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Mammalian Biology

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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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ARTICLE INFO

Article history:

Received 23 January 2015

Accepted 19 August 2015

Handled by Heiko G. Rödel

Keywords:

Introduced species

Range expansion

Habitat suitability

Space use

Callosciurus erythraeus

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.

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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., $\leq 3\%$ 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

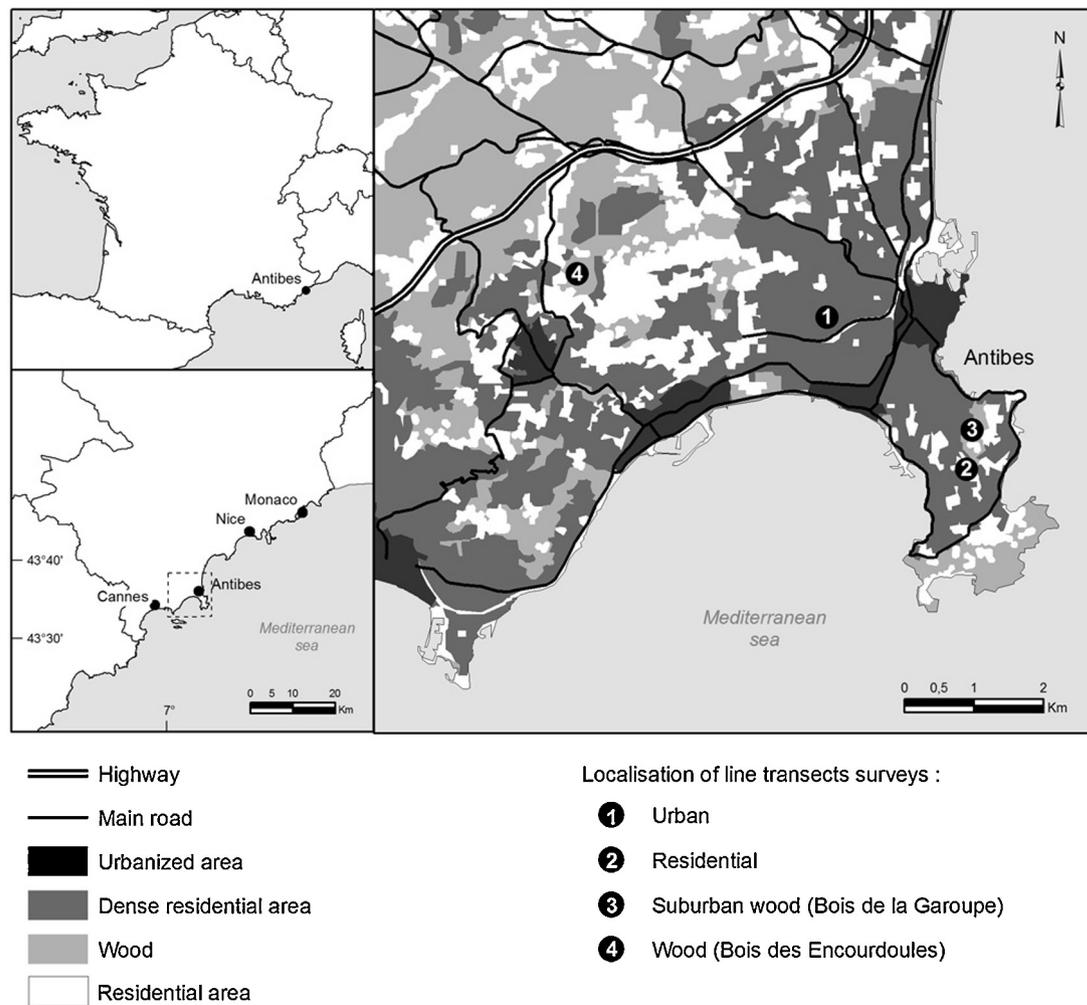


Fig. 1. Location of the study sites in the Antibes region (Alpes-Maritimes district). Sites 1–4: line transects; Site 4: radio-tracking area.

