

Factors affecting male and female reproductive success in a chipmunk (*Tamias sibiricus*) with a scramble competition mating system

Julie Marmet · Benoît Pisanu · Jean-Louis Chapuis ·
Gwenaél Jacob · Emmanuelle Baudry

Abstract While sexual selection in mammals with female defense systems has historically received considerable attention, much less is known about the factors affecting reproductive success in mammalian species with scramble competition mating systems. Using mark–recapture techniques and DNA microsatellite loci to assign parentage, we examined the mating system and factors affecting the variation of the annual reproductive success in an introduced population of the Siberian chipmunk, *Tamias sibiricus*, a small, monomorphic, solitary squirrel. Our analyses showed that breeding females were spatially dispersed, setting the stage for a scramble competition mating system. Male reproductive success was positively associated with the size of the home range. The strength of sexual selection on

this behavioral trait was very strong, equaling previous estimates for morphological traits in female defense mating systems. These findings suggest that a behavioral trait, space use, strongly influences the annual reproductive success in males, which is consistent with expectations in a scramble competition mating system. In both sexes, reproductive success was influenced by habitat, with twice as many juveniles produced in semi-open than in closed habitat, possibly due to differences in food availability between the two habitats.

Keywords Sexual selection · Scramble competition mating system · Annual reproductive success · Siberian chipmunk · *Tamias sibiricus*

Introduction

Among mammals, females usually have greater reproductive investment than males (Gittleman and Thompson 1988). Sexual selection theory predicts that because of this asymmetry, female reproductive success is mainly limited by access to resources, whereas male reproductive success is mainly limited by access to females (Bateman 1948; Trivers 1972). Depending on the distribution of receptive females in space and time, males can develop different strategies to increase their access to females (Shuster and Wade 2003). At one end of the spectrum, in species in which females are gregarious or estrus is predictable, dominant males should be able to defend access to receptive females, giving rise to a female defense mating system (Emlen and Oring 1977; Ims 1987). In this system, male reproductive success is determined by the ability to guard a mate and fight off rival males. At the other end of the

J. Marmet · B. Pisanu · J.-L. Chapuis
Conservation des Espèces, Restauration et Suivi des Populations,
UMR 7204 MNHN-CNRS-P6,
Muséum National d'Histoire Naturelle,
61 rue Buffon,
75005 Paris, France

G. Jacob · E. Baudry (✉)
Laboratoire Ecologie, Systématique et Evolution,
CNRS-UMR 8079, Université Paris-Sud,
91405 Orsay Cedex, France
e-mail: emmanuelle.baudry@u-psud.fr

Present Address:

G. Jacob
Department of Biology, Unit of Ecology & Evolution,
University of Fribourg,
Chemin du Musée 10,
CH-1700 Fribourg, Switzerland

spectrum, in species where receptive females breed synchronously or are spatially dispersed, males are not able to monopolize females, giving rise to a scramble competition mating system in which male reproductive success depends primarily on the ability to locate receptive females (Murphy 1998). Most work done to date has focused on female defense systems, and we have comparatively little information on scramble competition systems (Lane et al. 2009).

Scramble competition is considered a common mating system in insects (e.g. Thornhill and Alcock 1983; Moya-Larano et al. 2007) and anurans (Arak 1983; Szatecsny et al. 2006), but it has been reported only rarely in most other taxa. In mammals, scramble competition was not considered to be frequent (but see Schwagmeyer 1988; Kappeler 1997). However, studies of mammals are usually biased towards large-bodied diurnal, social species (Stockley and Bro-Jorgensen 2011) that typically show female defense systems (Waterman 2007). Scramble competition mating systems seem, however, to be a frequent occurrence in rodents (Waterman 2007). In particular, in many species of sciurids, females are home-range owners and are therefore spatially dispersed. This prevents males from defending access to receptive females and favors scramble competition mating systems (Murphy 1998; Waterman 2007; Lane et al. 2009). In these systems, sexual selection favors traits that increase a male's ability to locate females rapidly and accurately (Schwagmeyer and Wootner 1986). Such traits are often behavioral or are related to the sensory systems employed by the animals to locate potential mates and are hence usually more difficult to study than the morphological adaptations that are typically favored by selection in female defense systems (Lane et al. 2009). Consequently, the factors that determine male reproductive success in scramble competition mating systems are currently not well understood. Several studies have shown that in species with scramble competition, male mating or reproductive success is strongly correlated with the success of mate searching (Schwagmeyer and Wootner 1986; Schwagmeyer and Parker 1987; Schwagmeyer et al. 1998; Spritzer et al. 2005). To our knowledge, only one study (Lane et al. 2009) thus far has quantified the intensity of selection on male searching behavior in a scramble competition mating system.

