ORIGINAL PAPER

Home range, range overlap, and site fidelity of introduced Siberian chipmunks in a suburban French forest

Julie Marmet · Benoît Pisanu · Jean-Louis Chapuis

Abstract Home range size, range overlap, and multiyear site fidelity were investigated for introduced Siberian chipmunks (*Tamias sibiricus*) in a French suburban forest from bimonthly trapping sessions for 4 years (2004–2007). Annual home range sizes (100% minimum convex polygon, ±SE) were estimated from 39 trapping histories of 28 different adult residents. Males ($N=13$, 1.86 ± 0.32 ha) had a home range 2.5 times larger than females ($N=26$, 0.71 ± 0.08 ha); a male home range included significantly more trapping centers (arithmetic mean of capture locations) of females (5.5 ± 0.7) than of males (2.3 ± 0.5). Chipmunks exhibited strong multiyear site fidelity: mean distance between annual trapping centers of individuals trapped over two successive years was small ($N=82$, 26 ± 2 m) compared to the largest home range length (ranging from 36 to 281 m); overlap between annual home range sizes of residents was $84\pm5\%$ ($N=11$). These results improve our understanding of the space occupation of this unknown species in a novel environment.

Keywords Capture–mark–recapture ·
Introduced chipmunk · Home range · Multiyear site fidelity ·
Range overlap · *Tamias sibiricus*

Introduction

The Siberian chipmunk *Tamias sibiricus* Laxmann, 1769 (Rodentia: Sciuridae) is a small ground-dwelling squirrel

J. Marmet (✉) · B. Pisanu · J.-L. Chapuis
Département Ecologie et Gestion de la Biodiversité,
Muséum National d'Histoire Naturelle,
UMR 5173 MNHN-CNRS-P6,
61 Rue Buffon,
75005 Paris, France
e-mail: jmarmet@mnhn.fr

originally distributed from northeastern Europe to the Bering Strait and in the East of Asia (China, Korea, Japan; Obolenskaya 2007; Ognev 1940). Several papers deal with the biology and ecology of this squirrel (Kawamichi 1980, 1989, 1996, 1999; Kawamichi and Kawamichi 1993, in Japan; Obolenskaya 2007; Ognev 1940, in Russia) but little is known about its spatial behavior. In its native area, Siberian chipmunks live in different habitats extending from continental Siberia to temperate regions of Asia (Obolenskaya 2007; Ognev 1940). Diurnal, solitary, and sedentary, this rodent uses a nest located principally in a burrow consisting simply of one entrance, one tunnel, and one nest chamber where it also hibernates (Kawamichi 1989). It frequently changes nests but stays within the same home range, which is <1 ha in forest or dense bushy areas; high overlap of home ranges exists between sexes throughout the active seasons (Kawamichi 1996). The chipmunk's diet consists mainly of seeds, buds, young leaves, and animal matter; they forage more on the ground than in trees and store food in nests and by scatter hoarding (Kawamichi 1980).

Sold in pet shops in Europe in the 1960s, this squirrel was accidentally or intentionally released into forests in Belgium, Germany, Austria, The Netherlands, Italy, and Switzerland (see Chapuis 2005). In France, the Siberian chipmunk was found to be naturalized (Richardson et al. 2000) since the late 1970s. Since 2007, 11 populations have been recorded in the wooded suburban areas of Ile-de-France and Picardie (Chapuis 2005; Marmet and Chapuis 2005). The consequences of the Siberian chipmunks' introduction to European forests are poorly documented (Riegel et al. 2000). In 2004, a research program was launched in order to study the ecology of this species, its ability to colonize new habitats, and its potential impacts on the ecosystem and human health (Chapuis 2005).

The behavioral characteristics of the introduced species are poorly known. Native and introduced populations

provide contrasting situations to study the plasticity of behavioral traits involved in colonization and establishment processes (Holway and Suarez 1999). Introduced species also offer significant opportunities to improve our basic understanding of population biology (Holway and Suarez 1999). The study of spatial patterns may provide information on the behavioral component of a species spreading into a new habitat. Home range size (Burt 1943) and range overlap provide information on the species ability to use space and interactions between sexes, thus on the capacity for reproduction of the population (Boellstorff and Owings 1995; Emlen and Oring 1977; Wauters and Dhonts 1992). The study of site fidelity provides information on the capacity of adults to spread (Switzer 1993).

Taking advantage of trapping data collected from 2004 to 2007 using capture–mark–recapture methods in a suburban forest near Paris, the main aims of this study were (1) to compare annual home range size of residents according to sex, (2) to analyze intersexual and intrasexual home range overlap, and (3) to assess annual site fidelity. The results of this study provide original observations about the spatial organization of the Siberian chipmunk introduced into France. When it was possible, we compare our results with those from the single available study of a native population of *T. sibiricus* in Hokkaido, Japan (Kawamichi 1996).

