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Grey squirrel *Sciurus carolinensis* management in Italy - squirrel distribution in a highly fragmented landscape

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American grey squirrels *Sciurus carolinensis* introduced to northern Italy in 1948 have caused damage to commercial poplar plantations and have replaced the native red squirrel *Sciurus vulgaris* from most of the 350 km^2 of the Piedmont Po-plain they currently occupy. In order to plan a control programme aiming to stop grey squirrels from further spreading and to decrease their numbers, the current distribution and population size in the highly fragmented landscape of the Po-plain were studied. The probability of finding grey squirrels in woodland fragments increased with habitat quality (diversity of trees producing large, consumable seeds), woodlot size and the proportion of poplar. Adding isolation variables did not improve the fit of the logistic regression model that predicted squirrel presence. The density of squirrel dreys, an index of population density, in the large Stupinigi forest also increased with tree species diversity. An estimate of the minimum population size for all woodlots assessed for squirrel presence was 1,260 animals in the summer of 1996. This extrapolates to a total of ca 2,500 grey squirrels in Piedmont. Grey squirrels continue to increase their range and are getting close to the continuous mixed forests of the pre-Alps and to large hazel plantations. Control measures to stop the spread of grey squirrels, and eventually to eradicate them, should be implemented immediately.

Key words: distribution, fragmented landscape, grey squirrel, population control, Sciurus carolinensis, tree species diversity

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Introduced exotic species that succeed in establishing viable populations and increase their distribution, often become pests. They can cause considerable damage to agriculture or forestry, and/or become a threat to related native species occupying a similar niche. One example of an introduced mammal pest in Europe is the American grey squirrel *Sciurus carolinensis* released at several locations in the U.K. between 1876 and 1930 (Middleton 1930, Shorten 1954, Lloyd 1983, Gurnell 1987), and at two locations in northern Italy (Candiolo, Stupinigi forests in Piedmont in 1948; Nervi Park, in Liguria in 1966, Currado, Scarramozzino & Brusino 1987, Currado, Mazzoglio, Amori & Wauters in press). In the U.K., grey squirrels remove the bark of many broadleaf tree species, and cause serious economic damage to commercial hardwood timber production (Rowe & Gill 1985, Gurnell & Pepper 1988, Kenward, Parish & Robertson 1992). In northern Italy, similar damage has been reported in commercial poplar plantations, cultivated for pulp and softwood production (Currado et al. 1987, in press). In Italy, grey squirrels are still increasing their range and are close to reaching the prealpine forests in the north and the economically important hazel plantations in the south (Currado et al. in press). Moreover, in both countries the introduced grey squirrel competes with the native Eurasian red squirrel *Sciurus vulgaris*. Red squirrels have been replaced by grey squirrels in most broadleaved and mixed forests of England and Wales (e.g. Reynolds 1985, Gurnell & Pepper 1993). Recently, replacement of red by grey squirrels has also been reported in northern Italy, where the latter species now occupies about 350 km^2 of the high Po-plain south and southwest of Turin, Piedmont (Currado et al. 1987, in press).

In Italy, urgent steps are being taken to implement a grey squirrel control programme in order to stop them from spreading into continuous forests north of Turin, where control would become impossible, and to decrease their population size (Currado et al. in press). In order to carry out such a control programme, detailed data on the current distribution and the factors affecting grey squirrel presence are needed. We therefore studied the presence/absence of grey squirrels in an area of 373 km^2 covering its current distribution range. We also estimated population size in the large forested area of Stupinigi, and tested for several woodland characteristics that might affect squirrel densities. The importance of woodlot size, habitat quality and degree of isolation, factors known to affect tree squirrel distribution and densities in fragmented landscapes (Verboom & van Apeldoorn 1990, Fitzgibbon 1993, Celada, Bogliani, Gariboldi & Maracci 1994, van Apeldoorn, Celada & Nieuwenhuizen 1994, Wauters, Casale & Dhondt 1994a, Wauters, Hutchinson, Parkin & Dhondt 1994b) were studied in order to explain current grey squirrel distribution and to determine 'hot spots': important woodlots for targeting grey squirrel control.