radio-collars. A person handled the squirrel, and masked its head while another fixed the brass collar. In March, two females were pregnant (400 g and 435 g) and none lactating, and in June one female was lactating (410 g). Tracking began three days after collaring to eliminate any influence of capture and manipulation on movement behaviour (Witey et al., 2001). We used a directional three-element Yagi antenna and a Sika receiver (150–152 MHz Bio-track Ltd., Wareham, Dorset, UK). Radio locations were obtained using a standard triangulation technique from geo-referenced points, spaced 50–100 m apart, or by homing to the radio signal (Romeo et al., 2010; Wauters and Dhondt, 1992). Radio-collared individuals were monitored from early April to mid-November 2009, with three to five fixes per day, between 7:30 AM and 8:00 PM (local time). Fixes were included in three seasons: spring (early April–late May), summer (late June–late August), and autumn

(early to mid-November). We located each animal with a minimum of 90 min between each fix (Steele and Koprowski, 2001; Swihart and Slade, 1985) to avoid temporal autocorrelation, which can lead to a biased estimation of the size of the home range and movement (Hansteen et al., 1997). No trapping session was set to remove the collars, while a control session by shooting was initiated.

The estimation of the home range was conducted using the 'adehabitatHR' package (Calenge, 2006) in R 2.15 software (R Development Core Team, 2012). We used two estimators to approximate the size of the squirrel's home range: the minimum convex polygon (100% MCP), to compare our results with other studies, and the fixed Kernel method (Worton, 1989), which produces more reliable estimates. The smoothing parameter is a critical component in Kernel density estimation (Borger et al., 2006) because it strongly affects home range size. Horne and Garton (2006a,b) recommended

Table 1

Averaged relative densities (ind./ha) from line transect counts of Pallas's squirrels according to habitat and season in the Alpes-Maritimes district in 2010.

Habitats	Localisation (43° N, 7° E)	L (km)	W (m)	ESA (ha)	Relative density ± SE							
					n	Feb.	n	May	n	July	n	Nov.
Urban	35°03' N, 06°54' E	4.1	–	–	5	0	5	0	10	0	5	0
Residential	33°36' N, 08°00' E	3.0	60	18.0	5	<0.1	5	0.2 ± 0.1	9	<0.1	5	~0.1
Woodlands												
Garoupe	33°56' N, 07°54' E	1.1	40	4.4	5	1.7 ± 1.0	5	3.6 ± 1.3	10	0.8 ± 0.2	5	1.7 ± 0.6
Encourdoules	35°18' N, 03°44' E	1.1	40	4.4	5	1.1 ± 0.3	5	2.3 ± 0.4	10	1.0 ± 0.2	5	1.6 ± 0.6

Note. L: transect length (km); W: estimated bandwidth; ESA: effective sampling area; n: number of transect surveys.

comparing the shape of the home range obtained with different smoothing parameters against the shape expected from a theoretical spatial distribution. We tested our data to determine whether it supported the assumption of a unimodal, bimodal or multimodal distribution using the Animal Space Use 1.3 software (Horne and Garton, 2009). Seasonal home range sizes were calculated using the 95% Kernel density estimation method (95% KDE), with the adjusted smoothing parameter of Wauters et al. (2007) that best matched the expected multicore shapes of the home ranges. We calculated the averaged h_{LSCV}/h_{ref} ratio, which was not different according to sex (i.e., females: 0.52 [range: 0.27–0.88]; males: 0.55 [0.40–0.68]) in order to multiply h_{ref} (i.e.: $h_{adj} = 0.54 h_{ref}$) for each individual. Core area sizes were estimated using the 85% Incremental Cluster Polygon (85% ICP) recommended for multicore shaped home ranges (Wauters et al., 2007). We characterised the percentage of intra- and inter-sexual core overlap among individuals. Core-overlap was calculated using the 'Home Range Analysis' tool in ArcGIS 9.3.

