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Original Investigation

Range expansion of Pallas's squirrel (*Callosciurus erythraeus*) introduced in southern France: Habitat suitability and space use

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ABSTRACT

The study of space use and population density in different habitats is an important step in understanding the expansion process of an introduced species and in gathering useful knowledge for management actions. Pallas's squirrel (*Callosciurus erythraeus*) was introduced on the Cap d'Antibes (southeastern France) at the end of the 1960s. We used direct observations from a grid map centred onto the known historical distribution to document the expanding range of Pallas's squirrel. We assessed habitat suitability in the invaded area through distance sampling and nest counts and examined space use by quantifying the size of the home range and intra- and inter-sexual overlap based on radio-tracking in a suitable habitat. Our results confirm that Pallas's squirrel has expanded its range exponentially over the past two decades, although with low diffusion coefficients (0.08–0.20 km/yr). Squirrels reached the highest relative densities in suburban woodlands, in which females showed no territorial behaviour. Our results indicate that Pallas's squirrel was able to establish in various habitats in Antibes, preferentially in woodlands and gardens. Densely urbanised areas and the presence of the highway A8 (E80) acted as barriers that slowed range expansion. Such information is crucial to improve the control programme started in 2012 to limit the spread of this potentially invasive squirrel.

Introduction

The persistence and growth of a population requires individuals to move and meet in suitable breeding habitats (Kokko and Lopez-Sepulcre, 2006). More specifically, the key factor in explaining the expansion of a population relies on how—and how many—individuals are able to disperse and select suitable and/or adapt to new habitats (Bowler and Benton, 2005). As a consequence, landscape structure is a determinant in predicting species movement and distribution (Hanski, 1999), and the identification of suitable habitats is a prerequisite in foreseeing which paths the spread of an established species might take during its proliferation. Population density and how individuals use space are also essential in determining the potential for a species to expand spatially (White et al., 2012). An introduced species that is expanding offers the opportunity to test what population and habitat characteristics facilitate or hinder expansion (With, 2002; White et al., 2012). Additionally, understanding the expansion process of an introduced species makes it possible to both pre-empt its impacts and adapt population management methods (Hulme, 2006).

Among mammals, exotic tree squirrels are particularly successful invaders when introduced outside of their native range (Bertolino, 2009; Bertolino and Lurz, 2013; Bertolino et al., 2014). Pallas's squirrel (*Callosciurus erythraeus*), an arboreal species native to Southeast Asia (Lurz et al., 2013), has been introduced in seven countries across the world, mainly for ornamental purposes or by escape from captivity (Aprile and Chicco, 1999; Hori et al., 2006). Of the 29 introduction events recorded worldwide (Bertolino and Lurz, 2013), 20 have resulted in the establishment of populations: Japan (Miyamoto et al., 2004; Oshida et al., 2007), Hong Kong (Ho, 1994), Argentina (Aprile and Chicco, 1999), France (Jouanin, 1986), Belgium (Stuyck et al., 2009), the Netherlands (Dijkstra et al., 2009) and Italy (Bertolino and Lurz, 2013). In Japan and Argentina, studies have described the exponential growth of populations of Pallas's squirrels that accompany the species' spread (Benitez et al., 2013; Guichon and Doncaster, 2008; Tamura, 2004). *C. erythraeus* is

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considered to be an invasive species in Japan (Tamura, 2012) and is potentially invasive in Europe and Argentina (Bertolino and Lurz, 2013). To date, no study has shown the impact of *C. erythraeus* on native arboreal sciurid species. However, a detrimental effect on the native Japanese squirrel *Sciurus lis* has been suspected (Tamura, 2012). In the Antibes region, a few European red squirrels (*S. vulgaris*) have been observed between 2012 and 2014, mainly at the periphery of the area on which Pallas's squirrels have become established (see the online map of the national survey: Chapuis et al., 2012; see also Supplementary Fig. S1, at http://dx.doi.org/10.1016/j.mambio.2015.08.004), likely suggesting an eviction of the native species by the introduced one (e.g., Bertolino and Lurz, 2013).

The aims of this paper were as follows: (i) to determine the rates of expansion by estimating the range of Pallas's squirrel introduced on the Cap d'Antibes in a peculiar geographic situation (i.e., a peninsula with anthropogenic barriers) since the early period of introduction; (ii) to infer habitat suitability by comparing relative densities in areas with a gradient of urbanisation (i.e., from densely urbanised to suburban woodlands); (iii) to gather general information on social behaviour (i.e., intra-sexual overlap) and mating systems (i.e., inter-sexual overlap) by analysing space use according to sex in a suitable habitat. Such investigations are essential for setting the parameters to be used in the modelling of the expansion of this species in the south of France (Dozières, 2012) and to improve the national control plan of this species launched in 2011 (Chapuis et al., 2011).

Material and methods

Study area and species

The study was conducted at the Cap d'Antibes, southern France (43°33′ N–7°07′ E) (Fig. 1), which has a Mediterranean climate characterised by average temperatures of 26–27 °C in July and 8–9 °C in January and an annual cumulative rainfall of 843–934 mm in 2009–2010 (Météo France). In this area, Pallas's squirrel was introduced in the late 1960s (J.-M. Gourreau, Personal communication). The origin of its introduction is not known, but the most likely scenario is the deliberate or accidental release of individuals brought back from a trip to Asia by a resident of the Cap d'Antibes.