Methods

Study area

In northern Italy, grey squirrels occur in two distinct areas. A small population (<300 squirrels) lives around the town of Nervi, Liguria (44°24'N, 9°03'E) in private gardens and public parks where they receive food from the general public (Currado et al. in press). The main, large population occupies woodlands, poplar plantations and parks in a ca 350 km^2 area of the Po-plain south of Turin, Piedmont (between 44°47' and 45°00'N, and 7°28' and 7°44'E). The distribution of the Piedmont population is strongly fragmented. The 6.09 km^2 (1.25 km^2 poplar *Populus canadensis*, 4.84 km^2 mixed deciduous woodland) of the Stupinigi forests covers 12% of the area west of the Turin agglomeration. In the remaining 321 km^2 of the Po-plain that were checked, only 3.24 km^2 (1%) are covered by deciduous woodland, and 17.25 km^2 (5.4%) by poplar plantations (Fig. 1). Woodlands and poplar plantations are mainly surrounded by arable fields (main crops are maize, wheat, and winter wheat) and meadows. Many small woodlands were urban or suburban parks and large industrialised areas extend on the northern and northwestern borders of the squirrel's range.

Data sampling

We checked 61 of the 125 identified woodlands and poplar plantations, ranging from 0.2 to 70 ha in size, for the presence or absence of grey squirrels. The majority of woodlots (42, 69%) were <5 ha (Table 1), and the average distance between woods or plantations was ca 1 km (mean ± S.D. = 0.96 ± 1.07 km, range 0.1 - 5 km). The woodland size limit of 0.2 ha is well below the home range size of grey squirrels in high quality woodlands in England (Kenward 1985). To establish grey squirrel presence or absence, woodlots were examined for dreys, and/or obvious feeding signs. Since red squirrels were no longer present in

Table 1. The distribution of woodlot size and the percentage of woodlots occupied by grey squirrels (present) according to size. The 95% confidence limits of the observed presence/absence data (proportion of woodlots occupied) are compared with the presence predicted by the random sample hypothesis (see Methods).

Size class (ha)	Number of woodlots N	Number of woodlots Present (%)	Proportion occupied (95% confidence limits)	Predicted presence (Random sample hypothesis)
0.1 - 1	16	1 (6)	0 - 0.32	0,06
1.1 - 5	26	14 (54)	0.21 - 0.74	0,27
5.1 - 10	3	3 (100)	0.52 - 1.00	0,47
10.1 - 20	3	1 (33)	0.05 - 0.78	0,71
20.1 - 30	5	4 (80)	0.42 - 1.00	0,84
>30	8	6 (75)	0.60 - 1.00	0,96
Total	61	29 (48)		

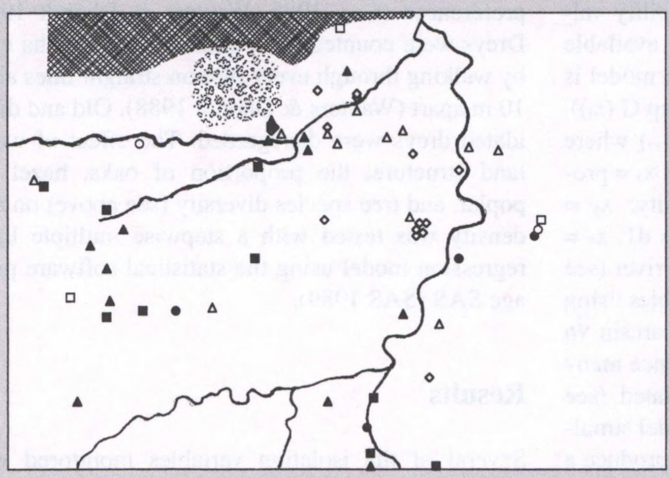

Figure 1. Map of the distribution area of grey squirrels in the Po-plain in northern Italy, indicating the main rivers. Shaded area is the Turin agglomeration, spotted area is the large Stupinigi forest. Woodlots <1 ha: squirrels present ♦, squirrels absent ◇; woodlots 1.1-5 ha: squirrels present ▲, absent △; woodlots 5.1-20 ha: squirrels present ●, absent ○; woodlots >20 ha: squirrels present ■, absent □.

