



Invasion dynamics of an introduced squirrel in Argentina

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Biological invasions are one of the major threats to both ecosystem and economic functioning. Their management typically involves culling of the pest or removal of its habitat. The Asiatic red-bellied beautiful squirrel *Callosciurus erythraeus* is the first known introduction of a squirrel into South America. It established from five releases in 1973, using exotic trees to spread through Argentinean Pampas. It now causes substantial economic damage in agricultural and urban areas across >680 km², and its continued spread threatens indigenous species. We developed a spatially explicit model of the invasion for the likely range of life-history parameters, matched against empirical data on patch occupancy in 2004. The two best-fitting models suggest the current population to be on the cusp of an explosive expansion. These models were used to predict future trends under alternative scenarios of strategic culling or habitat removal aimed at slowing the spread. The predictions for 18 yr into the future were that 1) the present lack of systematic management will lead to a 5-fold increase in area of occupancy, 2) removal of habitat down to half carrying capacity will thin the population but accelerate its spread, 3) 10 yr of culling above the maximum sustainable yield (MSY) will precipitate declines in abundance and patch occupancy towards extinction, but with immediate recovery upon cessation of the cull. We recommend continuous culling above the MSY in priority patches, aimed at slowing arrival to valuable conservation areas. This study demonstrates the need for prompt action to terminate invasions before they establish. The squirrel invasion is now irreversible after 30 yr of slow spread across fragmented habitat. Although culling requires public awareness campaigns and sustained governmental commitment, it is now the best feasible strategy for managing this invasion.

Biological invasions are now considered one of the major threats to biodiversity and ecosystem functioning, together with habitat degradation (Mack et al. 2000). Although exotic species are key components of the economies of several countries (e.g. most crops), they can provoke huge economic losses when they escape human control (e.g. many agricultural pests; Wittenberg and Cock 2001). The problem of biological invasions has long been recognised (Elton 1958) but concern about exotics has increased over the last decade. Recent studies have provided new evidence of the complexity of invasion dynamics and the interdisciplinary approach needed to inform management plans for preventing or mitigating negative impacts (Mack et al. 2000, Grosholz 2005).

Ecological models can provide valuable insight into the process of biological invasions, both for predicting the direction of colonisation and for exploring the consequences of alternative management options. Spatially-explicit population models (SEPMs) present a powerful tool in this context because of their capacity to incorporate the complexity of real-world landscapes in their predictions of spatial distribution, abundance, and viability of populations (Dunning et al. 2006). SEPMs have been applied

mainly to predictions of population viability for endangered or harvested species (see examples in Akçakaya 2000 and Akçakaya et al. 2004). The same approach has enormous potential for modelling the new environment of an invader in terms of corridors and barriers to dispersal and suitable habitat for reproduction, to predict its future distribution, quantify environmental impacts, compare alternative management strategies, and guide new research by identifying key variables that most affect the model predictions (Rushton et al. 1997, Lurz et al. 2001, Tattoni et al. 2006).

We developed a spatially explicit model to predict the spread of the red-bellied beautiful squirrel *Callosciurus erythraeus*. This tree squirrel is native to southeast Asia and was introduced to Argentina as a pet in 1970 (Aprile and Chicco 1999). By 1973, 2–5 animals had established from a single release point in the Pampas region. After 31 yr of slow spread, the wild population occupied a region of 680 km² around the release point by 2004 (Guichón et al. 2005). This is the first known introduction of a squirrel into South America. Although no systematic studies have yet been conducted on the ecology of the species in Argentina, anecdotal data (Aprile and Chicco 1999) and recent observations (Guichón unpubl.) indicate that its

feeding and nesting habits are associated with exotic trees in commercial and ornamental plantations in rural and urban areas of the pampas. This represents another example of how the success of new exotics can be facilitated by human-modified environments and positive interactions among introduced species (Mack et al. 2000, Grosholz 2005).

In the Argentine Pampas, economic damage has been reported by some inhabitants and local producers to fruit plantations, forestations, and electric and irrigation systems. The presence of this attractively patterned species is welcomed by other inhabitants, however, who regard it as a local tourist attraction given that no native squirrels inhabit this region, and some of whom catch individuals to sell or keep as pets (Guichón et al. 2005). Observations of predation on the nests of native birds have been reported in the Pampas (Pereira et al. 2003). Studies conducted in Japan, where it was first introduced in 1935, have reported high population growth and adaptability to new environments, damage to plantations, garden trees, and cables, and predation of native birds (Tamura et al. 1988, 1989, Azuma 1998, Miyamoto et al. 2004). The species was also introduced into France in the 1970s, where it now causes damage to trees and crops (Jouanin 1992). In its native habitat, it has been subjected to control actions to limit economic damage to the forestry industry caused by its debarking of coniferous trees which then become prone to fungal infection (Lin and Yo 1981, Yo et al. 1992a).

The current distribution of this squirrel in Argentina lies within a highly modified rural area of the Pampas region to the west of the city of Buenos Aires (Guichón et al. 2005). The northerly spread is within 30 km of the Paraná River Delta which sustains important commercial forests and unique and bio-diverse riparian forests composed of both temperate and subtropical flora and fauna (Malvárez et al. 1999). The Otamendi Natural Reserve within this delta protects several endemic birds potentially susceptible to nest predation by the red-bellied squirrel. No programme of proactive management has yet been developed for this population, and currently the only control is sporadic lethal trapping by local producers in response to damage. Proactive control actions require long-term commitment and funding from government, NGOs, wildlife managers and scientists, and the local community (Mack et al. 2000, Genovesi 2005), which may take several years. Some localized control actions could be taken more immediately, however, to slow the invasion towards critical areas, and to establish methods and test the commitment of stakeholders (Bertolino and Genovesi 2003). Here we simulate alternative control scenarios as a first step to evaluating the feasibility and success of both localized and region-wide actions.