Materials and methods

Study site

The Forest of Sénart is a 3,200-ha suburban forest located 22 km southeast of Paris (48°39′ N, 02°29′ E; 80 m a.s.l.) in a temperate climate. To limit public access (about three million visitors each year), the study was carried out within a fenced area of 12 ha, the Parc de la Faisanderie (Fig. 1). In this park, Siberian chipmunks have been present since the end of the 1990s (G. Spagnol, personal communication). However, the first observations were carried out in the early 1970s in the western part of the forest 5 km from the monitored site (see Chapuis 2005). The founders of this population were pets originally brought over from Korea (E. Baudry and A. Lissovsky unpublished).

The study site is dominated by oak-hornbeam forest (CORINE Biotopes: 41.24; Bissardon et al. 1997), with more open canopy cover in the northern part (5 ha) than in the southern part (5.5 ha) of the site. Stone-walled buildings and lawns occupy the remaining 1.5 ha. The dominant tree species are pedunculate and sessile oaks (*Quercus robur, Q. petraea*) and European hornbeam (*Carpinus betulus*). Other species include the common lime (*Tilia platyphyllos*), blackthorn (*Prunus spinosa*), wild cherry (*Prunus avium*), common hawthorn (*Crataegus monogyna*), Scots pine
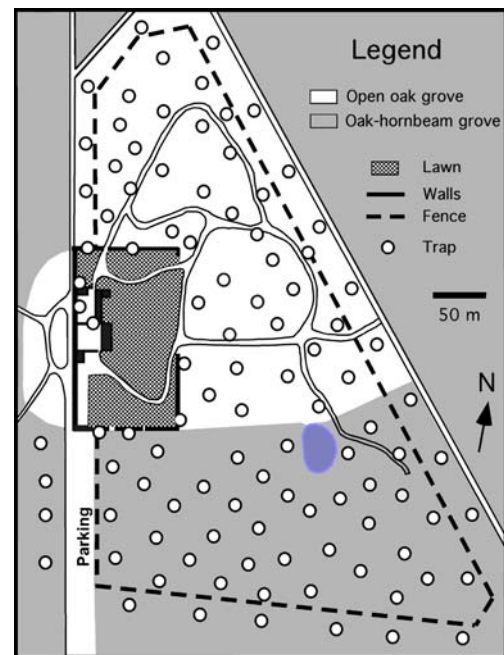
Fig. 1 Description of the study site and distribution of traps

(*Pinus sylvestris*), aspen (*Populus tremula*), sycamore maple (*Acer pseudoplatanus*), and silver birch (*Betula pendula*).

Trapping procedure

Trapping was conducted outside the hibernation period from March to October 2004, March to November 2005, February to December 2006, and February to November 2007. The trapping system consisted of live traps (8×8× 26 cm, H.B. Sherman Traps©) sited using a GPS Leitz® (±1 m) and distributed throughout the study site (distance between two neighboring traps=38±9 m, N=169; Fig. 1). Trapping sessions occurred twice a month for two to three consecutive days in 2004 and three to five consecutive days between 2005 and 2007. Every day, traps were opened early in the morning, baited with a mixture of peanut butter and sunflower seeds, checked four times during the day, and closed at the end of the afternoon. In 2004, 80 traps covered the 12 ha, and between 2005 and 2007, 24 traps were added to the periphery of the 2004 trapping scheme thereby increasing the trapping area to 14 ha.

Chipmunks captured for the first time were tagged with a subcutaneous transponder chip (PIT tag) and a numbered ear tag. At each capture, the chipmunks were weighed (±1 g) and released at the capture point. Individuals were aged according to four categories: adult, spring cohort juvenile (J1), summer cohort juvenile (J2), or an unknown age. Between February and the beginning of May, individuals captured for the first time were considered to be adults. Individuals with a body mass of <70 g at their

first capture were aged as spring cohort juveniles from the end of May to the end of July and as summer cohort juveniles from the end of August to November. For these individuals, mean body mass curves with 95% confidence intervals were generated as a function of time in order to age unknown individuals. According to our data and to that of Blake and Gillett (1984), spring and summer cohort juveniles can reproduce during the first period of the following year. Therefore, all juveniles were considered to be adults the year following their first hibernation period. All trapping and handling procedures were conducted in accordance with French legislation.

Data analysis

We used Ranges 6 software (Kenward et al. 2003) to estimate annual home range size, home range overlap, and multiyear site fidelity of adults.