In mammals, variance in reproductive success frequently seems to be greater among males than among females and sexual selection is therefore often expected to be stronger in this sex (Bateman 1948; Payne 1979; Stockley and Bro-Jorgensen 2011). This hypothesis has led some authors to assume that female variance in reproductive success is minimal, with the expectation that in natural populations, all of the females would be breeding close to the maximum of their reproductive

capacity (Stockley and Bro-Jorgensen 2011). As a consequence, female reproductive competition has received comparatively little attention. However, a growing number of studies have shown that in natural populations of mammals, the variance in female reproductive success could be substantial (Schulte-Hostedde et al. 2004; Clutton-Brock et al. 2006) and that female competition, particularly competition for resources, is therefore a potentially important evolutionary pressure. Because most of the current evidence concerns gregarious species, where social rank is a major determinant of female reproductive success (Clutton-Brock 2009), it is especially interesting to study a solitary mammal, where the determinant of female reproductive success are presumably very different.

We studied an introduced population of Siberian chipmunks (*Tamias [Eutamias] sibiricus barberi*), a small, diurnal, monomorphic squirrel. The biology and ecology of this chipmunk have been studied in its native range in Japan and in an introduced population in France (Kawamichi 1980, 1989; Chapuis et al. 2011). Siberian chipmunks are solitary and sedentary rodents (Kawamichi 1996; Marmet et al. 2009). Male chipmunks have larger home range than females, but they do not defend a territory (Kawamichi et al. 1987) and are thus unable to monopolize access to females, setting the stage for a scramble competition mating system (Andersson 1994; Murphy 1998). We first evaluated the spatial clustering of breeding female to test our hypothesis of a scramble mating system in this species. We then tested the hypothesis that males' reproductive success was correlated to their effort to locate females, using home range size as an estimator. Finally, we tested whether female reproductive success varied between two habitats with different resource levels.

Material and methods

Study species and site

The Siberian chipmunk is a diurnal ground squirrel native from north to southeastern Eurasia (Obolenskaya et al. 2009). Adults weigh approximately 100 g (no sexual dimorphism). They use burrows to hibernate and reproduce (Chapuis et al. 2011). From an age of 8 months, female chipmunks can enter estrus once per year in Japan (late April–early May; Kawamichi and Kawamichi 1993) or twice per year in France (in March and in June; Chapuis et al. 2011). The period of estrus lasts 1–2 day(s) during which a female utters distinctive estrous calls (Blake and Gillett 1984, 1988). Several males then aggregate near the female and pursue her (Kawamichi et al. 1987). Juveniles are born after a gestation period of about 1 month and remain in the nest at least another month (Chapuis et al. 2011). Young

begin their dispersal shortly after their emergence from the nest (Marmet et al. 2011).

Sold in pet shops in Europe starting from the 1960s (Chapuis 2005), Siberian chipmunk populations were observed a decade later in several European suburban forests and urban parks (Chapuis et al. 2011). Our study site, called La Faisanderie, is a 12-ha fenced area located in the Forest of Sénart, a 3,200-ha suburban forest situated 22 km south-east of Paris (48°39'N, 02°29'E). Two main kinds of habitat are found within the site: a semi-open oak grove (6.5 ha; herbaceous layer 90 %, shrubby layer 5 %, arboreal layer 60 %) and a closed oak-hornbeam grove (5.5 ha; herbaceous layer 10 %, shrubby layer 30 %, arborescent layer 90 %) (Marmet 2008).