The objectives of this study are 1) to develop a spatially explicit population model (SEPM) to simulate the invasion dynamics of the red-bellied squirrel in the Pampas region, and 2) to evaluate population viability and spread under various scenarios in order to recommend a management plan to slow the invasion. In particular we modelled the alternatives of harvesting and habitat removal. Local culls to harvest the population above its maximum sustainable yield can potentially precipitate extinction, but require sustained effort. Removing the squirrel's habitat can be done in a single operation but may have a stabilising effect on the

population, associated with its reduced efficiency of exploiting resources (Kent et al. 2003).

Materials and methods

Study area

The study area comprised 8100 km² (90 × 90 km) of northeastern Buenos Aires Province, Argentina, centred at the liberation site of the squirrels close to the town of Jáuregui in the district of Luján (34°36'S, 59°11'W). Ten red-bellied squirrels were bought from a pet shop in Holland and introduced to Argentina in 1970. They were kept caged for 3 yr until 2–5 individuals escaped or were liberated, originating a wild population. The species now principally occupies highly fragmented woodland patches in rural and urban areas of the Pampas (Aprile and Chicco 1999). Native grasslands of the Pampas region have been extensively modified by agriculture, livestock, and urbanisation. In our study area, fruit (mainly *Actinidia* sp., *Citrus* spp., *Juglans* spp., *Prunus* sp.) and timber plantations (mainly *Eucalyptus* spp., *Populus* spp.) add to an arboreal vegetation comprising exotic species used as wind curtains, for shade, or as ornaments in gardens and along roads, railways, and rivers (mainly *Ailanthus* sp., *Araucaria* spp., *Casuarina* spp., *Cupressus* spp., *Gleditsia triacanthos*, *Ligustrum* spp., *Melia azedarach*, *Morus* spp., *Pinus* spp., *Quercus* spp., *Tilia* spp.). All of these introduced trees are used by the squirrels (Aprile and Chicco 1999, Guichón et al. 2005, Guichón unpubl.). The temperate moist climate has mean temperatures of 23.8°C in January and 9.1°C in July, and mean annual precipitation of 944 mm.

The model

We developed a spatially-explicit, stage-structured stochastic model to simulate the invasion dynamics of the red-bellied squirrel in the Pampas region. Given that no previous studies have been conducted on the demography of the red-bellied squirrel in Argentina, we took estimates of life history parameters principally from published data on the squirrel in its indigenous habitat in Taiwan and in its colonised range in Japan. We used the population viability analysis program RAMAS/GIS 4.00 (Akçakaya 2002), which is designed to link a metapopulation model with landscape data from a geographical information system (GIS).

Habitat data

Published data on density and home range area were used to estimate habitat suitability for the different habitat types. The lowest density of red-bellied squirrels, 2–3 individuals ha⁻¹, was reported in a Taiwanese plantation of Japanese fir (*Cryptomeria japonica*) (Lin and Yo 1981), whilst 5–7 adults ha⁻¹ were found in temperate mixed forest in Japan and in native habitat (Tamura et al. 1989). Home range size and overlap was always larger in males than females (Tamura et al. 1989, Yo et al. 1992b). Tamura et al. (1987, 1989) reported mean home range sizes of females of 0.5–0.7 ha, which greatly overlapped with male home

ranges but not with those of other females, and mean home range sizes for males of 2.2–3.8 ha, which greatly overlapped with both male and female home ranges. On average, 8 males overlapped each female home range (Tamura et al. 1989), leading to densities as high as 7–9 sexually mature squirrels ha⁻¹. These data were used to estimate carrying capacity of the main habitat types identified in our study region.

Squirrels in the Pampas region reproduce in both urban and woodland areas (Aprile and Chicco 1999, Guichón unpubl.), as was reported for Japan (Miyamoto et al. 2004). We defined 4 types of suitable habitat (woodland, residential, suburban, and urban) in a matrix of non-suitable habitat. Woodland habitat included all forested areas, woodland patches, and wooded corridors; in the absence of more specific information, all woodlands were considered of equal quality. Residential, suburban, and urban areas differed in their increasing degree of urbanization and decreasing degree of arboreal cover. Non-suitable habitat was defined as open areas with no trees, mainly comprising arable and pasture fields and water bodies. Woodland was considered to have the highest habitat suitability, followed by residential, suburban, and urban, with non-suitable habitat receiving a zero value (Table 1). This habitat classification was used to construct a 90 × 90-km habitat map with a resolution of 40 m to encompass the current distribution of the squirrel, using GIS Idrisi 32 (Clark Labs) and ArcGIS 8.3 (Esri). With no land-cover maps available for this area, we built this habitat map by visual interpretation of satellite image Landsat 7 TM orbit 225-084, October 2002 (licensed by PRODITEL, Univ. Nacional de Luján), and then calculated habitat values as the number of individuals that a 40 × 40-m cell of each habitat type could support.