Data analysis

The variation in relative squirrel densities according to habitat, season, and their interaction was investigated using a two-way analysis of variance. Variations in the space use metrics according to season and sex were investigated using a linear mixed model (Pinheiro and Bates, 2000). Due to the small sample size, the interaction between these two factors was not included in the analysis. An individual random effect (noted σ_{ID}) was applied to account for pseudo-replication biases due to the repeated observations of the same individuals through time. The significance of the random effect was tested using a likelihood ratio test, by comparing models with the random effect to models without (Pinheiro and Bates, 2000). When not significant, simple linear models were run. Model selection was performed by retaining the subset of the best models based on the differences in Akaike's information criterion, corrected for a small sample size of less than 2.0 units (Symonds and Moussalli, 2011). The relative importance of each variable was determined from the selected models using an averaging procedure that calculates the adjusted standard errors and their corresponding 95% confidence intervals (Burnham and Anderson, 2004). The selected models were checked for variance, homogeneity and normality in the distribution of the residuals (Zuur et al., 2010). All analyses were performed on rank-encoded dependent variables in R 2.15 (R Development Core Team, 2012) using the package

'nlme' (Pinheiro et al., 2014) to run LMMs and the package 'MuMIn' (Baroń, 2009) for model selection.

Results

Distribution

Direct observation revealed a squirrel presence in 60 of the 226 cells, while other indices of presence (debarking, food remains) indicated squirrel activity in an additional 12 cells, corresponding to an area of 1800 ha (Fig. 2; see also Fig. S1, Supplementary Material). The diffusion coefficient of Pallas's squirrel in the Alpes-Maritimes district has increased from 1970–1990 (0.08 km/yr) to 1990–2010 (0.20 km/yr).

Relative density

The relative densities of Pallas's squirrels in 2010 (Table 1) differed significantly according to site and season, but there was no significant interaction between site and season (Table 2). In urban areas (Site 1), no squirrels were counted along 102.5 km of transects. In other habitats, seasonal relative densities were low in residential areas (Site 2; range: <0.1 to 0.2 ± 0.1 ind./ha) and highest in the Bois de la Garoupe (Site 3) and the Bois des Encourdoules (Site 4) (range: 0.8 ± 0.2 to 3.6 ± 1.3 ind./ha; 1.0 ± 0.2 to 2.3 ± 0.4 ind./ha, respectively; Table 1). Overall, relative densities were highest in the spring, compared to other seasons (Table 1).

The number of nests/km varied with habitat type. In November 2010, we counted 20 nests/km in the Bois de la Garoupe (16 nests on *P. halepensis* and 6 on *Q. ilex*), 14 nests/km in the residential area (43 on *Pinus pinea*), 6 nests/km in the Bois des Encourdoules (6 on *P. halepensis* and one on *Q. ilex*), and 0.2 nest/km in the urban area (one on *P. halepensis*).

Home range and core area

The number of annual fixes obtained per individual ranged from 86 to 253 (Table 3). No effect of season was found in the variation of home ranges (Table 4). The mean annual value of the home range size (KDE 95%) was significantly smaller for females (3.2 ± 0.5 ha) than for males (8.1 ± 1.3 ha). Considering both sexes, Pallas's squirrels had larger core areas in the summer than in the autumn (Table 4) but not among the other seasons (Tables 3 and 4).