Home range size was estimated using two nonparametric methods (Powell 2000): 100% minimum convex polygons (100% MCP; Mohr 1947) and 95% fixed kernels (95% FK; Worton 1989). Only adults with a home range located within the trapping network (<33% of trapping locations on the periphery of the study site) and captured at least 20 times (see Mares et al. 1980) during at least four consecutive trapping sessions were used in the analysis. The term "resident" refers to individuals for which a home range could be estimated. For each resident, we also measured the maximum distance between locations where it was trapped.

The percentage of home range overlap could not be estimated because we could not obtain information on the home ranges of all individuals in the population. Instead, an index was calculated in order to distinguish differences between intersexual and intrasexual home range overlap. For each resident female and male considered, we estimated the home range overlap index by counting the number of other female and male trapping centers (arithmetic mean of capture locations) present in each resident's home range (100% MCP). Only the trapping centers of chipmunks captured at least five times (nontransients) and present during the same period as the resident were considered. Thus, we compared the number of female trapping centers with the number of male trapping centers counted within the home range of a male and within the home range of a female. If there is no difference between intrasexual and intersexual overlap in home ranges, then the number of female and male trapping centers should not be different within any given area.

Multiyear site fidelity was estimated for chipmunks trapped during two consecutive years as the distance between annual trapping centers. In the analysis, we used adults trapped at least twice a year. Additionally, we estimated the percentage of overlap between the two annual

home ranges (100% MCP) for residents trapped in two successive years using the second year as the base for the calculation.

Statistical analysis

Due to our small sample sizes and a lack of normality in the data distribution, we used nonparametric statistics (Siegel and Castellan 1988). As excluding repeated observations of the same animal did not change the results, these additional observations were kept in the statistical analyses. The Spearman rank correlation coefficient, ρ, was calculated to fit home range size as a function of the number of locations and number of days of monitoring (i.e., number of days between first and last capture of the animal). We used the Wilcoxon matched-pair test, T^+, to compare the mean home range sizes estimated from 100% MCP and 95% FK, the mean annual home range sizes of residents trapped in two consecutive years (multiyear site fidelity analysis) and the mean number of male and female trapping centers within resident home ranges (overlap index analysis). For unpaired data, the Mann–Whitney U test was used to compare the mean distance between annual trapping centers between sexes (multiyear site fidelity analysis). Deviance analysis of our generalized linear model (McCullagh and Nelder 1989) using a Poisson distribution and logarithm link function was performed to explore variations in home range size according to sex and year. Calculations were made using the Genstat 6.0 software (Genstat 5 Committee 1994) and all mean values are presented with ±1 SE.

Results

During the study period, we recorded 6,420 captures and recaptures. The number of unique individuals trapped each year increased from 156 in 2004 to 337 in 2007 (Table 1). The number of adults was similar in 2004 ($N=68$) and 2005 ($N=76$) and in 2006 ($N=123$) and 2007 ($N=116$) (Table 1). For adults, the sex ratio (females/males) was always skewed in favor of females (2004, 1.2; 2006, 1.5; 2007, 1.3), particularly in 2005 where 2.5 times more females than males were trapped. The number of young varied depending on the year and season. Generally, more young were trapped in spring (J1) than in summer (J2) except in 2006 (Table 1).

Home range size

Home range size was estimated for one individual in 2004, six in 2005, and 16 individuals both in 2006 and 2007 (Table 2; Fig. 2). No significant correlations were found between the number of trapping locations or the number of days of

Table 1 Number of unique individuals trapped between 2004 and 2007 in the Forest of Sénart, according to year, sex, and age

Year	Trapping area (ha)	Trapping events	Age class								Total number of individuals
			Adult		J1		J2		Unknown		
			F	M	F	M	F	M	F	M	
2004	12	657	37	31	21	16	18	22	5	6	156
2005	14	1,609	54	22	44	52	18	13	5	7	215
2006	14	1,856	74	49	5	7	42	52	2	7	238
2007	14	2,299	65	51	59	59	29	48	7	19	337

F female, *M* male, *J1* spring cohort juvenile, *J2* summer cohort juvenile

monitoring and estimated home range size using either 100% MCP ($N=39$, $\rho=0.036$, *NS* and $N=39$, $\rho=-0.107$, *NS*, respectively) or 95% FK ($N=39$, $\rho=-0.155$, *NS* and $N=39$, $\rho=-0.117$, *NS*, respectively). Estimated mean home range size (Table 2) were not significantly different between the two methods for resident females ($N=26$, 100% MCP= 0.71 ± 0.08 ha; 95% FK=0.69 ± 0.09 ha; $T^+=163.0$, *NS*), but were significantly higher ($T^+=20.0$, $P<0.05$) for resident males when calculated using 95% KF ($N=13$, 1.86 ± 0.32 ha) rather than 100% MCP (1.71 ± 0.30 ha). Consequently, in order to simplify our discussion, we will only use 100% MCP estimates hereafter (Fig. 2). Home range size ranged from 0.05 to 1.81 ha for resident females and from 0.80 to 4.48 ha for resident males.