The minimum habitat suitability value below which the habitat is not suitable for reproduction and the distance that individuals travel for daily activity provide the link between the habitat map and the metapopulation model. Miyamoto et al. (2004) considered that if the distance between woods was < 163 m, which is the largest linear dimension of a

female home range (Tamura et al. 1987), females could move among them to establish home ranges and reproduce. Lin and Yo (1981) reported maximum movements of 326 and 484 m for mature and immature females, respectively; however, these distances may be an overestimate for daily movements within non-contiguous wooded areas. The “perceptual range” of a species describes the maximum distance from which an animal can perceive the presence of remote patches of habitat (Lima and Zollner 1996) and it becomes relevant for modelling gap crossing. We assumed daily movements of 160 m, after combining published information on the use of space by the red-bellied squirrel with data from other sciurids (Zollner 2000: perceptual range of 120 m for *Tamias striatus* and 300 m for *Sciurus carolinensis*; Gurnell et al. 2002: movement between patches up to 200 m apart by *S. vulgaris*; Verbeylen et al. 2003: trivial range of *S. vulgaris* encompasses patches separated by up to 50 m; Selonen and Hanski 2004: fields 100–150 m wide seldom traversed by *Pteromys volans*). The estimate of daily movements takes into account the potential for squirrels to use cables, isolated trees and bushes, and high vegetation on field borders when crossing open fields and rivers (unpubl.). Hedgerows, bushes, and isolated trees increase the connectivity of fragmented forest for *S. vulgaris* and *S. carolinensis* (Fitzgibbon 1993, van Apeldoorn et al. 1994, Wauters et al. 1994, Selonen and Hanski 2004). Therefore, in our habitat map, nearby cells within 160 m with habitat suitability at least equalling the threshold (i.e. woodland and urban habitat) were grouped together as a “patch”. The group of individuals occupying a discrete patch is hereafter referred to as a “population”, connected through dispersal to neighbouring populations. Nearest edge-to-edge distances yielded inter-patch distances. We used highways and main rivers to divide patches close enough to be assigned to the same patch but that would not be easily crossed by squirrels. The carrying capacity of each patch was calculated as the total habitat suitability within the patch (i.e. the sum of habitat values of woodland, residential, suburban, and urban cells). The habitat is extremely fragmented because of small forested patches used for shade or wind curtains in this agricultural landscape. Patches with a carrying capacity (K) < 75 individuals, were absorbed into the dispersal matrix as “stepping-stone” fragments that facilitate dispersal between permanent local populations. These smaller patches accounted for only 8% of suitable area and their incorporation as independent patches would have vastly inflated the patch matrix without contributing substantially to the metapopulation dynamics. In effect, their inclusion in the matrix of unsuitable habitat gave us a conservative estimate of the expansion rate across a total of 497 suitable patches.

Demographic data

We modelled the dynamics of the population within each patch with a composite age-structured Leslie matrix, with 3 age classes for each sex: juveniles in their first year of life, yearlings in their second year, and adults in their third year and above. We assumed that: 1) all births in the population take place in a relatively short breeding period in spring, 2) the population is censused immediately before the annual

Table 1. Parameter estimates used as model inputs (with range of values in parenthesis where applicable).

Parameter	Classification	Value (range)
Habitat quality (K)	Woodland	8 ind. ha ⁻¹
	Residential	6 ind. ha ⁻¹
	Suburban	4 ind. ha ⁻¹
	Urban	2 ind. ha ⁻¹
	Non-suitable	0 ind. ha ⁻¹
Survival rates (p _x)	Juveniles	0.8 (0.72–0.88)
	Yearlings	0.6 (0.54–0.66)
	Adults	0.3 (0.27–0.30)
Fecundity rates (F _x)	Juveniles	0.6 (0.54–0.66)
	Yearlings	1.2 (1.08–1.32)
	Adults	1.2 (1.08–1.32)
Finite rate of increase (λ)		1.53 yr ⁻¹ (1.38–1.68)
Mean dispersal distances		1 km (0.5–1.5)
Maximum dispersal distances		5 km (2.5–7.5)
Male:female relative dispersal	Juveniles	1.0:0.4
	Yearlings	0.7:0.3
	Adults	0.4:0.2
Density-dependent dispersal constant		0 (0.001)

birth pulse, 3) no deaths occur between litters within the reproductive season, and 4) the Leslie matrix applies across all populations.

We used mean yearly survival rates, p_x , reported by Tamura (2003) for the red-bellied squirrel in Japan, except for the survival rate of adults older than 3 yr for which we used a value of 0.3 (Table 1), influenced by Gurnell (1987) who reported that patterns of survival appear similar among Holarctic tree squirrels: once they have achieved their second year of life, year-to-year survival is 50–70%. The mean number of viable offspring per individual of each age (fecundity, F_x) was calculated as the age-specific offspring production (maternity, m_x) multiplied by the survival of juveniles (p_j) (Akçakaya 2002). As in most tree squirrels (Gurnell 1987), the mating system of the red-bellied squirrel is promiscuous. Females care for the young, and each female may mate with 4–11 different males while a male can mate with at least 6 females within a year (Tamura et al. 1988, 1989). In our model we assumed that each male can mate with up to 6 females each year. We also assumed that all females breed each year and that the sex ratio is 1:1 (Yo et al. 1992a). Females establish their own home ranges when they become sexually mature at ca 1 yr old, and they may have 1–3 litters yr^{-1} (Tamura et al. 1988, 1989). Multiplying the mean juvenile survival of 0.6 (Tamura 2003) by a litter size of 2 (from a range of 1–4 given by Tamura 1999) yields a value of 1.2 weaned juveniles per litter, which is within the range estimated for the red-bellied squirrel, of 1.1 to 1.4 (Tamura et al. 1988, Tamura 1999). We obtained estimates of fecundity (F_x) per year from the survival of juveniles ($p_j = 0.6$) times the litter size (2) times the number of litters per year (juveniles: 1, yearlings and adults: 2) times the sex ratio (0.5) (Table 1). The resulting Leslie matrix predicted a finite rate of increase, $\lambda = 1.53 \text{ yr}^{-1}$; because of uncertainty in these values for the red-bellied squirrel in Argentina, their influence on model outputs was explored by varying these estimates by $\pm 10\%$ (Table 1).