Live trapping

Throughout 2006, trapping was conducted twice a month for three and five consecutive days during the entire chipmunk active period, from February to December (Marmet et al. 2009). The trapping system consisted of 104 live traps (8×8×26 cm, H.B. Sherman Traps®) located with a GPS Leitz® (±1 m). The traps were distributed on a grid throughout the study site (80 traps) and on its periphery (24 traps) (Fig. 1) and were spaced on average 38±9 m apart (Marmet et al. 2009). A total of 52 traps were placed in the closed habitat and another 52 in the semi-open habitat. Every day, the traps were opened between 7:00 and 8:00 AM, baited with a mixture of peanut butter and sunflower seeds, checked four times during the day, and closed between 17:00 and 18:00 PM. At first capture, chipmunks were sexed and tagged with both a subcutaneous passive integrated transponder chip (PIT tag biolog-id, Bernay, France, 27303) and a numbered ear tag (National Band Tag Co, Newport, KY, 41071). For each individual, a hair sample was taken and stored at room temperature in 95 % ethanol. During capture, females were recorded as “receptive” if they showed a swelling of the vulva indicating their estrous status (Blake and Gillett 1988). They were considered “lactating” if the size and color of the nipples indicated lactation activities. After examination, the chipmunks were released at the capture point. Using trap history and body mass, age categories were defined: juvenile born in spring or in summer in 2006 and adult born in 2005 or earlier.

Habitat and space use

Because the large majority of the chipmunks in our study were either captured only in the semi-open habitat or only in the closed habitat, the habitat index was coded as a qualitative variable with two categories, semi-open habitat or closed habitat. Home range sizes were calculated using the

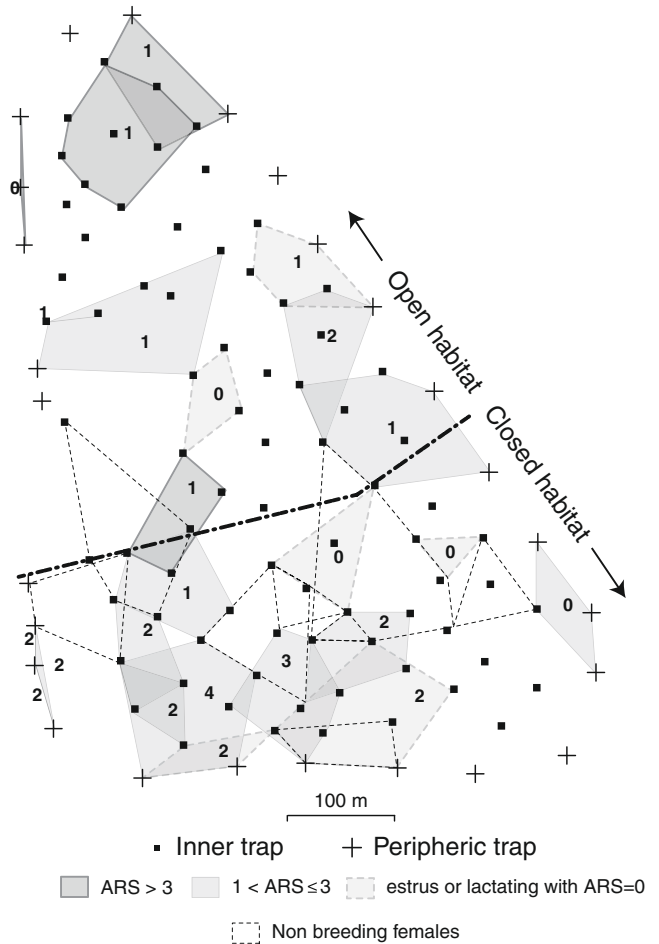


Fig. 1 Spatial distribution of adult breeding females of Siberian chipmunks *Tamias sibiricus* trapped at least five times on the Park de la Faisanderie (Forest of Sénart) in 2006. Number of overlapping breeding females per breeding female range in **bold**

100 % Minimum Convex Polygon method (100 % MCP, Mohr 1947) including all the trap coordinates used by each of the 63 adults (Table 1) caught at least five times over the study period. This measure of space use could be biased due to the truncation of the movements at the edge of the trapping grid and according to the number of time a chipmunk was trapped (see Boyer et al. 2010; Powell 2000). These potential biases were statistically controlled and yielded in a home range size index (Supplementary Material 1).

Females were considered to have been breeding if they were recorded as receptive and/or lactating and/or had successfully reproduced (inferred from molecular analyses, see below). Based on a graphical representation of the spatial distribution of the home range of breeding females and of males on the study area, the average number of overlapping ranges of breeding females in a breeding female's home range was calculated, along with the number of overlapping females in a male's home range. The average number of

Table 1 Number of adult Siberian chipmunks *Tamias sibiricus* trapped at least five times on the Park de la Faisanderie in the Forest of Sénart in 2006, and mean number of captures, home range size, and annual reproductive success

Habitat and sex	Number of chipmunks	Capture number	Home range size (ha)	ARS
Males				
Semi-open	10	28±6	1.45±0.38	2.7±1.0
Closed	19	18±4	0.63±0.11	1.5±0.4*
Females				
Semi-open	10	26±6	0.56±0.11	2.1±0.6
Closed	24	20±4	0.41±0.06	0.7±0.2

* Two males with no ARS available

overlapping ranges of breeding females was then used to calculate *P*, the degree to which breeding females are clumped in space, according to the method proposed by Shuster and Wade (2003), pp. 43–45.