most of the investigated area (unpubl. data), confusion between the two species did not pose a problem. In woodlands that might still contain both squirrel species, the presence of grey squirrels was controlled by direct observations. In some cases, when access could not be acquired, owners of private parks were contacted and interviewed about grey squirrel presence on their property.

To analyse the effects of patch size and isolation on the distribution of grey squirrels, woodlot size, interpatch distance, distance to the nearest woodlot and to the large woodlands of Stupinigi (source area), distance to wooded river banks (dispersal corridors), and density of surrounding woods and treerows were calculated from maps at a scale of 1:25,000 (Table 2). Differences in habitat quality were measured using three variables: 1) the proportion (per woodlot) covered by oak trees *Quercus robur* and *Q. petraea*; 2) the proportion covered by poplars; and 3) tree species diversity, represented by the number of seed-bearing conifer species (*Pinus strobus, Picea abies*) and deciduous tree species with large, consumable seeds (i.e. oaks, red oak *Q. rubra*, chestnut *Castanea sativa*, horse chestnut *Aesculus hippocastanum*, beech *Fagus sylvatica*, walnut *Juglans regia*, black walnut *J. nigra*, ash *Fraxinus excelsior*, hornbeam *Carpinus betulus*, cherry *Prunus avium*, and hazel *Corylus avellana*). Moreover, since grey squirrels were observed feeding in nearby maize-fields, we also monitored whether or not a woodlot had adjacent maize-fields (see Table 2a).

Statistical analysis

If a woodlot contained grey squirrels it was scored 1, if not it was scored 0. A logistic regression model was used to determine the effect of size, habitat quality and isolation variables on the binary dependent variable, grey squirrel presence, with the GLIM statisti-

Table 2. Variables pertaining to habitat quality, patch size and isolation (a). Pairwise Pearson's correlation coefficients among woodlot size and different isolation variables (b). (N = 61 in all cases, correlations of >0.252 are significant at P < 0.05).

a)

Habitat quality	Patch size	Isolation		
% oaks	woodlot size (ha)	d1	=	distance (km) to nearest woodlot ≥ 0.5 ha
% poplars		d2	=	distance (km) to nearest woodlot ≥ 10 ha
diversity		b1	=	number of woodlots within 500 m of woodlot edge
maize fields		b2	=	number of woodlots within 1000 m of woodlot. edge
		dis	=	distance to Stupinigi forest (km)
		hr	=	length (km) of hedge- and treerows within 500 m of woodlot edges
		river	=	distance (km) to wooded river bank

b)

	d1	d2	b1	b2	dis	hr	river
Size	0.12	0.11	-0.09	-0.06	0.40	0.30	0.001
d1		0.35	-0.47	-0.43	0.22	-0.20	0.13
d2			-0.36	-0.46	0.13	-0.05	0.16
b1				0.73	-0.25	0.19	-0.06
b2					-0.37	0.23	-0.11
dis						0.11	0.03
hr							0.12

cal package (Baker & Nelder 1978). The logistic regression converts binary data into probability values by fitting a logistic curve through the available points (Baker & Nelder 1978). The logistic model is described by: $P(Y_i = 1) = \exp G(x_i)/(1 + \exp G(x_i))$, and $G(x_i) = (A + B_1x_1 + B_2x_2 + ... + B_{12}x_{12})$ where x_1 = woodlot size (ha); x_2 = proportion oaks; x_3 = proportion poplars; x_4 = tree species diversity; x_5 = maize-fields (1 = absent, 2 = present); x_6 = d1; x_7 = d2; x_8 = b1; x_9 = b2; x_{10} = dis; x_{11} = hr; x_{12} = river (see Table 2a); and A and B_i are constants. Variables using proportions (p) were transformed using the arcsin $\sqrt{p}$ transformation before statistical analysis. Since many of the isolation variables were intercorrelated (see Table 2b), they could not be fitted in the model simultaneously (Fitzgibbon 1993). Therefore, to produce a model that best fitted the data a stepwise forward procedure was used, including one or more variables in the model, until addition of a variable no longer significantly increased the total deviance (e.g. Verboom & van Apeldoorn 1990, Fitzgibbon 1993).