Antagonistic behaviours and hierarchies among both male and female red-bellied squirrels reportedly influence their habitat use, foraging, and reproductive activities (Tamura et al. 1988, Yo et al. 1992a, b). We therefore assumed density-dependent population growth on all vital rates (mortality as well as fecundity) due to contest competition.

Dispersal

Dispersal refers to the movement of squirrels between habitat patches. We assumed that dispersal occurs annually and that dispersal rate (i.e. the proportion dispersing from a source population to a target population) was determined by: 1) the distance between the source and the target populations, and 2) the age and sex of the potential disperser. We modelled dispersal rate as a negative exponential function of distance (Akçakaya 2002), where distances were measured between patch edges. No study of dispersal distances is available for this species, and only one record of a dispersal event has been reported, of over 1 km (Lin and Yo 1981). The mean longest linear dimension of a home range in Japanese populations has been estimated to be 435 m for males and 130 m for females (Tamura et al.

1987), while Taiwanese populations have a mean of 250 m (Lin and Yo 1981). A distance of 1 km is well within the range of dispersal of *Tamiasciurus hudsonicus*, *S. carolinensis*, and *S. niger* (Goheen et al. 2003). For *S. vulgaris*, dispersal distances range from 0.6–1.3 km (Lurz et al. 1997), up to 3.2–3.5 km (Magris and Gurnell 2002) and a maximum of 4 km (Verbeylen et al. 2003). *Pteromys volans* has a mean and maximal dispersal distance of 2.5 and 9 km, respectively (Selonen and Hanski 2004). Taking into account differences in body size and mode of dispersal, we assumed mean and maximum dispersal distances of 1 and 5 km respectively, and varied both estimates by 50% of their value to account for uncertainty (Table 1). As some individuals are likely to move beyond this maximum dispersal distance, model predictions were intentionally conservative. We assumed that juvenile males had the highest dispersal rate and that adult females had the lowest rate (Table 1) based on Tamura et al. (1989) who reported male- and juvenile-biased dispersal, although they observed transient squirrels of both sexes and all ages. We evaluated the effect of density-dependent dispersal in population spread by varying dispersal rate in direct proportion to the size of the source population (Akçakaya 2002), using an arbitrary constant of proportionality (Table 1), which results in a greater proportion of individuals leaving a population at high than at low densities.

Stochasticity

Environmental stochasticity was incorporated at each time step of 1 yr by random sampling from lognormal distributions around the set of vital rates used to project the dynamics of each population, with means taken from the Leslie matrix described above and standard deviations of 5% (Akçakaya 2000). Demographic stochasticity was incorporated by sampling the numbers of survivors and dispersers from a binomial distribution, and the numbers of offspring from a Poisson distribution (Akçakaya 2002).

Validation of the model

We varied the following 3 input parameters to account for uncertainty (Akçakaya and Sjögren-Gulve 2000): finite rate of increase, mean dispersal distance, and maximum dispersal distance (Table 1). Three levels (low, medium, and high estimates) of each parameter were tested using complete Latin square sampling in the standard form, which delivers a spatially balanced design (Gomes et al. 2004) suitable for identifying any interacting pairs amongst the three input variables. This design yields a total of 9 parameter combinations. We explored numerous other combinations in order to verify that the inputs to the balanced Latin square were representative of the full set of combinations. Each model was run for 1000 replications, always specifying an initial abundance of 5 squirrels (3 adult females and 2 adult males) in the patch where they were originally liberated in 1973.

We first modelled the spatial distribution of the squirrels over 31 yr, representing its spread from 1973 to 2004, in order to compare the predicted patch occupancy to that observed in field reconnaissance in 2004 (Guichón et al. 2005). This comparison provided a valid test of the model inputs, because the dataset of observations was independent

of the one used to generate the model. Although the observed data are limited to presence/absence at a single point in time, they are the only available information for the species in Argentina, and provide a useful reference against which to discard significant under- or overestimations of regional occupancy.

All of the patches lying within the observed distribution of squirrels in 2004 were classified as “occupied”, which yielded 114 km² of occupied suitable habitat. The total area predicted to be invaded after 31 yr was calculated by adding up the areas of the patches that had an average of at least 5 individuals at the end of the simulation period. The “simple matching coefficient” (SMC, Krebs 1999) was used to measure the similarity between the observed area of distribution and the area predicted to be occupied by squirrels under the different parameter combinations (Rushton et al. 1997). To this end, the proportion of pixels with matching predicted and observed occupancy was calculated as: $(a+b)/c$, where a is the number of pixels predicted and observed to be occupied (positive matches), b is the number of pixels predicted and observed to be unoccupied (negative matches), and c is the total number of pixels of suitable habitat and thus belonging to a patch (matches + mismatches).

Prediction of expansion and alternative management scenarios

The 2 models that most closely matched the observed spread of squirrels to date were selected to predict the dynamics of invasion over the following 20 yr (i.e. over a total simulation period of 51 yr up to 2024), under different management scenarios taking effect within the next 10 yr. Longer simulation periods were also analysed to address particular questions, such as the year of invasion of Otamendi.

