

Natal dispersal of introduced Siberian chipmunks, *Tamias sibiricus*, in a suburban forest

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Abstract The Siberian chipmunk, *Tamias sibiricus*, was introduced into the suburban forest of Sénart in the late 1970s where it naturalised. Juvenile dispersal of this solitary ground-dwelling squirrel is not known, while it is an important component of the invasion process. From 2003 to 2007, mark–recapture techniques were used to determine how dispersal movements differed between year, cohort, sex and body mass. Distances moved were calculated between the location of first capture during the year of birth and the arithmetic centre of the trapping locations obtained the next year. Excluding heaviest individuals, e.g. 80 g, that must have already dispersed and thus lowered the estimation of averaged distance moved, our results shows that the dispersal distance in juvenile males (168 ± 24 m, $n = 39$) was greater than in females (83 ± 11 m, $n = 66$), with no effect detected for either year or cohort. Juveniles are thus involved in the spread of this ground squirrel, bearing in mind that movements estimated may have been underestimated due to the use of capture–mark–recapture methods on a limited trapping area.

Keywords Siberian chipmunk · *Tamias sibiricus* · Introduced species · Natal dispersal · Capture–mark–recapture

Introduction

The rate of spread of an invading species, i.e. the rate at which individuals colonise new territories, depends on two population parameters: the growth rate and the dispersal ability (Levine 1989; Mooney and Drake 1989). The dispersal process has profound effects on the structure and dynamics of populations (Hanski 2001). According to Clobert et al. (2001), two types of dispersal can be distinguished: natal dispersal, i.e. movement between the natal area or social group and the area or social group where breeding first takes place, and breeding dispersal, i.e. movement between two successive breeding areas or social groups. Two parameters that are generally estimated based on the observations of animals are the dispersal rate and the distance moved by each disperser. The distances travelled by juveniles during the natal dispersal period are an essential element of demography, population distribution, colonisation and gene flow (Berteaux and Boutin 2000; Sutherland et al. 2000). However, for many species, dispersal data are still missing because they are difficult to collect and often require intensive, large-scale and long-term demographic studies (Koenig et al. 1996).

Many factors influence the ability of juveniles to disperse or to maintain philopatry; these factors include resource competition, intrasexual mate competition, parasitism and predation (Clobert et al. 2001). Natal dispersal distances vary considerably among species due to the aforementioned factors (Sutherland et al. 2000), and different patterns of dispersion can exist within a single species (Bray et al. 2007). In many mammalian species, the frequency of dispersers decreases with increasing distance from the natal area (Taylor 1980), and long-distance dispersal occurs regularly, but at a relatively low frequency (Sutherland et al. 2000). Moreover, in mammals, the

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Table 1 The trapping system for Siberian chipmunks, *Tamias sibiricus*, installed inside and outside the study area in the Sénart Forest in each sample year

Yearly trapping system	2003	2004	2005	2006	2007
Inside					
Period	Mar–Oct	Mar–Oct	Mar–Nov	Feb–Dec	Feb–Nov
Trapping effort (days/month)	4	5		8	
No. of traps	60	80		104	
Surface (ha)	12	12		14	
Outside					
Period			July–Oct	May–Nov	May–Oct
Trapping effort				2 days/month	
No. of traps	–	–	88	100	80
No. of lines	–	–	4	4	4
Orientation and distances of lines from study area (m)	–	–	50 (W); 50, 100, 150 (E)	50, 100, 150, 200 (E)	May, Aug: 150, 200 (W&E) June, Sep: 450, 500 (W&E) July, Oct: 1,000, 1,050 (W&E)
No. of adults previously trapped as juvenile (annual capture rates)					
Females	–	5 (29.4%)	15 (38.5%)	29 (46.8%)	29 (61.2%)
Males	–	3 (23.1%)	4 (10.5%)	23 (35.4%)	24 (40.7%)
Distance moved (mean ± SE, in m)					
Females	–	68 ± 39	60 ± 9	106 ± 21	73 ± 12
Males	–	27; 40; 52	32; 74; 83; 275	175 ± 35	122 ± 22

W west, E east

probability and distance of dispersal is often observed to be sex-biased (Greenwood 1980), although this bias varies greatly among species (Loew 1999). More specifically, sex-biased dispersal in Sciurids was found related to males (Devillard et al. 2004), more rarely to females (Hanski and Selonen 2009), or even unbiased (Wauters and Dhondt 1993).