Genetic methods and parentage analyses

DNA was extracted from approximately 20 hairs per individual using the Qiagen Tissue Kit and following the manufacturer's protocol for DNA extraction from tissue samples. The DNA was eluted in 50 µl of AE buffer (Qiagen) and stored at −20 °C. Nine microsatellite markers were used to assess the parentage. We tested 16 loci originally cloned from *Tamias striatus* (Peters et al. 2007) and 11 loci originally cloned from *Tamias amoenus* (Schulte-Hostedde et al. 2000) for amplification and polymorphism, using DNA obtained from ear tissue of ten *Tamias sibiricus* chipmunks captured in the Senart forest. Nine loci (Supplementary Material 2) amplified successfully and were polymorphic. Among these loci, the primers specific for *T. sibiricus* were redesigned for five loci. The original primers were used for the four remaining loci because specific primers could not be designed, usually because of the short size of the amplified fragment.

We amplified the nine microsatellite loci in two 10-µL polymerase chain reaction (PCR) multiplexes containing five and four markers, labeled with the fluorescent dyes FAM, VIC, NED, or PET. All of the PCRs contained 1× Multiplex Master Mix (Qiagen). The amount of marker used varied among the markers from 0.1 to 0.3 µM. The PCR conditions were as follows: 15 min at 94 °C for DNA denaturation, 35 cycles of a 30-s denaturation step at 94 °C, a 3-min hybridization at 54 °C, and a 30-s elongation at 72 °C, and a final elongation step of 15 min at 72 °C. The PCR products were mixed with an internal size standard and analyzed using an ABI 3700 capillary DNA sequencer (Applied Biosystems). The size of the microsatellite alleles was calculated using the Genescan and Genemapper software

(Applied Biosystems). Among 36 linkage disequilibrium tests, only two were significant at the 0.05 level, and none were significant after a Bonferroni correction. All the loci can therefore be considered as genetically independent. One of the Hardy–Weinberg tests was significant at the 0.05 level, but it did not remain so after a Bonferroni correction.

A duplicate analysis performed on 96 individuals showed a low overall error rate: one allelic dropout was observed at one locus for one individual, i.e., an error rate of 0.1 %. To account for other possible types of errors, we assumed an overall conservative error rate of 2.0 % in the final genotypes. Most of the loci showed moderate variation, with a mean allele number of 5.5 and mean heterozygosity levels of 0.62. The overall amplification success was 94.3 %, and all of the individuals included in the analyses were scored for a minimum of six loci. Three candidate fathers (among 32) and one candidate mother (among 35) were excluded from the analyses because of this criterion.

We used the program CERVUS 3.0 (Kalinowski et al. 2007) to identify parent–offspring trios. CERVUS uses a likelihood-based approach to assign parentage, combined with a simulation of a parentage analysis to determine the confidence of the parentage assignments. Using this approach, parent pair-assignment analyses were conducted for all of the juveniles of the population using strict (95 %) and relaxed (80 %) levels of statistical confidence. The simulations were based on 10,000 cycles with a genotyping error rate of 2 %. For each offspring, parentage was assigned to the most-likely candidate parent pair. If a parent pair could not be assigned at least at the 80 % confidence level, we assigned either maternity or paternity alone, using the same method. When parentage could not be assigned at the 80 % confidence level (see “Results” section), it can be due to young having been born from a non-resident adult or from a never-captured resident adult or because the young was born outside our study site but dispersed into it.

We then used the parentage inferences to estimate the annual reproductive success (ARS) of the 63 adults, defined as the genetically detected number of offspring for an individual in 2006. We then calculated the opportunity for sexual selection *I_s*, quantified as the square of the coefficient of variation of the ARS for a given sex (Arnold and Wade 1984a, b).