The first scenario described a continuation of the present condition of no systematic management. We then simulated 2 control strategies to slow down the expansion of squirrels: 1) increase mortality by removing individuals; 2) decrease available resources of food and refuge by a reduction in patch carrying capacities (see the Discussion for an appraisal of ways to implement these strategies). We simulated the removal of squirrels for 10 consecutive years from 2008 in the form of yearly culls from each population of a small amount more than the maximum sustainable yield ($MSY \times 1.1$, where MSY is attained at half carrying capacity under logistic growth). We simulated a reduction in available patch resources from 2008 onwards by halving the carrying capacity of each patch. These management actions were modelled for three areas of implementation: 1) all patches; 2) a priority area of 59 patches selected on the basis of the direction of the wave of advance and of the conservation value of the area beyond the front of invasion at Otamendi Natural Reserve (see Results); and 3) 2 central patches selected because of their location and large size (the release patch and a neighbouring patch that summed up 54% of the invaded area by 2004), where local producers would be more willing to control squirrels. Invaded area is expressed as the sum of all habitats occupied by at least 5 squirrels on average. Spread rate was estimated following Andow et al. (1993) from the square-root of the mean R_i^2

where R_i are the shortest and longest radial increases in the minimum convex polygon encompassing the invaded area (Jenness 2004).

Results

The habitat suitability map shows the highly fragmented habitat occupied by the red-bellied squirrel in the Pampas region, with contiguous tracts only in the north-eastern urbanised area (Fig. 1). The 90 × 90-km² study area encompasses 1117 km² of suitable habitat (14% of total area), which partitioned into 353 km² of woodland and 764 km² of residential, suburban, and urban areas. This suitable habitat contained 497 patches with $K > 75$, ranging in size from 0.09 to 95 km² and covering 1027 km² (13% of total area). All of these patches had some positive dispersal rate under the set of tested models, indicating some degree of connectivity for all.

Validation of the model

Medium and high estimates of population growth (λ) overestimated the area of squirrel occupation after the first 31 yr, in comparison to the observed distribution of 114 km² (Table 2). The congruence of predicted and observed areas was relatively high for the model with low λ , regardless of dispersal distance ($SMC = 0.96$). The inclusion of density-dependent dispersal increased similarity between observed and predicted areas of occupancy in all models (Table 2), yielding lowest differences between observed and predicted occupied areas for models 2 and 3 with low λ , and model 4 with medium λ . Since the predictions of models 3 and 4 fell just either side of the observed area, and both had high SMCs, we used these 2 models for predicting the expansion of squirrels into the future. Model 3 yielded slightly conservative projections from low λ combined with a high mean, and low maximum, dispersal distance; model 4 slightly overestimated the likely rate of spread from a higher λ combined with low mean and maximum dispersal distances.

Prediction of expansion and alternative management scenarios

In the absence of control measures, the models predicted expansion to occupancy of 707 to 808 km² of suitable habitat in the 20 yr following 2004 (Table 3) within a total convex polygon of 3102–3308 km². The area invaded by 2024 comprises 63–72% of habitat susceptible to colonisation within the 90 × 90 km map, including most of the available urban settlements and the forests of the Delta Region with natural and commercial afforestations (Fig. 2). In particular, the models predicted invasion of the Otamendi Natural Reserve in the next 16–24 yr (Table 3). Given that the predicted expansion is mainly north-easterly and Otamendi is a first step into the Delta Region in this direction, we selected a priority area (Fig. 1) where urgent management actions could be conducted to slow or prevent colonisation in this direction, until a long-term strategy can be undertaken with broad consensus. Culling