The Siberian chipmunk, *Tamias sibiricus* (Laxmann 1769) (Rodentia: Sciuridae), is a small ground-dwelling squirrel originally distributed from the north-eastern portion of Europe to south-eastern Asia (Obolenskaya et al. 2009). In France, the Siberian chipmunk has been naturalised since the late 1970s (Chapuis 2005). Sold in pet shops, the chipmunk was accidentally or intentionally released in wooded suburban areas in the Ile-de-France and Picardie regions (Marmet and Chapuis 2007).

Few papers have dealt with the biology of Siberian chipmunks in either their native range (Kawamichi 1980,

1989, 1996; Kawamichi and Kawamichi 1993; Ognev 1940) or in introduced areas. According to our knowledge, natal dispersal patterns in Siberian chipmunks have never been described. In order to study the ecology of this little known species and its ability to spread in a new habitat, we investigated its natal dispersal pattern. We used mark–recapture data collected over 5 years in order to compare natal dispersal distances between the sexes and between cohorts to describe the colonisation capacity of the species.

Materials and methods

Study site and species

The Sénart Forest 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. The forest is embedded in an urbanised



Fig. 1 The trapping system installed inside and outside the study area, according to year, for the survey population of Siberian chipmunks, *Tamias sibiricus*. Each circle represents a trap location

area, and is unfragmented in the western and central portions. Wood production in this region of the forest is managed by the National Forest Office. The study was carried out within and around a 14-ha area bounded by an oak–hornbeam forest (CORINE Biotopes: 41.24; Bissardon et al. 1997; Marmet 2008) in the southern part of the forest.

The Siberian chipmunk is a diurnal, solitary and sedentary rodent. It nests principally in burrows that are also used as hibernation sites. Its diet consists mainly of seeds, buds, young leaves and animal matter (Kawamichi 1980). In France, the mating season extends from early February until the first half of July, with two peaks of births. Juveniles emerge from their natal burrows from May to June and from August to September (Chapuis 2005; Marmet 2008). The reported home ranges of males (1.9 ± 0.3 ha, $n = 13$) are 2.5 times larger than those of females (0.7 ± 0.1 ha, $n = 26$), with a high rate of overlap between the sexes and strong multi-year site fidelity (Marmet et al. 2009).

Trapping procedure

Trapping occurred outside the hibernation period from 2003 to 2007. The trapping system consisted of live traps

($8 \times 8 \times 26$ cm, H.B. Sherman Traps[®]) that were site referenced with a GPS Leitz[®]. A trap grid (between 60 and 104 traps depending on the year) was laid inside the main study area and was set 4–8 days per month according to the year of study (Table 1; Fig. 1). Additionally, to detect long-distance movements, trap lines were positioned outside the study area (Fig. 1), every 50 m from the periphery toward the east and west sides, and up to 150 m in 2005, to 200 m in 2006, and to 1,050 m in 2007 (Table 1). Trap lines were deployed 2 days per month from 2005 to 2007 and were composed of 80–100 traps according to years (Table 1; Fig. 1). Once every study day, the traps were opened early in the morning, baited with peanut butter, checked four times during the course of the day and closed at the end of the afternoon. At first capture, chipmunks were sexed and tagged with a subcutaneous transponder chip (PIT tag) and a numbered ear tag. At each capture, animals were weighed (± 1 g) and released at the capture point. Individuals were classified by age according to four categories: adult, spring cohort juvenile (J1), summer cohort juvenile (J2) or unknown age. Between February and early May, individuals captured for the first time were considered as adults. Individuals were aged according to body mass at first capture and date of trapping (Marmet 2008). All juveniles were considered to be adults in the year following the first hibernation period (Marmet 2008). Individuals that were captured for the first time between February and early May were considered to be adults. Trapping and handling procedures were conducted in accordance with French legislation.

Data analysis

Natal dispersal distance was calculated for each juvenile trapped in two consecutive years as the straight-line distance between the estimated birthplace and the settlement location. The birthplace was approximated by the location of the first capture and the settlement location was determined as the arithmetic centre of the trapping locations in the next year. For each sex, recapture rate was calculated as the number of juveniles trapped as adult the following year divided by the total number of juveniles trapped during a given year (see Marmet et al. 2009). Difference in recapture rates between sexes was calculated using Fisher's exact test, noted as P_{Fisher} . We tested for the effects of sex, cohort, year and body mass on natal dispersal distances using a generalised linear model, noted hereafter GLIM, with a negative binomial distribution and a log-link function (McCullagh and Nelder 1989; Wilson et al. 1996; Wilson and Grenfell 1997). The deviance is a statistic assessing the goodness-of-fit of a model and has an approximate Chi square distribution. Models were built beginning with a 3-way interaction between the factors,

followed by stepwise exclusion until only a single factor remained. The significant contribution of a minimum sufficient model to the explanation of the variation in the data is calculated as the change in deviance between two models. This parameter also has a chi square distribution, where the degree of freedom is the change in the number of degrees of freedom between the two models.