The maximum distance between trapping locations ranged from 36 to 246 m for females ($N=26$, 136 ± 10 m) and from 134 to 281 m for males ($N=13$, 189 ± 12 m). In 2006 and 2007, home range size varied according to sex of the residents, but not with year (Table 3). Males had a home range ($N=11$, 1.80 ± 0.34 ha) that was on average 2.5 times larger than that of females ($N=21$, 0.71 ± 0.07 ha). Due to the few number of individuals, data obtained in 2004 (one female) and in 2005 (four females and two males) were not considered in this analysis.

Home range overlap index

Using the 39 home ranges estimated between 2004 and 2007, we compared the number of trapping centers of males and females found inside each range. Within the home range of resident males ($N=13$), the mean number of female trapping centers (5.5 ± 0.7) was significantly higher than the mean number of male trapping centers (2.3 ± 0.5; $T^+=0.0$, $P<0.05$). Conversely, within the home range of resident females ($N=26$), the mean number of female trapping centers (1.7 ± 0.3) was not significantly different from the mean number of male trapping centers (1.3 ± 0.2; $T^+=80.50$, *NS*).

Multiyear site fidelity

Among the 68 adult individuals trapped in 2004, 28 were trapped again in 2005, with 20 at least twice a year. In 2006, we trapped 39 of the 76 adults trapped in 2005 with 31 at least twice a year. In 2007, 38 of the 123 adults trapped in 2006 were captured with 31 at least twice a year.

In the 2004 to 2005 comparison, the mean distance between annual trapping centers was significantly higher for males ($N=5$; 42 ± 9 m) than for females ($N=15$; 24 ± 4 m;

Table 2 Mean home range size of Siberian chipmunks estimated by 100% MCP and 95% FK methods for resident females and males trapped in the Forest of Sénart between 2004 and 2007

Year	Sex	Number of residents	Mean number of		Mean home range size (ha)	
			Locations	Days[a]	100% MCP	95% FK
2004	F	1	20	189	0.16	0.26
2005	F	4	49±9	195±8	0.85±0.40	0.53±0.21
	M	2	44; 24	185; 213	1.36; 1.14	1.84; 0.98
2006	F	10	45±6	138±15	0.70±0.10	0.65±0.14
	M	6	40±7	124±26	1.84±0.61	1.98±0.66
2007	F	11	40±8	140±20	0.72±0.12	0.83±0.18
	M	5	37±6	195±23	1.74±0.47	1.89±0.45
2004–2007	F	26	43±4	149±11	0.71±0.08	0.69±0.09
	M	13	38±4	163±17	1.71±0.30	1.86±0.32