Statistical and selection analyses

The degree of spatial clumping of breeding females and the number of female range overlapping the range of males was compared between habitats using a Kolmogorov–Smirnov test for paired sample noted D (Siegel and Castellan 1988).

The variation in ARS, Log(+1) transformed was analyzed as a function of habitat, sex, and home range size index using simple linear models including two-way interactions.

Model validation was checked from graphical examination of the quantile–quantile plots, and the heterogeneity of variance using residuals vs. fitted plot (Zuur et al. 2009, 2010). Missing data were excluded. Models were selected using change in at least 2 U in Akaike Information Criterion corrected for small sample size (Δ_{AICc}) and best candidate model determined by ranking AIC weights (Symonds and Moussali 2011). Parameter estimates were obtained from full averaged model method (Symonds and Moussali 2011).

Standardized linear (also called directional Lande and Arnold 1983) selection gradients were calculated for each sex separately by regressing the relative ARS on the standardized home range size. Estimates and standard errors were generated using a “delete-one” jackknifing technique from simple regressions (Sokal and Rohlf 1995; Crawley 2007). Due to the small sample size, non-linear gradients were not calculated.

All of the analyses were completed with R 2.14.1 software (R Development Core Team 2011), using the “adehabitat” package (Calenge 2006) for home range analyses, the “MASS” package (Venables and Ripley 2002) for generalized linear models, the “MuMIn” package (Barton 2012) for information theory-based model selection. The R-code for the “delete-one” jackknife procedure is given in Supplementary Material 1. Mean is always followed by a standard error, unless otherwise stated.

Results

We recorded 1,856 captures and recaptures between February and December 2006, corresponding to a total of 226 chipmunks (120 adults and 106 young). The parentage was inferred from genetic data for all of the captured young. Maternity was successfully assigned to 66 of the young and paternity to 71, with at least 80 % confidence. For each adult captured at least five times, mean number of captures, home range size, and annual reproductive success according to sex and habitat are shown in Table 1.

Mating system and opportunity for sexual selection

The variance in ARS was significantly higher in males than in females (variance ratio test, $P < 0.001$). The difference between the male and female variance in ARS decreased when removing an outlier corresponding to a male with an assigned ARS of 9 young, but ARS of males remained significantly higher ($P = 0.02$). However, the opportunity for sexual selection, I_s , was very similar between sexes, with a value of 1.55 for females and 1.51 for males (outlier excluded).

All the females trapped at least five times in the semi-open habitat (Table 1) were found to be in breeding

condition ($n = 10$), while the percentage fell to 58 % ($n = 14$) for females in the closed habitat (Fig. 1). The mean number of breeding females overlapping the range of a breeding female was 0.9 ± 0.2 ($n = 10$) in the semi-open habitat (Fig. 1), whereas the value was significantly higher ($D = 0.61$, $P = 0.02$) in the closed habitat (1.7 ± 0.3 ; $n = 14$). The degree of spatial clumping of females (Fig. 1) in the semi-open habitat was $P = 0.25$, 3.5 times lower than in the closed habitat where $P = 0.83$. Some of the females that were captured in estrus or lactating had an ARS of zero (Fig. 1), possibly because we failed to assign their young or because it died before emergence from the burrow or disperse before being captured.

The number of overlapping females in a male's range was 4.1 ± 0.6 ($n = 10$) in the semi-open habitat (Fig. 2), which was not significantly different ($D = 0.26$, $P = 0.73$) from the number in the closed habitat ($n = 17$, 4.6 ± 0.6). The home range size of males in the semi-open habitat was on average 2.3 times larger than in the closed habitat (Table 1; Supplementary Material 1).