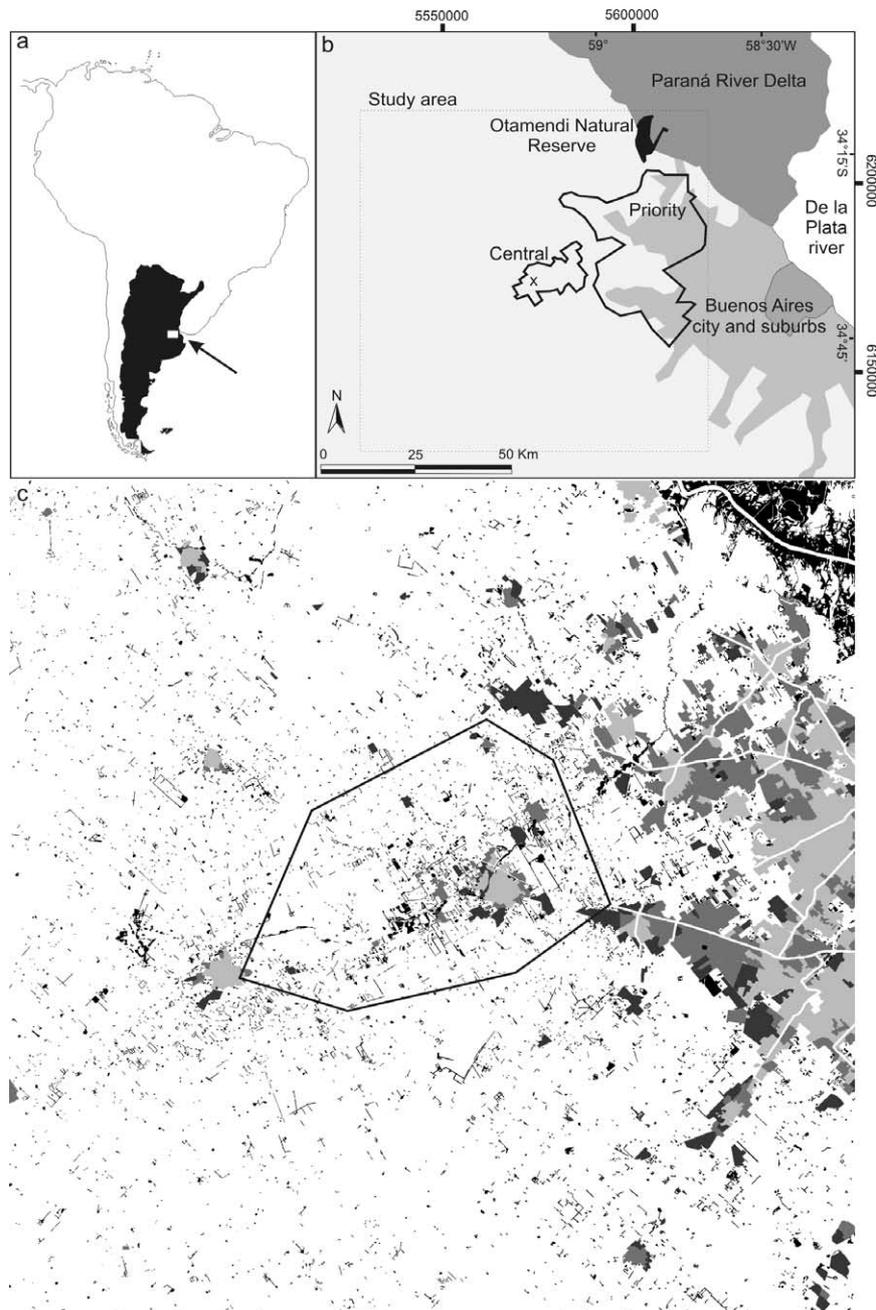


Fig. 1. (a) Location of study site in Argentina, (b) study area with the release point of the squirrels in the centre (×), the area covered by the city of Buenos Aires and its large suburbs, the Lower Delta Region of the Paraná River, Otamendi Natural Reserve, and the central and priority areas used for modelling alternative management scenarios, and (c) map showing suitable habitat for squirrels (wooded habitat in black and urban habitats in grey) and the matrix of unsuitable habitat (non-forested areas in white), indicating the range expansion observed by 2004 (polygon).

squirrels in this area was at least as effective at delaying their arrival in Otamendi as culling in all patches, and more effective than culling the central area which did not have any delaying effect (Table 3). Habitat removal to reduce K only shortened the time to reach Otamendi, particularly when applied in the priority area (Table 3).

The models predicted a relatively slow expansion in occupancy during the first 34–37 yr after liberation in 1973 and then a steep increase in the invaded area (Fig. 3a). This indicates that the spread of squirrels may be at the cusp of

an explosive expansion. The rate of spread shows a tendency to increase (Fig. 3b), though large variations are observed (mean \pm SD, model 3: 1.28 ± 1.14 km yr⁻¹ and model 4: 1.44 ± 1.23 km yr⁻¹).

The increase in abundance was rather flat for the first 20 yr of exponential growth, and then increased dramatically (Fig. 4). High numbers predicted by model 4 showed signs of an intermediate plateau 30–40 yr into the invasion, in response to density-dependent regulation within colonised patches (Fig. 3a and 4b). Culling and reducing K resulted in

Table 2. Model inputs to the Latin Square design: finite rate of increase (λ), mean dispersal distance (MeanDD), and maximum dispersal distance (MaxDD), predicted area of occupancy after 31 yr of invasion (difference from observed occupancy of 114 km² in 2004 in parentheses), and simple matching coefficient (SMC). The last 2 columns show predictions for models incorporating density dependent dispersal.

	λ	MeanDD	MaxDD	Area (km ²)	SMC	Density dependent dispersal	
						Area (km ²)	SMC
1	1.38	0.5	7.5	73 (-41)	0.96	88 (-26)	0.97
2		1.0	5.0	72 (-42)	0.96	111 (-3)	0.96
3		1.5	2.5	73 (-41)	0.96	93 (-21)	0.98
4	1.53	0.5	2.5	374 (+260)	0.70	124 (+10)	0.94
5		1.0	7.5	672 (+558)	0.46	283 (+169)	0.84
6		1.5	5.0	447 (+333)	0.68	404 (+290)	0.72
7	1.68	0.5	5.0	804 (+690)	0.33	361 (+247)	0.72
8		1.0	2.5	825 (+711)	0.31	412 (+298)	0.70
9		1.5	7.5	934 (+820)	0.20	493 (+379)	0.64

broadly similar patterns of predicted abundance, with the former tending to outperform the latter (Fig. 4). Numbers of squirrels and occupancy area could be significantly diminished by culling each population with a constant harvest for 10 yr, though populations would start to recover immediately upon interruption of the harvest (Fig. 4, note the particularly sharp reversal in fortune of the “cull all” scenario when culling stops after 10 yr). It would take >30 yr (model 3) or 60 yr (model 4) of continuous harvest in all patches to eradicate squirrels. No significant advantages result from reducing the number of squirrels in central patches though concentrating efforts in a priority area would restrict abundance and area of occupancy while delaying the predicted invasion of Otamendi by 10–15 yr (Table 3). Decreasing the carrying capacity of all or only priority patches has an unwanted effect of increasing the spread rate, such that Otamendi is reached before the no-action scenario (Table 3).