[a] Number of days between first and last capture
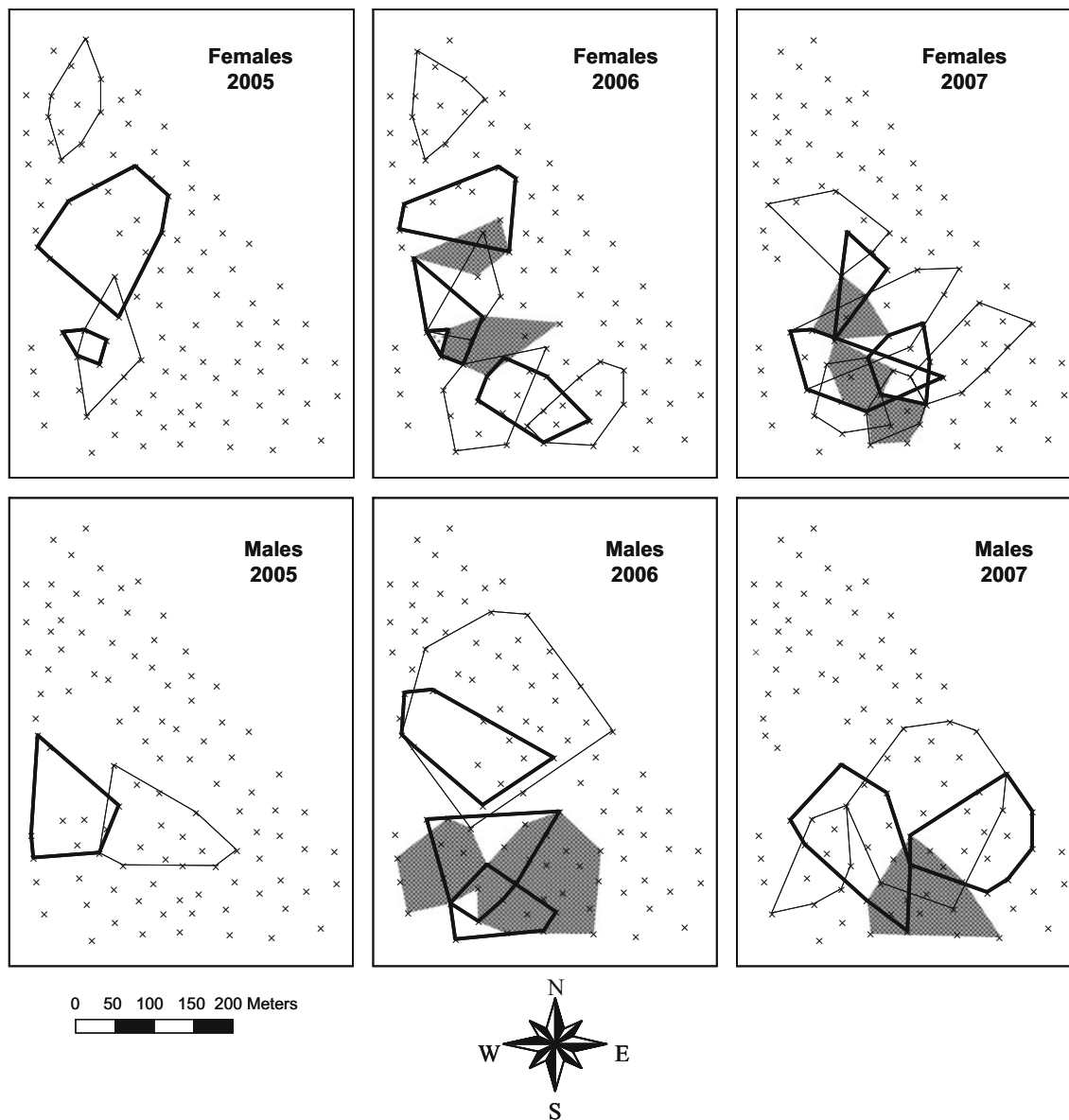
Fig. 2 Home ranges (100% MCP) of six resident Siberian chipmunks (two males and four females) in 2005, 16 (six males and 10 females) in 2006, and 16 (five males and 11 females) in 2007 trapped in the Forest of Sénart. *Shaded* home ranges and *thickened lines* have been used for clarity. Trap stations locations are represented by *crosses*

Table 3 Deviance analysis of generalized linear models exploring the variation in home range size of resident chipmunks according to sex and year (2006 and 2007)

Source of variation	df	Deviance	p value
Total	31	16.82	<0.01
Sex	*1*	*7.40*	*<0.01*
Year	1	0.05	NS
Sex × year	3	7.42	<0.001

Selected model is italicized

$U=12.0$, $P<0.05$). There was no significant difference between the sexes in 2005 to 2006 (males: $N=7$, 32±5 m; females: $N=24$, 23±3 m; $U=47.0$, NS) and in 2006 to 2007 (males: $N=11$, 26±7 m; females: $N=20$, 24±4 m; $U=109.0$, NS). The distance between annual trapping centers ranged from 3 to 88 m ($N=82$, 26±2 m).

The annual home ranges of ten residents, eight females and two males, trapped during two consecutive years (one female was trapped three consecutive years, thus $N=11$) overlapped by 84±5%. The mean distance between annual trapping centers was 18±5 m ($N=11$). The mean home range size of the eight females decreased significantly ($T^+=1.0$,

$p<0.05$) between the first year (0.88±0.17 ha) and the second year (0.55±0.09 ha).

Discussion

Hayne (1949) underlined difficulties in interpreting trapping data to define home range size. Trap spacing, bait food, grid size, shape and placement, or even trap shy and trap happy behavior may affect estimates (Andrzejewski 2002; Jewell 1966). In addition, obtaining sufficient locations per individual to assess home range size is often difficult. However, for easy-to-capture species like chipmunks, capture–recapture techniques allow for the monitoring of individuals on longer time scales, even over several years, as well as the study of occupation of space including a greater number of individuals than other methods such as radiotelemetry.

Although the MCP method is the most commonly used technique because it is easy to draw and useful in comparing different studies, it is highly sensitive to sample size (see Powell 2000). In order to minimize the effect of sample size on the estimates, we chose to calculate annual home range size to have enough number of captures per individuals. Ranges obtained with a minimum of 20 locations (Mares et al. 1980) and over at least four consecutive trapping sessions, i.e., 2 months, were not correlated with the number of locations or the number of days of monitoring, suggesting the good reliability of estimates. We are aware that home ranges for chipmunks can vary seasonally, even from week to week (Martinsen 1968). Unfortunately, despite the frequency of trapping sessions, our data are insufficient to analyze the effect of seasonality on the size and use of home ranges.