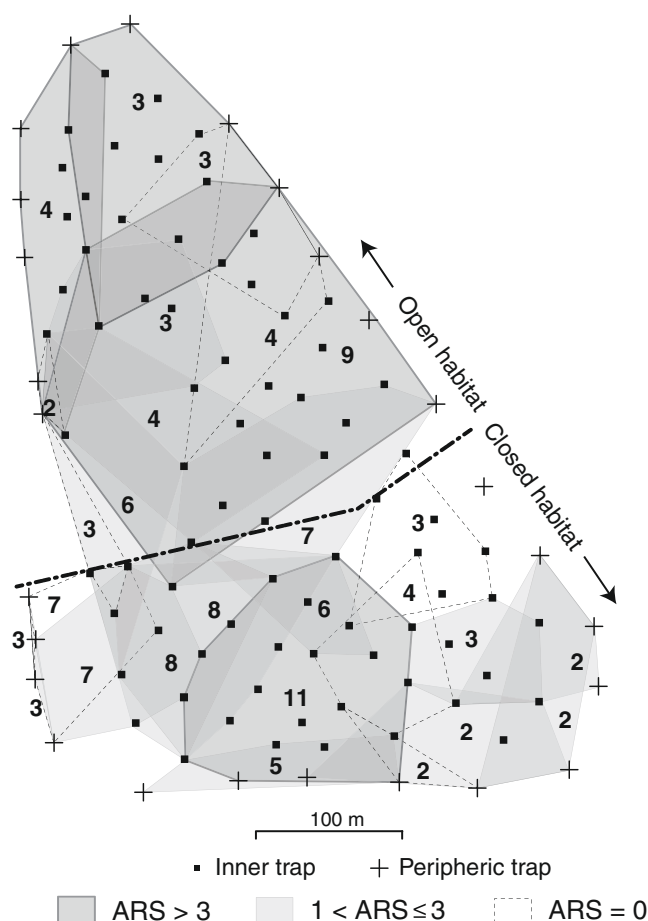


Fig. 2 Spatial distribution of adult males of Siberian chipmunks *Tamias sibiricus* trapped at least five times on the Park de la Faisanderie (Forest of Sénart) in 2006. Number of overlapping breeding females per male's range is indicated

Annual reproductive success and selection analyses

Model ranking based on AICc weights indicated that the interaction between sex and home range size best explained variation in ARS (Table 2). Male ARS markedly increased with home range size (averaged coefficients±adjusted SE, 1.56 ± 0.72 , $P=0.030$), whereas home range had little influence on the female ARS (Fig. 3). Moreover, ARS differed according to habitat (coefficient for the semi-open habitat, 0.42 ± 0.12 , $P=0.019$), being more than 2.1 times higher in the semi-open habitat ($n=20$, 2.3 ± 0.5) than in the closed habitat ($n=41$, 1.1 ± 0.2).

We performed a selection analysis for the trait that was observed to influence the ARS, namely home range size according to sex. In males, the selection gradient of the standardized home range size on the relative ARS was very strong ($n=27$, $\beta=0.57\pm0.11$, $P<0.001$), while it was weak for females ($n=34$, $\beta=0.10\pm0.03$, $P<0.001$).

Discussion

The hypothesis of a scramble competition mating system in the Siberian chipmunks of Sénart is supported by the observed spatial distribution of breeding females in relation with the home range size of males and the number of overlapping females in a male's home range according to habitat. The degree of spatial clumping of breeding females <1 indicates a more evenly distribution of breeding females over resources than expected by chance (Shuster and Wade 2003), thus setting the stage for a scramble competition mating system (Shuster and Wade 2003). Furthermore, a male home range in the semi-open habitat is approximately twice larger than in the closed habitat but the mean number of overlapping female in a male's home range is equivalent between the two habitats. Such a pattern reinforces the hypothesis that males increase their space use to increase their chances of meeting and fertilizing females (Marmet et al. 2009).

Table 2 Best candidate models ranked according to AIC's weight, w_i , examining the variation of the annual reproductive success, Log(+1) transformed, according to habitat, sex, and home range index using a simple linear model

Best candidate models	K	AICc	Δ_{AICc}	w_i
Habitat(HAB)+sex (SEX)+home range index (HRI)+SEX:HRI	6	116.94	0.00	0.44
HAB+SEX+HRI+HAB:SEX+HRI:SEX	7	119.04	2.09	0.15
HAB+SEX+HRI+HAB:HRI+HRI:SEX	7	119.34	2.40	0.13
HAB+HRI	4	119.67	2.73	0.11
HAB+SEX+HRI	5	119.90	2.96	0.10
HAB+HRI+HAB:HRI	5	120.86	3.92	0.06

Selected model in bold.