In order to know the maximum distance that an individual can travel, we increased the sample size used previously by calculating the distance between the site of first and last capture in the same year for all juveniles in the population that were captured at least two times.

Calculations were made using Genstat 6.0 software (Genstat 5 Committee 1994). Mean values are presented with \pm SE.

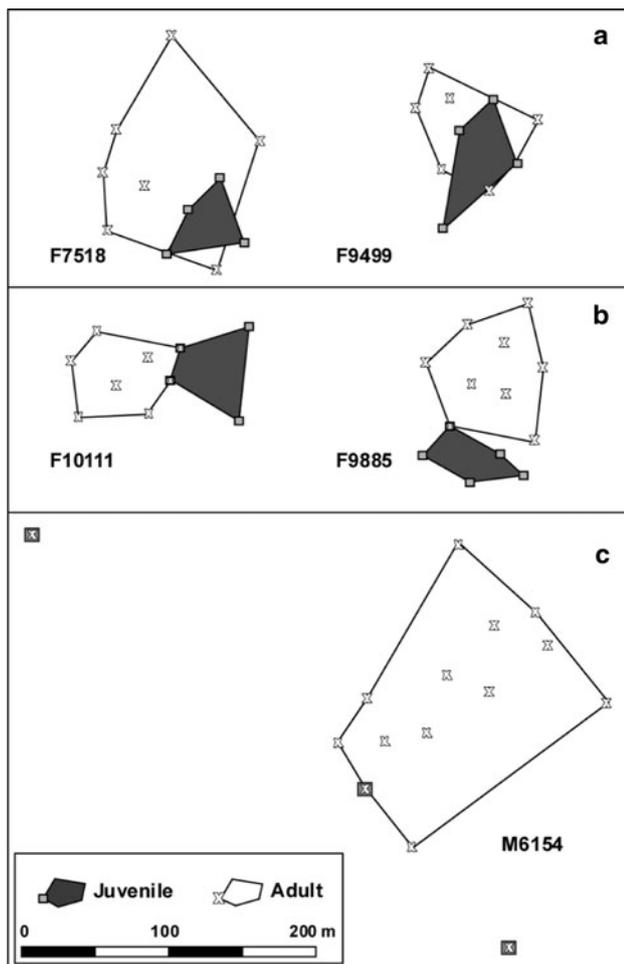


Fig. 2 The trapping areas for five Siberian chipmunks trapped in two consecutive years: **a** overlap for females *F7518* and *F9499*; **b** no overlap and proximity of the areas for females *F10111* and *F9885*; **c** long-distance movement for male *M6154*

Results

During the 5-year study period, 580 juveniles were marked: 285 from the spring cohort (141 males and 144 females), 284 from the summer cohort (152 males and 132 females) and 11 undetermined cohort juveniles (7 males and 4 females). The mean body mass at first capture for the spring cohort juveniles was 68 ± 1 g ($n = 141$; range, 33–96) for males and 68 ± 1 g ($n = 143$; 46–90) for females. For the summer cohort juveniles, the mean body mass at first capture was 64 ± 1 g ($n = 151$; 30–86) for males and 63 ± 1 g ($n = 131$; 35–89) for females.

Natal dispersal distances

Thirty-seven females (72 ± 2 g) and 27 males (77 ± 2 g) from the spring cohorts, and 41 females (63 ± 2 g) and 27 males (66 ± 2 g) from the summer cohorts were trapped during two consecutive years. Annual recapture rates ranged between 29.4 and 61.2% for females and between 10.5 and 40.7% for males (see Table 1). Males were significantly less often recaptured than females in 2005 ($P_{\text{Fisher}} < 0.01$), but not in 2004 ($P_{\text{Fisher}} = 0.24$) and 2006 ($P_{\text{Fisher}} = 0.21$), and only a tendency was found in 2007 ($P_{\text{Fisher}} = 0.05$).