According to our results, adult male chipmunks had a mean annual home range 2.5 times larger than those of adult females in 2006 and 2007 in the Forest of Sénart. Kawamichi (1996) also reported adult male home ranges to be 1.7 times larger than those of adult females in a native Siberian chipmunk population found in a coastal oak forest in Northern Japan. Differences in home range size between sexes has also been observed in other sciurids (e.g., *Sciurus vulgaris*, Wauters and Dhonts 1992; *Sciurus griseus*, Linders et al. 2004). In the only other publication on the ecology of an introduced population of Siberian chipmunk in Europe, Geinitz (1980) found that females had larger home ranges than males. However, this study was based on a small number of individuals and locations observed over a short period of time within a small area, all of which may have biased the results. In *Tamias striatus*, a species closely related to *T. sibiricus*, such a difference have been relied upon extension of male home ranges during the breeding seasons (Bowers and Carr 1992). Other studies indicate that

male and female chipmunks have the same home range size (Lacher and Mares 1996; Mares et al. 1982) but the study periods did not correspond to the breeding season. Additionally, resident males had more adult female trapping centers than adult male centers within their home ranges, whereas there was no difference within resident female home ranges. Since estimating home range size for all individuals within the population was not feasible, we chose to calculate an index to examine how sex differences influence the establishment of chipmunk home range. These results show that range overlap is different between sexes; the overlap between a male home range and its neighbor females is more frequent than overlap between female home ranges or between male home ranges. This difference is not due to a lower density in males because there is no difference between the numbers of trapping centers of either sex in home ranges of resident females. These results are also in agreement with the observations of Kawamichi (1996) who used the number of burrows as an indicator of overlap between home ranges.

For chipmunks, mates and the distribution of food resources are the main factors influencing home range use (Bowers and Carr 1992; Martinsen 1968; Yahner 1978). In polygynous and promiscuous species, intersexual differences in home range size may be due to different strategies concerning these limiting resources (Edelman and Koprowski 2006). During the reproductive period of Siberian chipmunks, the principal limiting resources are food for females and estrous females for males (i.e., females are receptive only 1 day per reproductive period; Kawamichi and Kawamichi 1993). Despite the fact that home range sizes were estimated without regard to the breeding season in our study, differences in home range size and range overlap exist between the sexes in this introduced population of *T. sibiricus*. Therefore, by having a large home range and a high degree of range overlap with females, males can increase their chances of meeting and fertilizing females and maximize their reproductive success. According to these results, it appears that this species has a promiscuous mating system.

Food quality, predation avoidance, and burrow or refuge availability can affect the home range size of sciurids (Edelman and Koprowski 2006; Harestad and Bunnel 1979; Lacher and Mares 1996; Mares et al. 1976; Martinsen 1968; Wauters and Dhonts 1992). The home range size of squirrel species can also vary with density (Forsyth and Smith 1973; Lurz et al. 2000). According to the few data that we disposed, it appears that when number of trapped adult Siberian chipmunks increase between years, mean home range size tends to increase for males and decrease for females. Males may expand their home ranges to encounter more females, but we need more data to demonstrate a potential effect of density on home range size.

Site fidelity reflects stability in spatial use, either in resources availability or social organization in ground squirrels (*T. striatus*, Elliott 1978; Lacher and Mares 1996; *Spermophilus* spp., Boellstorff and Owings 1995; Harris and Leitner 2004). From the individuals trapped during two consecutive years (41%, 51%, and 30% between 2004 and 2005, 2005 and 2006, and 2006 and 2007, respectively), we showed that the distances between annual trapping centers were small (ranged from 3 to 88 m) relative to the largest home range length for both sexes (ranged from 36 to 246 m for resident females and from 134 to 281 m for resident males). For this analysis, we used animals with at least two captures by years in order to have the greatest number of individuals. Of course, we cannot consider the individuals who disappeared from the study area. It is probable that they move partially out of the area. The largest distance between annual centers observed in our 14-ha study site was 88 m, a relatively small distance compared to the size of the study area. Annual home ranges of resident Siberian chipmunks overlapped on average by 84%. We can thus suggest that the Siberian chipmunk shows strong multiyear site fidelity. Moreover, the observed yearly decrease in the home range size of females would indicate a better exploitation of their range. Kawamichi (1989) demonstrated that this squirrel tends to stay in the same place despite frequent changes in nest sites. He also showed that the distance between burrows is relatively short and that males travel over greater distances than females. For the Eastern chipmunk, the distance between annual trapping centers is small relative to the home range size for both sexes (Lacher and Mares 1996).