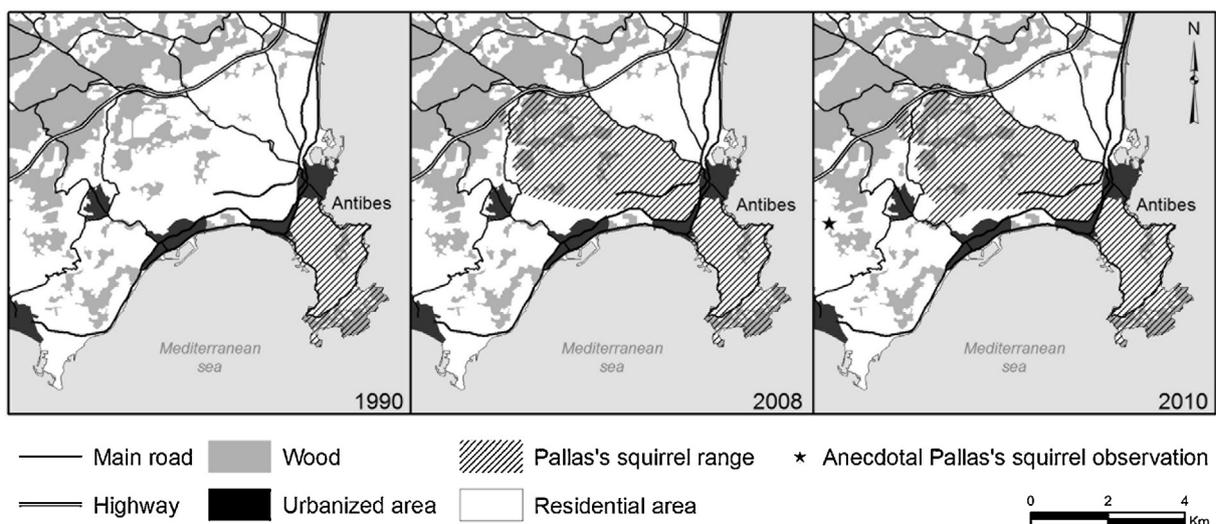


Fig. 2. The distribution of Pallas's squirrel in 1990 (from Jouanin, 1992), in 2008 (from Gerriet, 2009) and in 2010.

Table 2
Averaged parameters from the AICc-based selected linear mixed models exploring the variation of relative densities of Pallas's squirrel according to site and season at the Cap d'Antibes in 2010. Non-zero parameter in bold. Parameter estimates: β with standard error, 95% confidence interval (CI).

Sources of variation	Model selection				Coefficients		
	<i>K</i>	<i>-LL</i>	δ_{AICc}	<i>w_i</i>	$\beta \pm SE$	95% CI	<i>P</i>
Habitat + Season	7	303.2	0.00	0.996			
Habitat	4	312.7	11.7	0.003			
Habitat * Season	13	302.4	14.5	0.001			
Intercept					48.6 ± 4.0	40.7; 56.5	<0.001
Habitat _(Garoupe)					-4.3 ± 3.7	-11.4; 2.9	0.247
Habitat_(Residential)					-39.0 ± 3.7	-46.3; -31.7	<0.001
Season_(Spring)					17.0 ± 4.8	6.8; 25.6	<0.001
Season _(Summer)					-0.7 ± 4.2	-8.9; 7.5	0.860
Season _(Autumn)					7.2 ± 4.6	-1.8; 16.3	0.116

Table 3
Home ranges and core areas (ha) with the percent overlap for Pallas's squirrel in the Bois des Encourdoules in 2009.

Season	Sex	N. fixes	Home range (ha)		Core area (ha)	Sex overlap (%)	
			95% KDE	100% MCP		85% ICP	Intra
Spring	F (<i>n</i> =4)	86; 89; 106; 109	2.1 ± 0.4	2.2 ± 1.2	0.6 ± 0.1	35 ± 19	71 ± 21
	M (<i>n</i> =4)	97; 98; 104; 111	5.4 ± 1.1	6.5 ± 1.1	1.9 ± 0.4	71 ± 22	45 ± 13
Summer	F (<i>n</i> =5)	87 ± 17	4.0 ± 0.4	4.3 ± 0.8	1.4 ± 0.3	63 ± 15	83 ± 17
	M (<i>n</i> =5)	100 ± 2	7.7 ± 1.6	8.3 ± 1.2	2.1 ± 0.4	74 ± 14	67 ± 7
Autumn	F (<i>n</i> =3)	47; 49; 50	3.1 ± 0.4	2.4 ± 0.2	0.9 ± 0.1	37 ± 14	34 ± 15
	M (<i>n</i> =3)	42; 45; 48	9.3 ± 3.2	5.8 ± 1.4	1.3 ± 0.4	39 ± 17	27 ± 12

Note. MCP: minimum convex polygon; ICP: incremental cluster polygon. Values are mean ± SE.