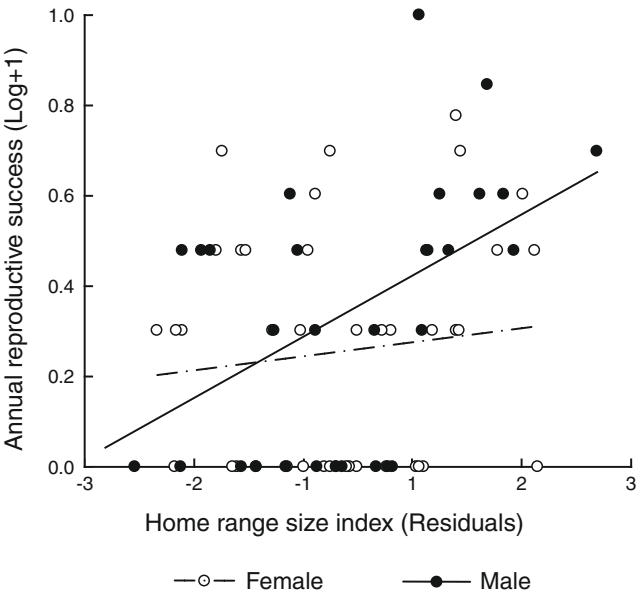


Fig. 3 Relationships between annual reproductive success and home range size index according to sex of Siberian chipmunks

We observed a relatively low value of 1.51 for the opportunity for sexual selection I_s in males (note however that, because our sample sizes are relatively small and because some juveniles were not successfully assigned parentage, our estimation of I_s is probably not very precise). This value is much lower than the one typically observed in species with female defense systems in which a few males monopolize the access to females. For example, in the highly polygynous and sexually dimorphic northern elephant seal (*Mirounga angustirostris*), Soay sheep (*Ovis aries*), and bighorn sheep (*Ovis canadensis*), the average I_s value for males were 21.8, 3.5, and 4.5, respectively (Le Boeuf and Reiter 1988; Coltman et al. 1999, 2002). The I_s values that we observed are in the order of those reported for other squirrel species. For instance, in the yellow-pine chipmunk (*T. amoenus*), a species with female-biased sexual size dimorphism, depending on the year, the opportunity for selection ranged between 0.86 and 1.55 for males and between 0.48 and 1.19 for females (Schulte-Hostedde et al. 2004). In the red squirrel, a species without sexual size dimorphism, Lane et al. (2009) observed an I_s value of 1.52 for males and of 0.16 for females. Interestingly, we observed very similar values of I_s in males and females (1.55 versus 1.51). Thus, even if males have a higher reproductive potential than females, in this population of Siberian chipmunks, the variance of the actual reproductive success is very similar between the sexes, suggesting that the potential for sexual selection is little different in males and females (Stockley and Bro-Jorgensen 2011). Notably, however, caution must be taken when interpreting I_s values because they reflect potential and not actual sexual selection (Klug et al. 2010).

Male's ARS increased with the size of their home range, whereas it had little influence on the female ARS. A likely explanation for this pattern is that a large home range allows male chipmunks to more efficiently locate the home range of females and the females within that home range, thereby increasing mating opportunities. Such a relationship between behavioral traits related to female localization and male reproductive success has already been described in a few species with a scramble competition mating system. Lane et al. (2009) have shown that in the North American red squirrel, *Tamiasciurus hudsonicus*, a species with a scramble competition mating system, male reproductive success was positively correlated with both search ability (measured as the number of estrous females located over the mating season) and effort (measured as the mating season home-range size). Similarly, Patterson and Schulte-Hostedde (2011) found that in eastern chipmunks, bolder males had more offspring, when the analyses were controlled for the endoparasite load, presumably because bolder males use larger home ranges, thus increasing the encounter rate with potential mates. Our findings suggest that a behavioral trait, i.e., space use, is determinant for ARS in males, consistent with expectations in a scramble competition mating system.

In our study population in 2006, female ARS was influenced by habitat. Females inhabiting the semi-open habitat had a significantly higher reproductive success than the ones inhabiting the closed habitat. This finding is probably due to the differences in food availability between the two habitats of our study site. The chipmunks of the Senart Forest feed mostly on acorns and hornbeam seeds during autumn and spring, and on cherries, herb seeds, and various insects during summer (Chapuis et al. 2011), resources that seem to be more abundant in the semi-open than in the closed habitat (J.L. Chapuis and C. Le Coeur, personal observations). Although it was not possible to calculate a selection gradient for the habitat variable, due to its qualitative nature, our results suggest that habitat has a very important influence on female fitness, given that females inhabiting the semi-open habitat have an ARS more than twice that of the females inhabiting the closed habitat. Such an influence of resource availability is in agreement with classical sexual selection theories that postulate that, in mammals, because of the high energetic demands of gestation and lactation, female reproductive success will often be limited by access to food (e.g., Emlen and Oring 1977; Sterck et al. 1997). In our study, males, like females, have higher ARS in the semi-open habitat. A male reproductive success depends on the number of females it mates with, and of the fertility of these females. Our spatial analyses show that males in the semi-open habitat have in average about the same number of females overlapping their range than males in the closed habitat. This suggests that males have higher ARS in the

semi-open habitat because they have access to more fertile females in this habitat.