Ecological studies of introduced populations can reveal shifts in the biological traits of a species toward its new habitat, a process involved in the successful colonization and expansion of the distributional range of a small population. According to our results, the occupation of space by adult Siberian chipmunks introduced to the Forest of Sénart seems similar to that of the Japanese native population. The males use larger home ranges than females, and the population shows a high rate of range overlap between the sexes and strong multiyear site fidelity. However, the first individuals introduced into France came from Korea where the subspecies (*T. sibiricus orientalis*) differs from the Japan subspecies (*T. sibiricus lineatus*, Ognev 1940); a recent study even suggested that *T. sibiricus* from South Korea could be considered to be a separate species (Lee et al. 2008). To compare space occupation between a native and an introduced population of Siberian chipmunk, it will be essential to have data from the Korean population.

The behavior of adult chipmunks is thus related to a high stability of space use across years, which could reduce or inhibit the rate of spread of the population. The potential ability of this introduced species to spread now needs to be investigated by studying the dispersal of young, which can elsewhere be influenced by stability of adults.

References

Andrzejewski R (2002) The home-range concept in rodents revised. Acta Theriol (Warsz) 47:81–101

Bissardon M, Guibal L, Rameau J-C (1997) CORINE biotopes. Version originale. Types d'habitats français. Nancy

Blake BH, Gillett KE (1984) Reproduction of Asian chipmunks (*Tamias sibiricus*) in captivity. Zoo Biology 3:47–63

Boellstorff DE, Owings DH (1995) Home range, population structure, and spatial organization of California ground squirrels. J Mammal 76:551–561. doi:10.2307/1382363

Bowers MA, Carr TG (1992) Home range shifts accompanying breeding in the eastern chipmunk, *Tamias striatus* (Rodentia: Sciuridae). Z Saugetierkd 57:288–293

Burt WH (1943) Territoriality and home range concepts as applied to mammals. J Mammal 24:346–352. doi:10.2307/1374834

Chapuis J-L (2005) Répartition en France d'un animal de compagnie naturalisé, le Tamia de Sibérie (*Tamias sibiricus*). Rev Ecol (Terre Vie) 60:239–253

Edelman AJ, Koprowski JL (2006) Influence of female-biased sexual size dimorphism on dominance of female Townsend's chipmunks. Can J Zool 84:1859–1863. doi:10.1139/Z06-181

Elliott L (1978) Social behavior and foraging ecology of the eastern chipmunk (*Tamias striatus*) in the Adirondack Mountains. Smithson Contrib Zool 265:1–107

Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223. doi:10.1126/science.327542

Forsyth DJ, Smith DA (1973) Temporal variability in Home ranges of eastern chipmunks (*Tamias striatus*) in a Southeastern Ontario woodlot. Am Midl Nat 90:107–117. doi:10.2307/2424271

Geinitz VC (1980) Beiträge zur biologie des streifenhörnchens (*Eutamias sibiricus* Laxmann, 1769) auf einem friedhof in Freiburg (Süddeutschland). Z Saugetierkd 45:279–287

Harestad AS, Bunnel FL (1979) Home range and body weight—a reevaluation. Ecology 60:389–402. doi:10.2307/1937667

Harris JH, Leitner P (2004) Home-range size and use of space by adult Mohave ground squirrels, *Spermophilus mohavensis*. J Mammal 85:517–523. doi:10.1644/1545-1542(2004)085<0517:HSAUOS>2.0.CO;2

Hayne DW (1949) Calculation of size of home range. J Mammal 30:1–18

Holway DA, Suarez AV (1999) Animal behavior: an essential component of invasion biology. Trends Ecol Evol 14:328–330. doi:10.1016/S0169-5347(99)01741-3

Jewell PA (1966) The concept of home range in mammals. Symp Zool Soc Lond 18:85–109

Kawamichi M (1980) Food, food hoarding and seasonal changes of Siberian chipmunks. Japanese Journal of Ecology 30:211–220

Kawamichi M (1989) Nest structure dynamics and seasonal use of nests by Siberian chipmunks (*Eutamias sibiricus*). J Mammal 70:44–57. doi:10.2307/1381668

Kawamichi M (1996) Ecological factors affecting annual variation in commencement of hibernation in wild chipmunks (*Tamias sibiricus*). J Mammal 77:731–744. doi:10.2307/1382678

Kawamichi M (1999) Ecological aspects of the solitary ranging squirrel, Siberian chipmunk (*Tamias sibiricus*). Mammalian Science 78:185–187