We also tested whether the occurrence of grey squirrels in woodlots of different size could simply be explained by the random sample hypothesis (Andrén 1994), which predicts that one has the same probability to encounter an animal in equally sized plots within different woodland fragments independently of the size and degree of isolation of the fragments (Andrén 1994, 1996). Consequently, according to the random sample hypothesis, a positive effect of fragment size on the presence of squirrels is expected by chance, and the expected presence (y) can be calculated with the formula: $y = (1 - (1-p)^{size})$, where p is the probability to find squirrels in a woodlot of size 1, the smallest size class (Andrén 1996).

At the Stupinigi forest a drey census was carried out to estimate squirrel density and determine habitat preferences (Don 1985, Wauters & Dhondt 1988). Dreys were counted in 37 census plots of 1 ha each, by walking through every plot on straight lines about 10 m apart (Wauters & Dhondt 1988). Old and dilapidated dreys were disregarded. The effect of woodland structure, the proportion of oaks, hazel and poplar, and tree species diversity (see above) on drey density was tested with a stepwise multiple linear regression model using the statistical software package SAS (SAS 1989).

Results

Several of the isolation variables monitored were intercorrelated (see Table 2b). Positive correlations were found between the distance to the nearest small (>0.5 ha, d1) and larger woodlot (>10 ha, d2), and between the number of woodlots within 500 m (b1) and within 1,000 m (b2) of woodlot edge (see Table 2b). Negative correlations between d1 and b1 and between d2 and b2 indicated that when the distance between woodlots increased the number of nearby woodlands decreased. More interestingly, the positive correlation between woodlot size and distance from Stupinigi, and the negative correlation between b2 and distance from Stupinigi (see Table 2b), suggest that the density of woodlots in the landscape decreased when further away from Stupinigi, but that the woodlots furthest away from Stupinigi were generally larger in size than those in the vicinity. Woodlot size was significantly correlated with the proportion of poplars ($r = 0.34$, $N = 61$, $P = 0.0079$), and the latter was negatively correlated with the proportion of oaks ($r = -0.38$, $N = 61$, $P = 0.0022$). Hence most of

Table 3. Goodness-of-fit tests for logistic models of grey squirrel presence/absence incorporating different combinations of size, habitat quality and isolation variables. Model B was compared with model A, models C and D were compared with model B. Models E-L were compared with model D (the selected model). The values of chi-square are for the inclusion of each extra variable in the model and are all with one degree of freedom.

Model	Variables included	Total deviance (%)	χ^2	P
A	diversity	32	26.7	0.00001
B	diversity + size	39	6.4	0.011
C	diversity + size + oak	40	0.21	NS
D	diversity + size + poplar	57	14.8	0.00018
E	diversity + size + poplar + d1	58	0.45	NS
F	diversity + size + poplar + d2	57	0.06	NS
G	diversity + size + poplar + b1	58	0.29	NS
H	diversity + size + poplar + b2	57	0.05	NS
I	diversity + size + poplar + dis	58	0.51	NS
J	diversity + size + poplar + hr	57	0.01	NS
K	diversity + size + poplar + river	57	0.07	NS
L	diversity + size + poplar + maize	57	0.02	NS

the larger woodlots were poplar plantations with few oaks or were deciduous woods adjacent to poplar plantations.