Females, however, had an annual ICP 85% significantly smaller than males (1.3 ± 0.3 ha and 2.9 ± 0.5 ha, respectively). The percentage of intra- or inter-sexual overlap varied greatly, ranging between 0% and 100%. On average, 35–74% (56 ± 6%) of individual core areas were overlapped by same sex individuals, and 27–83% (60 ± 6%) by opposite sex individuals (Table 3). There was an effect of sex on the inter-sexual overlap (Table 4), with males sharing a

significantly higher percentage of females' core areas than of other males. There was no difference in the percentage of core overlap within sex (Table 4). In the summer, the percentages of both intra- and inter-sexual overlaps were greater than in the autumn (Table 4). Additionally, inter-sexual overlap was higher in the spring than in the autumn, but this was not the case for intra-sexual overlap.

Table 4
Averaged parameters from the AICc based selected linear mixed models exploring the variation of home range size, and core area size and overlap, according to season and sex of Pallas's squirrel in the Bois des Encourdoules in 2009.

S. of variation	Random effect			Model selection				Parameter estimate		
	σ_{ID}	<i>LRT</i>	<i>P</i>	<i>K</i>	<i>-LL</i>	δ_{AICc}	<i>w_i</i>	$\beta \pm SE$	95% CI	<i>P</i>
KDE 95%	0.44	1.44	0.231							
Season + Sex				5	72.2	0.00	0.62			
Sex				3	75.7	0.94	0.38			
Intercept								8.3 ± 2.1	4.1; 12.4	<0.001
Season _(Spring)								-4.6 ± 2.7	-9.9; 0.7	0.091
Season _(Summer)								1.0 ± 2.6	-4.0; 6.0	0.703
Sex_(Male)								10.3 ± 2.1	6.2; 14.4	<0.001
ICP 85%	0.26	0.40	0.526							
Season + Sex				5	76.4	0.00	0.75			
Sex				3	80.5	2.22	0.25			
Intercept								6.1 ± 3.0	0.3; 12.0	0.040
Season _(Spring)								1.9 ± 3.2	-4.4; 8.2	0.559
Season_(Summer)								7.4 ± 3.0	1.5; 13.3	0.014
Sex_(Male)								7.6 ± 2.5	2.8; 12.5	0.002
INTRASEX	0.22	0.35	0.557							
Season				4	80.9	0.00	0.49			
Season + Sex				5	79.9	1.15	0.28			
Intercept								7.6 ± 3.8	0.1; 15.1	0.046
Season _(Spring)								6.2 ± 3.7	-1.2; 13.5	0.098
Season_(Summer)								9.5 ± 3.5	2.6; 16.3	0.007
Sex _(Male)								3.5 ± 2.8	-2.1; 9.0	0.218
INTERSEX	0.48	0.87	0.351							
Season + Sex				5	74.4	0.00	0.89			
Sex * Sex				7	73.2	5.13	0.07			
Intercept								9.5 ± 2.4	4.6; 14.4	<0.001
Season _(Spring)								6.3 ± 2.8	0.5; 12.1	0.034
Season_(Summer)								11.2 ± 4.3	5.8; 16.7	<0.001
Sex_(Male)								-6.6 ± 2.1	-10.9; -2.3	0.005

Discussion

The spread of Pallas's squirrels in the Cap d'Antibes is supported by many of the reasons advocated for the success of invasion by tree squirrels (i.e., reviewed in Palmer et al., 2007; see also for *Callosciurus* species: Bertolino and Lurz 2013): ability to install and disperse even through densely urbanised areas, and to adapt human-impacted environment through the benefit of active feeding. We highlighted that the absence of territoriality in female, which is commonly observed in many tree squirrels (e.g., Koprowski 2007; Waterman 2007), may provide increased opportunity for mating success on small areas, and could explain high densities reported for this species worldwide.