Kawamichi T, Kawamichi M (1993) Gestation period and litter size of Siberian chipmunk *Eutamias sibiricus lineatus* in Hokkaido, Northern Japan. J Mammal Soc Jpn 18:105–109

Kenward RE, South AB, Walls SS (2003) Ranges 6 v1.2: for the analysis of tracking and location data (software). Anatrack, Wareham, UK

Lacher TE, Mares M (1996) Availability of resources and use of space in eastern chipmunks, *Tamias striatus*. J Mammal 77:833–849. doi:10.2307/1382689

Lee M-Y, Lissovsky AA, Park S-K, Obolenskaya EV, Dokuchaev NE, Zhang Y-P, Yu L, Kim Y-J, Voloshina I, Myslenkov A, Choi T-Y, Min M-S, Hang Lee H (2008) Mitochondrial cytochrome *b* sequence variations and population structure of Siberian chipmunk (*Tamias sibiricus*) in Northeastern Asia and population substructure in South Korea. Mol Cells 26:566–575

Linders MJ, West SD, Haegen WMV (2004) Seasonal variability in the use of space by Western gray squirrels in Southcentral Washington. J Mammal 85:511–516. doi:10.1644/1545-1542(2004)085<0511:SVITUO>2.0.CO;2

Lurz PWW, Garson PJ, Wauters L (2000) Effects of temporal and spatial variations in food supply on the space and habitat use of red squirrels, *Sciurus vulgaris* L. J Zool (Lond) 251:167–178. doi:10.1111/j.1469-7998.2000.tb00601.x

Mares MA, Watson MD, Lacher TE (1976) Home range perturbations in *Tamias striatus*. Oecologia 25:1–12. doi:10.1007/BF00345029

Mares MA, Willig MR, Bitar NA (1980) Home range size in Eastern chipmunks, *Tamias striatus*, as a function of numbers of captures: statistical biases of inadequate sampling. J Mammal 61:661–669. doi:10.2307/1380311

Mares MA, Lacher TE, Willig MR, Bitar NA, Adams R, Klinger A, Tazic D (1982) An experimental analysis of social spacing in *Tamias striatus*. Ecology 63:267–273. doi:10.2307/1938940

Marmet J Chapuis J-L (2007) Répartition de l'écureuil de Corée (*Tamias sibiricus*), animal de compagnie exotique introduit en France: résultats de l'enquête nationale de 2005. In: Les Mammifères Forestiers Cdf, editor; 2005; Rambouillet. pp 27–31

Martinsen DL (1968) Temporal patterns in the home ranges of chipmunks (*Eutamias*). J Mammal 49:83–91. doi:10.2307/1377730

McCullagh P, Nelder JA (1989) Generalized linear models, 2nd edn. Chapman and Hall, London

Mohr CO (1947) Table of equivalent populations of North American small mammals. Am Midl Nat 37:223–249. doi:10.2307/2421652

Obolenskaya EV (2007) Distribution patterns of the Siberian chipmunk (*Tamias sibiricus* Laxmann, 1769). Arch Mus Zool Univ Moscou 49:265–298

Ognev SI (1940) Zveri SSSR i prilezhashchikh stran: Gryzuny. (Zveri vostochnoi Evropy i severnoi Azii) [Mammals of the USSR and adjacent countries: Rodents (Mammals of eastern Europe and northern Asia)]. Akademiya Nauk SSSR, 4:1–615 (in Russian)

Powell RA (2000) Animal home ranges and territories and home range estimators. In: Boitani L, Fuller TK (eds) Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, pp 65–110

Richardson DM, Pysek P, Rejmanek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. Divers Distrib 6:93–107. doi:10.1046/j.1472-4642.2000.00083.x

Riegel J, Lafontaine R-M, Pasteels J, Devillers P (2000) Influence potentielle du Tamia de Sibérie *Tamias sibiricus* (Laxmann) sur la régression de l'avifaune en Forêt de Soignes. Cah Éthol 20:45–62

Siegel S, Castellan NJJ (1988) Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York

Switzer PV (1993) Site fidelity in predictable and unpredictable habitats. Evol Ecol 7:33–555. doi:10.1007/BF01237820

Wauters L, Dhonts AA (1992) Spacing behaviour of red squirrels, *Sciurus vulgaris*: variation between habitat and the sexes. Anim Behav 43:297–311. doi:10.1016/S0003-3472(05)80225-8

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168. doi:10.2307/1938423

Yahner RH (1978) Burrow system and home range use by eastern chipmunks, *Tamias striatus*: ecological and behavioral considerations. J Mammal 59:324–329. doi:10.2307/1379916