Of the 61 woods surveyed, 29 (48%) were found to contain grey squirrels. Squirrels were more likely to occur in woodlots with many species of large-seed producing deciduous trees (tree species diversity, Table 3, Fig. 2). They were not present in very small parks (<1 ha, see Table 1), but were more likely to be found in larger woods with a high proportion of poplar (see Table 3 and Fig. 2). The model which explained the highest proportion of deviance (57%) was model D, with G_{xi} = -11 (±3) + 1.8 (±0.5) tree species diversity + 0.004 (±0.003) woodlot size + 0.08 (±0.03) proportion poplar (see Table 3). None of the isolation variables that were added to the model significantly improved the fit (see Table 3, models E-K). However, the presence of grey squirrels in woodlots of different size as predicted by the random sample hypothesis (proportion of woodlots occupied per size class), fell within the 95% confidence limits of the observed presence values for five out of six size classes (see Table 1).

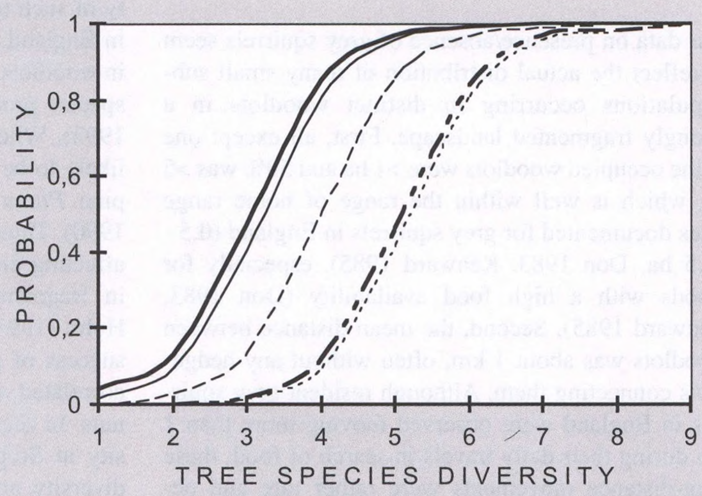

Figure 2. Logistic curves fitted to the probability of grey squirrels being present in a woodlot according to tree species diversity: woodlots of 50 ha with 80% poplar (———), woodlots of 5 ha with 80% poplar (———), woodlots of 5 ha with 50% poplar (- - - - -), woodlots of 50 ha with 20% poplar (— · —), woodlots of 5 ha with 20% poplar (·········).

The density of dreys in the 37 samples of the Stupinigi forest ranged from 0 to 6 dreys/ha^{-1} (mean ± SD = 1.14 ± 1.51). Using the relationship between drey and grey squirrel density calculated by Don (1985), this indicated a mean squirrel density of 0.5/ha^{-1}, and an estimated population size of ca 305 grey squirrels. Of all the habitat variables tested (N = 37), the proportion of oak was negatively correlated with the proportion of hazel (r = -0.49, P = 0.0021), and with poplar (r = -0.39, P = 0.018), suggesting that oak dominated plots had a relatively poor understory and that few oaks occurred in poplar dominated plots. The proportion of hazel was positively correlated with tree species diversity (r = 0.53, P = 0.0008), indicating that plots with many species of large-seed producing trees had a good understory of hazel. In a multiple linear regression model, variation in tree species diversity explained 29% of variation in drey density (R^2 = 0.29, F = 13.9, df = 1, 35, P = 0.0007; Fig. 3). When the proportion of oak was included in the model (partial r = 0.226, P = 0.12), both variables explained 34% of variation in drey density (R^2 = 0.34, F = 8.59, df = 2, 34, P = 0.001).