To describe the movements during dispersal process, we selected individuals that were trapped more than five times per year with a body mass at first capture of less than 50 g to ensure that they had not already dispersed. This resulted in the analysis of the movements of four females and one

Table 2 Deviance analysis of the generalised linear models exploring the variation in natal dispersal distances of Siberian chipmunks according to sex, cohort, year and body mass

Sources of variation	df	Deviance	<i>P</i>
Total	131	164.00	
Year	3	10.77	0.01
Cohort	1	<0.01	0.93
Sex	1	10.34	<0.01
Body mass	1	2.44	0.12
Year \times cohort	7	17.38	0.02
Year \times sex	7	22.43	<0.01
Year \times body mass	3	19.78	<0.01
Cohort \times sex	3	10.84	0.01
Cohort \times body mass	1	3.16	0.08
Sex \times body mass	1	17.65	<0.01
Year \times cohort \times sex	15	37.17	<0.01
Year \times sex \times body mass	7	47.43	<0.01
Year \times cohort \times body mass	7	24.08	<0.01
Cohort \times sex \times body mass	3	22.57	<0.01

The best model is indicated in bold

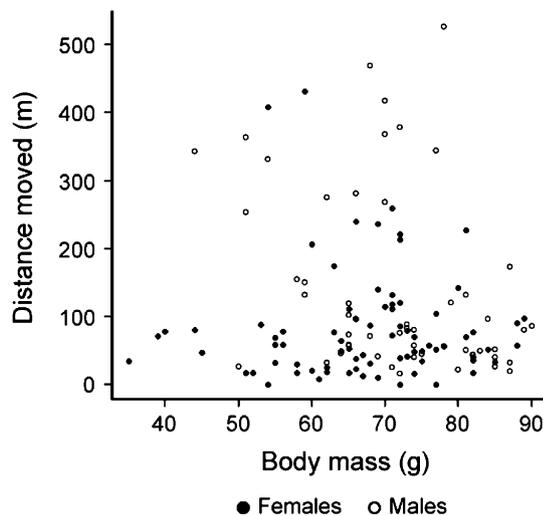


Fig. 3 Relationship between maximal distance moved and body mass at first capture of chipmunks by sex

male from the summer cohorts. For females F9499 and F7518, who were trapped for the first time at 39 and 45 g, respectively, no movement was observed either before or after the hibernation period (Fig. 2). For females F9885 and F10111, who were trapped for the first time at 35 and 40 g, respectively, no movement was observed before the hibernation period and there was a contiguous settlement in the next year (Fig. 2). For male M6154, who was trapped for the first time at 44 g, long-distance movements were observed before the hibernation period without return to the first trapping area. The body mass of this individual ranged between 52 and 55 g (Fig. 2) when it was recaptured during this period.

From the 132 juveniles recaptured as adults in the following year, the mean dispersal distance varied according to sex and body mass (GLIM: $\chi^2_1 = 17.65$, $P < 0.001$; Table 2). There was no better explanation in distance variation by including an effect of the cohort or of the year of capture, either solely or in interaction (Table 2), and body mass according to sex significantly improved the explanation in data variation than sex alone (GLIM: $\chi^2_1 = 10.34$, $P < 0.001$). Both females and males had decreasing distance moved with increasing body mass (Fig. 3), with females dispersing lesser than males (females: 83 ± 9 m; $n = 78$; males: 139 ± 18 m; $n = 54$). Excluding 27 individuals that weighted above 80 g (see Fig. 3) which may have already dispersed, mean distance moved by females was 83 ± 11 m ($n = 66$), and 168 ± 24 m ($n = 39$) for males.

Maximum natal dispersal distance

Among the individuals captured in two consecutive years, the greatest dispersal distances observed in females were 259 m for a spring cohort juvenile in 2005, and 430 m for a

summer cohort juvenile also in 2005. In males, these distances were 527 and 469 m, respectively, for the spring cohort in 2005 and the summer cohort in 2006.

By increasing the sample to include the maximal distances travelled by juveniles within their entire year of birth, meaning that these individuals did not install, we found the maximum distance travelled to be that of a female in the spring cohort which moved over 933 m in 2007 when maximal distance could be detected.

Discussion

According to our results, some juveniles of Siberian chipmunks were philopatric, meaning they continued to frequent their natal ranges past the age of reproductive maturity (Waser and Jones 1983), while others dispersed over both short and long distances.