Range expansion and landscape

Due to the geographical nature of the Cap d'Antibes, a peninsula, Pallas's squirrel can spread mainly towards the north, offering a simplified situation within which to monitor its expansion. In 2010, the range was approximately 18 km². This area is probably underestimated because of difficulties in detecting squirrels at low densities (Tamura and Yong, 1993), as is often the case at the edge of a species distribution. Moreover, we did not include cells in which only indirect indices were recorded where red squirrels co-inhabited with *C. erythraeus* (Fig. 1; see also Fig. S1, Supplementary Material I). Indeed, indirect indices of presence (nests and food remains) are not differentiable between species. However, Pallas's squirrel is quite noisy and bold, making it relatively easy to spot (Bertolino, 2009; Jouanin, 1986; Lurz et al., 2013). Therefore, we feel confident surveys performed on our grid covering 5650 ha gave a minimal but reasonable estimation of the distribution of *C. erythraeus* in the region of the Cap d'Antibes.

No specific methodology was used to detail the distribution of squirrels in the 1990s. Jouanin (1992) only stated that Pallas's squirrels inhabit the Cap d'Antibes peninsula without the ability to cross the barrier constituted by the city of Antibes (Fig. 2). In 2007–2008, Gerriet (2009) estimated the distribution of Pallas's squirrels using an unstandardised protocol formed by direct observations and hair tubes. After an initial phase of expansion of Pallas's squirrels at low speed during the first two decades following their introduction, the area occupied increased exponentially and was multiplied by a factor of 2.5 over the period 1990–2010. This spread appears to follow the same pattern that has been observed for *C. erythraeus* in other countries (Benitez et al., 2013; Bertolino and Lurz, 2013) and for another sciurid (*S. carolinensis*) introduced in Italy (Bertolino and Genovesi, 2003; Bertolino et al., 2014). However, the expansion of *C. erythraeus* in the region of Antibes (18 km² in 40 years) is low compared to the expansion observed in Japan (304 km² in 52 years; Tamura, 2004) and Argentina (1340 km² in 40 years; range in diffusion coefficient: 0.05–0.61 km/yr; Benitez et al., 2013). Habitat in Antibes must be less suitable for the expansion of the Pallas's squirrel compared to that found in Japan and Argentina. Indeed, the landscape forming the current range of Pallas's squirrels around the city of Antibes is urbanised, with a fragmented structure that is likely to reduce the connectivity between suitable woodland habitat patches. This situation explains the confinement of Pallas's squirrels to the peninsula of the Cap d'Antibes until the 1990s, with a bottlenecked expansion to the north formed by the city of Antibes. However, squirrels successfully reached the city and established themselves in a public garden (Jardin de la Pinède, 43°34'02" N, 7°06'54" E) where people fed them. The high number of squirrels on this site and their gradual adaptation to human presence must be at the origin of their crossing of the highly urbanised area in the 1990s. Since the late 2000s, the A8-E80 highway serves as another effective barrier limiting the expansion of *C. erythraeus* to the north. This highway is one of the most travelled by cars and trucks in

southern France, with an average of 82,900 vehicles/day recorded in Antibes in 2002, and car traffic is expected to grow in the next two decades (Reffet, 2004).

In Argentina, the expansion of Pallas's squirrels was facilitated by the landscape structure composed of small wooded areas connected by corridors (Benitez et al., 2013). As a case in point, the lowest diffusion coefficient detected in the city of La Cumbre was explained by the absence of arboreal cover outside the urbanised area (Benitez et al., 2013). Moreover, private initiatives from people to whom this squirrel had become emblematic in these localities, in a region devoid of a native sciurid, lead to translocations of individuals, driving an increase in the rate of expansion of the species (Benitez et al., 2010; Novillo and Ojeda, 2008; see also Bertolino and Lurz, 2013). On the Cap d'Antibes, squirrels were appreciated by residents in the early phase of their establishment (C. Jouanin, Personal communication), but we are not aware of translocation in the Antibes region until the late 2000s. On the contrary, with increasing density and related damages to gardens and orchards, this squirrel has come to be considered a pest by some people, who control these intruders by trapping, shooting or poisoning, with potential detrimental effects on non-targeted wildlife and domestic animals (Chapuis et al., 2011).