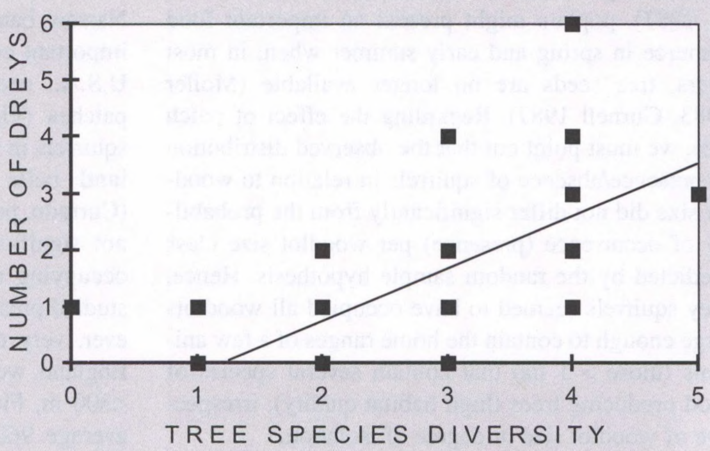

Figure 3. Linear regression of drey density (dreys/ha^{-1}) on tree species diversity. Drey density = -0.8 (±0.6) + 0.77 (±0.21) tree species diversity.

Discussion

Our data on presence/absence of grey squirrels seem to reflect the actual distribution of many small subpopulations occurring in distinct woodlots in a strongly fragmented landscape. First, all except one of the occupied woodlots were >1 ha and 50% was >5 ha, which is well within the range of home range sizes documented for grey squirrels in England (0.5 - 12.5 ha, Don 1983, Kenward 1985), especially for woods with a high food availability (Don 1983, Kenward 1985). Second, the mean distance between woodlots was about 1 km, often without any hedgerows connecting them. Although resident grey squirrels in England were observed moving more than 1 km during their daily travels in search of food, these long-distance movements were rather rare and occurred mainly towards very rich food patches (Kenward 1985). Therefore, we feel that interpatch distance and woodlot size in the Po-plain resulted in most resident grey squirrels occupying only one woodlot during the census period.

The distribution of grey squirrels in the strongly fragmented landscape of the Po-plain south of Turin was found to be influenced by both patch size and habitat quality variables. More than 85% of woodlots >1 ha adjacent to poplar plantations (≥50% poplar) that had >3 species of large-seed producing trees were occupied by grey squirrels (see Fig. 2). However, woodlot size and proportion of poplars were intercorrelated, complicating the interpretation of the effect of poplar on squirrel presence. However, since grey squirrels were known to strip bark from poplars in order to get to the nutrient-rich phloem (Currado et al. 1987), poplars might present an important food resource in spring and early summer when, in most years, tree seeds are no longer available (Moller 1983, Gurnell 1987). Regarding the effect of patch size, we must point out that the observed distribution of presence/absence of squirrels in relation to woodlot size did not differ significantly from the probability of occurrence (presence) per woodlot size class predicted by the random sample hypothesis. Hence, grey squirrels seemed to have occupied all woodlots large enough to contain the home ranges of a few animals (those > 1 ha) that contain several species of food producing trees (high habitat quality), irrespective of woodlot size or degree of isolation.

Large seeds of deciduous trees are the main food resource for grey squirrels throughout most of the year (Moller 1983, Gurnell 1987), which explains the close link of squirrel presence to the species diversity of such trees in the woodlots in the Po-plain. Also in England, grey squirrels were more likely to occur in woodlots containing oak, beech or hazel; these tree species produce preferred squirrel food (Fitzgibbon 1993). Whereas red squirrels in Holland were more likely to be present in woodlots dominated by Scots pine *Pinus sylvestris* (Verboom & van Apeldoorn 1990). Thus habitat quality was an important variable affecting presence/ absence of squirrels in woodlots in fragmented landscapes. Moreover, Kenward & Holm (1993) showed that both density and breeding success of grey squirrels in England was positively correlated with the abundance of acorns and hazelnuts. In accordance with this, grey squirrel drey density at Stupinigi forest increased with tree species diversity, an index of the overall availability of large, nutrient-rich seeds, such as hazelnuts, acorns, walnuts and hornbeam or ash seeds.