Discussion

Range expansion and squirrel numbers have grown slowly for the first 2 to 3 decades after liberation, but the models predict a steep increase in abundance and regional distribution over coming years. The pattern of rapid growth following slow establishment is typical of the expansion of many introduced species (Crooks and Soulé 1999). This is the first attempt to predict future expansion of the red bellied squirrel in Argentina and we acknowledge some limitations in the construction and validation of the model, mainly due to sparse life history and population data for our

study area. As with other studies using sparse data (Lurz et al. 2001, Tattoni et al. 2006), our input parameters for models are estimated from diverse sources of empirical information on behavioural and population ecology from the squirrel’s native and exotic ranges. The use of a Latin Square of simulations at least ensures realistic orders of magnitude for the invasion dynamics of this species.

Density-dependent dispersal reduced predicted range expansion when population rate of increase was medium and high but increased predicted spread for low values, and even showed a rescue effect from extinction when lower rates were used (e.g. $\lambda = 1.23$, unpubl. outputs). These results are consistent with the population regulating effects of density dependence (Akçakaya et al. 2007). The first priority for improving model predictions should be to obtain local and seasonal estimates of reproduction and survival rates in different habitat types (work in progress).

One of the principal aims of this modelling approach is to make recommendations based on objective evaluation of the success of alternative control actions. Management measures could be oriented towards mitigating damage, restricting colonization of new areas, regulating abundance, or complete eradication. The probability of achieving the desired result can be evaluated by simulating population responses to different control measures. Our results show that reducing the carrying capacity of the habitat would lower squirrel numbers but an unwanted accelerating spread would lead to a faster colonization of a key conservation area (Otamendi). Non-lethal techniques have a potentially greater efficiency than lethal control, since they avoid the density-dependent consequences that can follow culling, and are likely to be seen as more acceptable in welfare and

Table 3. Predicted expansion and abundance (\pm SD) of squirrels by the year 2024, and time to reach the Otamendi Natural Reserve under alternative management scenarios.

Scenario	Area	Area by 2024 (km ²)		Abundance by 2024		Year reaches Otamendi	
		Model 3	Model 4	Model 3	Model 4	Model 3	Model 4
No control	–	707	808	55 251 (25 136)	122 557(44 171)	2031	2023
Cull squirrels	all	140	381	17 525 (9854)	35 086 (9985)	2044	2038
	priority	288	408	36 277 (13 861)	40 380 (10 591)	2041	2038
	central	707	810	45 173 (24 755)	121 259 (42 752)	2031	2023
Reduce K	all	826	893	30 570 (14 173)	74 543 (24 526)	2024	2016
	priority	818	811	39 704 (16 800)	99 972 (29 096)	2021	2016
	central	713	793	45 712 (21 811)	110 861 (39 299)	2029	2023

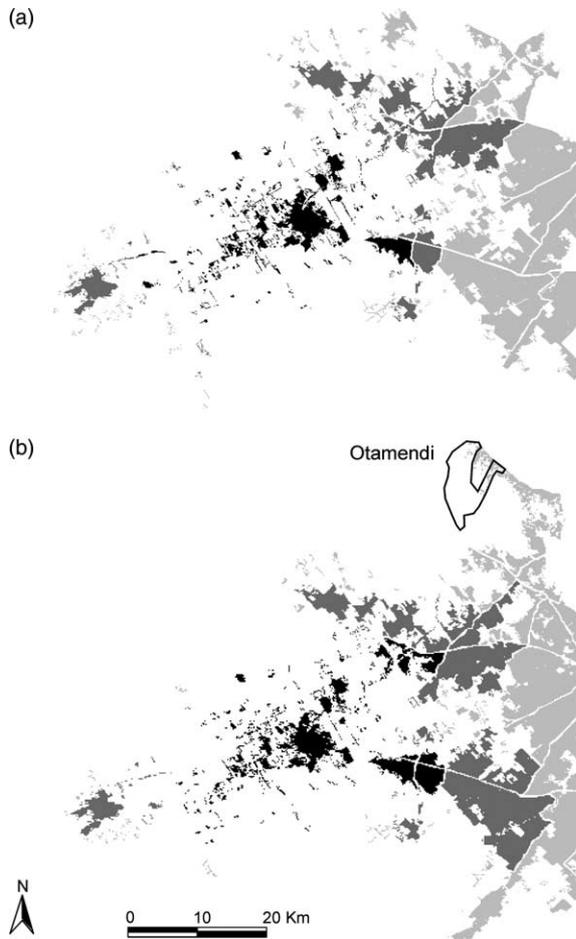


Fig. 2. Area of occupancy predicted under current scenario of no control by (a) model 3 and (b) model 4 in 2004 (black), 2014 (dark grey), and 2024 (light grey).

ethical terms (Barr et al. 2002, Baker et al. 2007). Decreasing the carrying capacity of suitable patches could be accomplished by reducing accessibility (e.g. place sheet metal and cones to impede or reduce use of trees and cables), persistence (e.g. nest destruction), and suitability of resources (e.g. pruning trees to thin canopy and reduce suitability for nesting; replace trees used for food and nesting by alternative, less suitable tree species). Regardless of the viability of implementing this action, however, it must be rejected as a viable option because of the predicted acceleration of the invasion front.