Habitat suitability

The relative densities of Pallas's squirrels in Antibes were higher in the late spring (i.e., May), likely in connection with an increased availability of food resources when many trees are flowering and fruiting and probably coincident with the peak in birth of young. The observed relative densities, ranging between 2 and 4 ind./ha (up to 6 ind./ha), were overall lower than or similar to those observed in the various habitats within the invading range: woodland areas in urbanised landscapes in Japan: 6–7 ind./ha (Tamura et al., 1989), wooded corridors in Argentina: 1–18 ind./ha (Benitez et al., 2010), and in its native range in Taiwan (tropical monsoon forest: 5–7 ind./ha, Lin and Yo, 1981; conifer plantation: 0.5–2.5 ind./ha, Yo et al., 1992). However, the lack of standardised methodologies to estimate densities between these studies precludes reliable comparisons with our results. Relative densities were lowest in the summer, probably due to low rates of individual encounters during the line-transect counts as a result of reduced activities during high daily temperatures. Intermediate densities were observed during the autumn when the squirrels may reduce their daytime activities under a period of reduced reproductive behaviour. At this time, young squirrels born during the main peak of birth (spring) have probably dispersed and settled a new home range. In the winter (i.e., February), most females are pregnant (Chapuis et al., 2014), which could explain a low daily rate of activity.

The absence of squirrels observed in fully urbanised areas supports the idea that these habitats are unfavourable to Pallas's squirrels in the Antibes region, most likely because of a lack of either private or public vegetated gardens. Woodlands were the most favourable habitat for *C. erythraeus*, as indicated by the highest relative densities recorded in our study area. In Japan, the diversity of tree species was found to be an important factor explaining the selection of habitats by Pallas's squirrels in a semi-urbanised area, likely due to the availability of food resources and nesting sites (Tamura et al., 1989). The largest number of squirrels in the Antibes region was observed in the site of La Garoupe; this area is dominated by holm oaks, which may provide an important food supply through acorns, and Aleppo pines for nesting sites. Houses where gardens are planted with many fruit trees also surround this area. Squirrels may thus benefit from the availability of food items preferred in their native range (e.g., fruits and flowers; see Tamura, 2012). Active feeding by people must also occur, playing a role in the facilitation of squirrel establishment, spread and adaptation

across relatively urbanised landscapes (e.g., Benitez et al., 2010, 2013; Bertolino and Lurz, 2013).

A large number of nests were also observed in residential areas, despite the low relative densities of squirrels. Hence, residential habitat may be favourable to this species. As no native European red squirrels have been observed in this habitat, we are confident that the nests belong to *C. erythraeus*. It should also be noted that the observation of nests in *P. pinea* is easy and that unused nests may persist longer than in other species of trees. This situation may have led observers to overestimate the role of residential areas as a suitable nesting habitat.

Space use

Studies dedicated to the analysis of the home range and core area sizes of *C. erythraeus* employed different methods: capture-recapture from a trapping grid in a coniferous forest in Taiwan (Tamura et al., 1987), radio-tracking in a suburban woodland in Japan (Tamura et al., 1989), and visual surveys in a monsoon forest in China (Yo et al., 1992). According to our results, home range areas based on 100% MCP in Antibes were 4–6 times larger than those reported by these studies for females and 2–5 times larger than those reported for males. Although the MCP is useful for a comparison between studies, it is very sensitive to sample size (Tamura et al., 1989) and must be used with caution, especially when the methods used to localise the positions of individuals are different.