In contrast to the other studies in strongly fragmented landscapes, not one of the isolation variables that were tested affected grey squirrel distribution in the Po-plain. The density of hedgerows and the vicinity of another wood >5 ha positively affected grey squirrel presence in English woodlands (Fitzgibbon 1993). For red squirrels in Holland, both the distance to a large source woodland, the amount of surrounding woodland and the amount of hedgerows affected the probability for squirrels to occupy a woodlot (Verboom & van Apeldoorn 1990). Likewise, red squirrels in the strongly fragmented Po-plain in the province of Pavia, northern Italy, were more likely to be found in woodlots that were close to large woodlands bordering the rivers (Celada et al. 1994). Narrow bands of hardwood along streams were an important component of grey squirrel habitat in the U.S.A., and facilitated movements between forest patches (Fischer & Holler 1991). Likewise, grey squirrels in Piedmont were observed using the woodland belts along rivers as dispersal corridors (Currado, pers. obs.). However, distance to a river did not significantly affect the probability of squirrels occupying a woodlot. The landscape in which we studied presence/absence of grey squirrels was, however, very different from those in other studies. In England, woodlands were closer together (on average <300 m, Fitzgibbon 1993) than in the Po-plain (on average 960 m) and there was a higher density of hedgerows. In Holland, there was also a denser network of hedgerows and the distance from a large 'source' woodland (>30 ha) varied between 40 m and

3.5 km (mean 843 m, Verboom & van Apeldoorn 1990), while in the Piedmont Po-plain the distance from a woodland >10 ha varied between 10 m and 8.5 km (mean 3.4 km) and the distance from the source population at Stupinigi varied between 400 m and 22 km (mean 8.5 km). Hence, there was a higher degree of fragmentation in our study site than in the others. This could result in a scenario where grey squirrels show little dispersal and only emigrate from good woodlands when these become completely saturated, moving through the landscape until they reach an unoccupied suitable woodland (or one with still a low density of grey squirrels) where they can settle. Such a scenario would be in agreement with the very slow colonisation of the Po-plain by the grey squirrels, with only an average increase of their distribution of 7 km^2 per year, compared to an average of 18 km^2 per year in East-Anglia, England (Okubo, Maini, Williamson & Murray 1989). Another explanation, not excluding the first one, might be that grey squirrels readily use maize-fields for dispersing, decreasing the importance of more traditional corridors (tree-rows, riversides, small woodlots) as dispersal routes and resulting in the lack of significance of isolation variables in explaining squirrel distribution.

Our data on presence/absence of grey squirrels in the different woodlots within their distribution range can also be used to make an informed estimate of minimum population size. The population of Stupinigi forest, based on drey counts and the regression of grey squirrel density on drey density calculated by Don (1985) for English woodlands, was estimated at 305 animals. However, the mean density of grey squirrels, 0.5/ha^{-1}, was rather low and might be the result of the above relationship not being applicable to the Stupinigi habitat. Therefore, the estimate should be considered as an absolute minimum and treated with caution. A second large grey squirrel population occurred in the 70 ha woodland of Racconigi park, an optimal habitat where densities, revealed by capture-mark-recapture, had reached ca 6 squirrels/ha^{-1} in the autumn of 1996 (Currado, unpubl. data), resulting in an estimated population size of 420 animals. Grey squirrels were further present in 28 other woodlots with a total area of ca 420 ha and mean tree species diversity of four. Combining the regression equation from the Stupinigi forest (see Fig. 3) to calculate drey density based on tree species diversity, and that of Don (1985) to calculate squirrel density from drey density, resulted in an average drey density of 2.25 dreys/ha^{-1} and an average squirrel density of 1.27/ha^{-1}. Thus at least 535 grey squirrels inhabited these 28 woodlots, which together with the two larger populations added up to 1,260 squirrels. Since only 50% of the woodlots occurring in the distribution area were checked, an estimate of total population size is more likely to approximate 2,500 animals.

We conclude that grey squirrels numbers and distribution in northern Italy are still limited, making an eradication campaign feasible. A pilot-study to evaluate the methods and manpower necessary for successful control is in progress. However, the squirrel's range being currently only 6 km from continuous deciduous forests of the pre-Alps towards the northwest, and only 9 km from extensive hazel plantations towards the south, habitats where control would become very difficult or even impossible, grey squirrel control should be started immediately.

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