In contrast, model predictions show that culling squirrels could be an effective measure to restrict invasion and reduce abundance, provided it targets priority areas. Culling all patches would have the largest impact on numbers and range distribution, but implementing such a vast campaign has doubtful feasibility. Culling populations only in central patches could create a vacuum that would rapidly be filled by local growth and dispersal from neighbouring patches. However, concentrating effort and resources in the priority area would delay colonization of Otamendi. This Natural Reserve would be the first step into the Paraná River Delta which hosts a unique and biodiverse region of riparian forests represented by both temperate and subtropical species and also important commercial forests (Malvárez

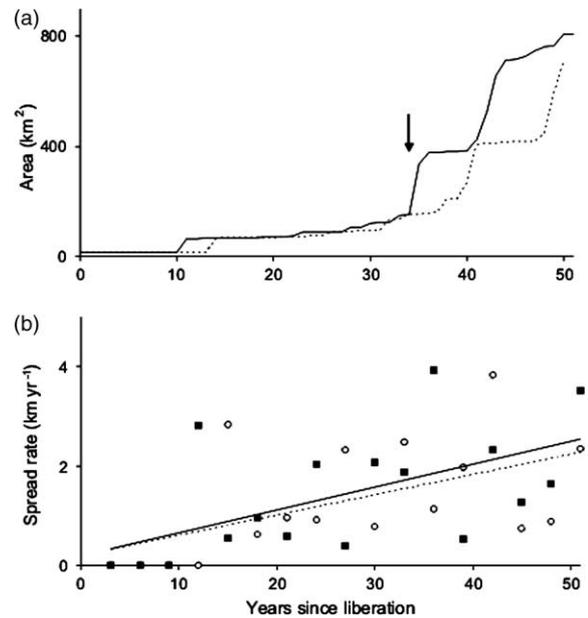


Fig. 3. Model predictions under current scenario of no control: (a) range expansion since liberation of squirrels in 1973 (area estimated using the minimum convex polygon method) predicted by models 3 (dashed line) and 4 (solid line), and (b) spread rate (dots indicate new invaded area every 3 yr after liberation with trend line showing predicted increase of colonisation speed) predicted by models 3 (open circles, dashed line) and 4 (black squares, solid line). Arrow indicates year 2007.

et al. 1999). Removing squirrels would require public awareness campaigns and long-term commitment of governmental authorities. Broad public support should be achieved through a communication strategy informing about the problem and addressing ethical issues, particularly given the charismatic appearance of the squirrel (Barr et al. 2002, Bertolino and Genovesi 2003). Additionally, an adequate legal basis is needed to initiate control actions, given that local authorities refuse to implement any measure until the species is declared a pest. A rapid response to new invasions is the best-case scenario to prevent vast invasions, when technical, financial, and logistic needs are more easily achieved (Mack et al. 2000, Genovesi 2005). When control actions are delayed, eradication of introduced mammals is usually not viable for financial, technical, or social reasons. Actions to diminish negative effects caused by already established exotic species are expensive and not always successful, as in the case of attempts in the United Kingdom to control *S. carolinensis* in order to protect *S. vulgaris* and reduce bark stripping (Sheail 1999, Huxley 2003, Lawton and Rochford 2007). Nevertheless, localized intensive control of introduced mammals in selected areas may help to reduce some negative effects and slow their spread (Bertolino and Genovesi 2003).

Because we seldom understand ecological systems completely, applications of models need to be flexible and management must be able to adapt to new information (Lynan et al. 2002). Our assessment of the most realistic and effective long-term action is to target culling in priority areas, and to mitigate damage in commercial plantations through local control. It is important that all such operations are closely monitored, and that the predictive

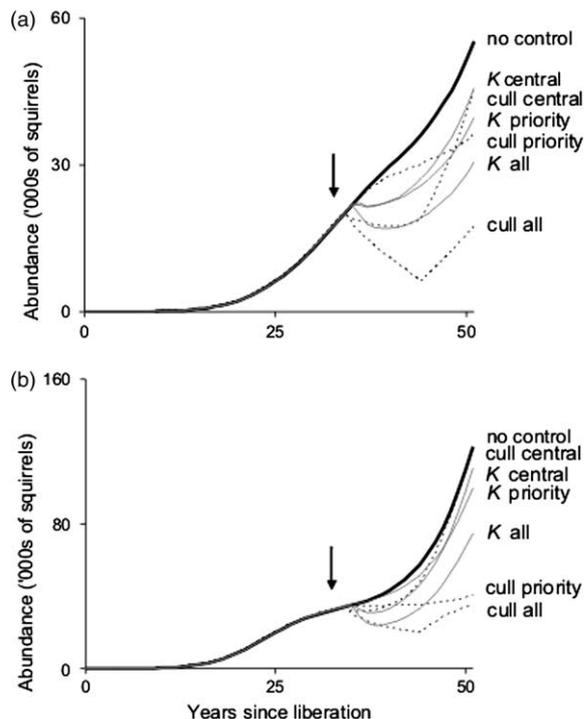


Fig. 4. Predicted abundance of population by (a) model 3, and (b) and model 4 since liberation of squirrels in 1973, under alternative scenarios described in Methods (no control, black solid line; culling, dashed lines; reduce k, grey solid line). Standard deviations are not shown for graph clarity though values never reached zero, see Table 2 for SD of no control scenario. Note different scales of y-axes in (a) and (b). Arrows indicate year 2007.

models are updated with information on control actions and on vital rates. With more empirical information it will be possible to carry out sensitivity analyses to determine the key variables that drive expansion, which can then guide the collection of future data.

Acknowledgements – We thank R. Akçakaya for helping with software specifications, L. Di Franco (PRODIGITEL, UNLu) for facilitating satellite imaging, F. Milesi for constructive discussions at all stages, and L. Wauters and an anonymous reviewer for their help with improving the manuscript. The study was funded by a UNESCO-L'Oréal Fellowship for young women in Life Sciences to MLG at the Univ. of Southampton and by a Small Ecological Project Grant awarded to MLG by the British Ecological Society.

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