Most knowledge of the biology and ecology of Pallas's squirrels has been recently reviewed by Tamura (2012) and Lurz et al. (2013). This arboreal squirrel is diurnal, with two main peaks in activity, one in the morning and one in the late afternoon. Individuals can be considered adults when their body mass is above 300 g, and there is no sexual dimorphism. In its introduced range, Pallas's squirrel lives in various types of forested habitats and in anthropogenic areas including orchards, bushes, gardens and city parks. Leaf nests are mainly built in evergreen broad-leaf and coniferous trees. The social structure of this species is poorly documented. However, the space use by females seems sensitive to habitat characteristics, with various patterns of home range overlap (Tamura et al., 1989). Additionally, the greater home range sizes of males compared to females and the high rate of inter-sexual overlap strongly suggest a promiscuous mating system. Breeding occurs throughout the year with two peaks. Most females breed 2 times a year with on average 2 embryos per litter (1–4). In urbanised areas, an important predator of the Pallas's squirrel is the domestic cat. All of these characteristics are found for the population on the Cap d'Antibes (Chapuis et al., 2014).

Distribution

The distribution of Pallas's squirrels was inferred from standardised observations made between February and early July 2010. A grid was centred on its previously estimated range (i.e., Gerriet, 2009) and expanded in all directions. The grid was formed by 256 squared units 25 ha each covering a total of 5650 ha (Fig. S1, Supplementary Material I). Each cell was visited during the main daily peaks of activity of the squirrels. A cell was surveyed for 1 h and up to three times (i.e., 3 h), as long as an individual was seen or heard. Traces of fruit consumption and the presence of nests or debarking were observed and noted as a probable presence. Observations were geolocalised and mapped in ArcGIS 9.3 (ESRI Redlands, CA, USA) to calculate the minimum convex polygon containing all indices of the presence of the squirrels except on the area where *S. vulgaris* and *C. erythraeus* inhabited in sympatry. The results of previous studies analysing the range area of *C. erythraeus* (Gerriet, 2009; Jouanin, 1992) were used to calculate the velocity of the population expansion since the estimated date of its introduction. We also calculated the rate of expansion of the population using the diffusion coefficient (Andow et al., 1993) which was estimated from the square-root of the mean square of the shortest and longest radial increase in the minimum convex polygon encompassing the invaded area (Benitez et al., 2013).

Line transect count

We estimated the relative abundance of Pallas's squirrels in different habitats by counting individuals and nests along transects (Gurnell et al., 2004). Four main types of habitat were chosen (Fig. 1; Table 1): urbanised (Site 1: large buildings with no or only small gardens), peri-urban residential areas (Site 2: dominated by houses with gardens), and two suburban woodlands (Site 3: Bois de la Garoupe, 9 ha; Site 4: Bois des Encourdoules, 25 ha). Squirrels were counted (N) along one transect per habitat in February, May, July, and November. In each month, a session consisted of five to ten consecutive days. Transect surveys were performed in the morning or in the afternoon, avoiding the warmest hours of the day and rainy weather due to a lower detection rate. The perpendicular distance of each squirrel to the survey line was recorded using a laser rangefinder. We calculated a proxy of the number of active squirrels per unit area per transect, hereafter referred to as relative density: $D = N/(L * W)$, in hectares. We estimated a bandwidth (W) equal to twice the maximal distance at which a squirrel was located from the transect line, which was multiplied by the length of the transects (L) to obtain the effective sampling area (in ha). The greatest distances representing 5% of the samples were discarded to avoid an overestimation of the effective sampling area (Buckland et al., 1993).

Nests were counted along the same transects in the four habitats in November 2010, taking advantage of the better visibility afforded after the autumnal leaf fall. A kilometric index of abundance was calculated. For each detected nest, the tree species was recorded.

Radio-tracking

The Bois des Encourdoules (Site 4, Fig. 1) is characterised by homogeneous tree cover dominated by *Quercus ilex*, *Q. pubescens*, *Pinus halepensis*, and by the shrubs *Laurus nobilis*, and *Pistacia lentiscus*. Pallas's squirrels were trapped between March 24 and April 1, and between June 29 and July 2, 2009, using 33 meshed live-traps placed on the ground, irregularly spaced 30–50 m, and covering approximately 5–6 ha. Traps were open in the morning (06:30 AM local time), baited with apples and peanut butter, checked every two hours, and closed in the afternoon (06:00 PM local time). Fourteen adult Pallas's squirrels, seven females (range in body mass: 375–435 g) and seven males (300–405 g), were fitted with radio collars (Biotrack Ltd., Wareham, Dorset, UK) weighing 10 g (i.e., ≤3% of the body mass): 9 (4 ♀; 5 ♂) in late March, and 5 (3 ♀; 2 ♂) in late June 2009. Animals were not anaesthetised when equipped with