As with most studies on the natal dispersal of mammals using mark–recapture methods with limited study areas, our estimation may have been biased, as the probabilities of detecting dispersal movements at differing lengths are uneven and depend largely on the sampling area (Koenig et al. 1996). The number of short-distance dispersers may have been overestimated. For ground-dwelling species such as chipmunks, mothers give birth in a burrow and dispersal from the birthplace can occur quickly after emergence. This dispersal can occur within 2 weeks of emergence in *Tamias striatus* juveniles (Elliott 1978). Thus, juveniles may have dispersed before being captured for the first time despite our intensive presence in the field (160 days between May and September from 2003 until 2007) and a narrow trap spacing grid that was approximately 30 m (Marmet et al. 2009). The influence of body mass at first capture obtained in our study confirms this assumption: heaviest individuals, e.g. above 80 g, showed shortest distance moved compared to lightest ones, traducing a bias due to individuals that may have had already dispersed. In the case of females, however, the bias was not so pronounced, and averaged distance moved must be a reliable indicate of their dispersal movements. In the case of males, the averaged distance moved during natal dispersal must have been underestimated. These lowered rates may have arisen because (1) there was a lack of coverage of the total dispersing area by our trapping system, and (2) there was a greater mortality of males compared to females (Marmet 2008). We had to restrain our dispersal trapping lines to the eastern and western area of our study site, which structured the degree of long-distance dispersal that we were able to measure (see Fig. 1). However, despite this constraint on the sample, and including both under- and overestimations, we still observed more males dispersing at longer distances than females (Fig. 3).

To our knowledge, there are no precise data on natal dispersal in Siberian chipmunks, either in the native range or introduced habitats, with which we could compare our results. In their treatise on the social organisation of solitary mammals, Kawamichi et al. (1987) described a population of Siberian chipmunks in Japan where the average distance between natal dens and settled hibernation burrows was 50 m for females and 140 m for males, suggesting that male offspring dispersed further than females. Although the methods, data or sample size were not indicated in this account, these observations are in accordance with our results.

Natal dispersal behaviour has been well studied in the eastern chipmunk, *Tamias striatus*, a species that is phylogenetically close to *T. sibiricus*. In this species, many juveniles (especially females) establish their home ranges adjacent to their mother's home range. In many cases, the ranges are also adjacent to one another (Elliott 1978). The distribution of dispersal distances overlapped between the sexes, with an average distance four times greater for males than for females. Male juveniles showed a significant tendency to disperse further than female juveniles, and only juvenile females shared their mother's home range (Loew 1999). The dispersal patterns described for the eastern chipmunk are similar to our results.

Mammals commonly show a sex-bias in the probability and distance of dispersal in favour of males (Clutton-Brock 1989). To explain male-biased dispersal, two dominant hypotheses are frequently proposed: competition for mates and inbreeding avoidance (Dobson 1982; Wauters and Dhondt 1993; Loew 1999; Devillard et al. 2004; Hanski and Selonen 2009). Firstly, competition for access to females is suggested to drive long-distance movements by males (Greenwood 1980). Such a hypothesis is under the assumption of a mate-defense mating system, e.g. where males do not defend resources but compete with other males for mates, which is often the case in mammals (Greenwood 1980; Hanski and Selonen 2009). Secondly, in a promiscuous species like the Siberian chipmunk (Marmet 2008), high movement rates of males may be ruled out by female choice to preferentially mate with unrelated males, which occurs when there is a high load of inbreeding between individuals (Lehmann and Perrin 2003).

In many species, long-distance dispersal occurs regularly but at relatively low frequencies (Sutherland et al. 2000)—this seems to be the case for the Siberian chipmunk in the Sénart Forest. Once initial colonisation and establishment have occurred, invasive species may spread by continuing long-distance dispersal and by short-distance dispersal (lateral expansion) of the established population. Nonetheless, long-dispersal distances are central to the invasion process because they can determine the speed at

which a population can invade a new habitat (Caswell et al. 2003). Dispersal into the surrounding environment is the final stage of a species' invasion and is the stage that yields serious problems for control and management. In a preceding work, we showed the multiyear site fidelity of 10 adult Siberian chipmunks (Marmet et al. 2009), as soon as they installed for the first time (e.g. 6 of the 10 adults monitored were juvenile the year before). Thus, juveniles play a role in the expansion process of the Siberian chipmunk with an ability to disperse over short and long distances. Moreover, even if there is a sex-bias in the natal dispersal distance, both genders are capable of long-distance movement, but only a subset of individuals move over great distances. More studies are, however, needed to precisely define such long-distance dispersal in a solitary small-sized ground squirrel such as the Siberian chipmunk by using radio-tracking methods (Hanski and Selonen 2009) that allows less biased estimations of distance moved due to an unlimited study area.

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