L., Gurnell, J., Martinoli, A., Tosi, G., 2001. Does inter-specific competition with grey squirrels affect the foraging behaviour and food choice of red squirrels? *Animal Behaviour* 61, 1079–1091.
- Wauters, L.A., Lurz, P.W.W., Gurnell, J., 2000. The effects of inter-specific competition by grey squirrels (*Sciurus carolinensis*) in the space use and population dynamics of red squirrels (*S. vulgaris*) in conifer plantations. *Ecological Research* 15, 271–284.
- Wittemberg, R., Cock, M.J.W., 2001. *A Toolkit of Best Prevention and Management Practices*. CAB International, Wallingford, Oxon, UK.