An inverse relationship between food abundance and home range size was also commonly observed in *C. erythraeus* (Tamura et al., 1989); habitats with low food availability are thought to drive individuals to explore larger areas to gather enough food. Thus, differences between the habitat characteristics investigated in our study sites and those reported by Tamura et al. (1989) may explain such discrepancies. Indeed, 27 and 43 species of trees per 0.1 ha were found in Japanese and Taiwanese study sites (Tamura et al., 1989), respectively, in contrast to the woodland of Encourdoules where less than ten species of trees per hectare can be found.

Moreover, increased predation pressure can be associated with a decrease in home range size of *C. erythraeus* (Tamura et al., 1989). Within the Antibes region, the only predators of squirrel are domestic cats and dogs. Assuming that there is a reduced number of predators for Pallas's squirrels in Antibes compared to Asiatic countries, such a lack of enemies may partly explain the large home ranges observed in our study sites. This hypothesis deserves further comparative studies between the native and invaded habitats of Pallas's squirrels.

In the Antibes region, male Pallas's squirrels had a mean annual home range size approximately 2.5 times larger than female home ranges, and they had 2.2 times larger core areas. These results are in agreement with the fact that this species has a promiscuous mating system, with males increasing their home range to overlap with the maximum number of females (Tamura et al., 1987), which is also commonly reported for other sciurids (Lane et al., 2009; Lurz et al., 2005; Marmet et al., 2009, 2012; Romeo et al., 2010). Moreover, overlap within sex is more important in males than in females (Di Pierro et al., 2008; Romeo et al., 2010; Wauters et al., 2001, 2005). Furthermore, we expected to observe intra-sexual territoriality among adult females, especially during the reproductive season, because females are known to defend the area around their nest against other females (Tamura et al., 1987). Intra-sexual overlap was not lower between females than it was between males. Moreover, adult females did not have exclusive core areas, which contradicts the results obtained by a radio-tracking study on the home range in an introduced *C. erythraeus* population in Japan (Tamura et al., 1987) and for a native population in Taiwan obtained by point censuses (Tamura et al., 1989). Again, differences in habitat characteristics between study sites in Japan or Taiwan and in

Antibes may explain the observed discrepancies. Seasonal differences in both the intra- and intersexual overlap found in our study are difficult to interpret in relation to the small number of animals that were followed in the autumn, potentially leading to an underestimation of the overlap.

Conclusion

The present study confirms that *C. erythraeus* is able to establish populations in various habitat types, including suburban forests, woodlands, and residential areas (e.g., Bertolino and Lurz, 2013; Benitez et al., 2013). We also confirm that Pallas's squirrel is now firmly established in the urbanised landscape of the Antibes region (e.g., Gerriet, 2009), reaching locally high relative densities in homogeneous woodland habitats within a slowly expanding range in relation to the peculiar geographic situation constituted by the peninsula of the Cap d'Antibes and to the presence of anthropogenic barriers. Specific to our study, the absence of territoriality indicates the ability for the squirrels to share space among a large number of individuals of both sexes, thus contributing to high densities. Consequently, establishment does not seem to require large areas, and numerous suitable habitat patches may be available at the landscape level, thereby having a significant role on the future expansion prospects of the species. Major public communication is also necessary to prevent any translocation events, new invasion foci (Benitez et al., 2010; Bertolino and Lurz 2013; Signorile et al., 2014) and detrimental effects to non-target species or to the environment by resident actions (e.g., unsupervised trapping and poisoning). The present study provides information on the key parameters involved in the expansion process of Pallas's squirrel in the Antibes region, allowing for the development of useful tools for the National Control Plan that has been set by the French Ministry of Ecology and launched in 2012 (Chapuis et al., 2011).

Acknowledgements

The French Ministry of Ecology (M.E.D.D.E.) funded this study. We are grateful to Catherine Ducatillon and Richard Belanger (INRA) for their help with the field logistics. Many thanks to Noëlie Maurel (MNHN), Gilles Plattner (MNHN), and Françoise Cardou for their useful comments and especially to two anonymous referees who fruitfully reviewed the manuscript.

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