Interestingly, while we observed a relatively low value for the opportunity of sexual selection in males ($I_s=1.51$), the selection gradient corresponding to the home range size ($\beta=0.57\pm0.11$) was very strong (i.e., $\beta>0.50$; Kingsolver et al. 2001), suggesting that a behavioral trait, space use, is under strong sexual selection in the males of our study population (note however that our study covers only 1 year, and that patterns of selection could very likely exhibit inter-annual variation). In the North American red squirrel, Lane et al. (2009) also found a high intensity of sexual selection on behavioral traits, male searching effort and ability ($\beta=0.56\pm0.20$ and $\beta=0.48\pm0.15$). Such high values are comparable to the ones observed for weaponry in female defense mating systems. For example, the standardized selection gradient of antler size in male red deer and of horn size in Soay sheep were found to be 0.44 ± 0.18 and 0.56 ± 0.28 , respectively (Kruuk et al. 2002; Robinson et al. 2006). Though more studies would be needed to reach a definitive conclusion, the study by Lane et al. (2009) and our present study suggest that, in species with a scramble competition mating system, even if sexual selection does not result in spectacular adaptations such as male weapons, the intensity of sexual selection is similar to the intensity in species with a female defense system.

Acknowledgements The authors wish to thank David Laloi, Denis Réale, and three anonymous referees for their thoughtful comments that improved the manuscript. Funds were received from the Région Ile-de-France, the Conseil Général des Hauts-de-Seine, and the Office National des Forêts. We thank G. Spagnol (ONF), for his help in the field and M. Devès for her help in the laboratory.

Ethical standards All conducted experiments complied with the current laws of France.

References

- Andersson M (1994) Sexual selection. Princeton University Press, Princeton
- Arak A (1983) Male-male competition and mate choice in anuran amphibians. In: Bateson P (ed) Mate choice. Cambridge University Press, Cambridge, pp 181–210
- Arnold SJ, Wade MJ (1984a) On the measurement of natural and sexual selection: applications. *Evolution* 38:720–734
- Arnold SJ, Wade MJ (1984b) On the measurement of natural and sexual selection: theory. *Evolution* 38:709–719
- Barton K (2012) MuMIn: Multi-model inference. R package version 1.7.2. <http://CRAN.R-project.org/package=MuMIn>
- Bateman AJ (1948) Intra-sexual selection in *Drosophila*. *Heredity* 2:349–368
- Blake BH, Gillett KE (1984) Reproduction of Asian chipmunks (*Tamias sibiricus*) in captivity. *Zoo Biol* 3:47–63

- Blake BH, Gillett KE (1988) Estrous cycle and related aspects of reproduction in captive Asian chipmunks, *Tamias sibiricus*. *J Mammal* 69:598–603
- Boyer N, Réale D, Marmet J, Pisanu B, Chapuis JL (2010) Personality, space use and tick load in an introduced population of Siberian chipmunks *Tamias sibiricus*. *J Anim Ecol* 79:538–547
- Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Model* 197:516–519
- 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
- Chapuis J-L, Obolenskaya EV, Pisanu B, Lissovsky AA (2011) *Tamias sibiricus* (Siberian chipmunk). The Invasive Species Compendium. Cambridge Agricultural Bureau International, <http://www.cabi.org/isc/>. Accessed 25 May 2011
- Clutton-Brock TH (2009) Sexual selection in females. *Anim Behav* 77:3–11
- Clutton-Brock TH, Hodge SJ, Spong G, Russell AF, Jordan NR, Bennett NC, Sharpe LL, Manser MB (2006) Intrasexual competition and sexual selection in cooperative mammals. *Nature* 444:1065–1068
- Coltman DW, Smith JA, Bancroft DR, Pilkington J, MacColl AD, Clutton-Brock TH, Pemberton JM (1999) Density-dependent variation in lifetime breeding success and natural and sexual selection in Soay rams. *Am Nat* 154:730–746
- Coltman DW, Festa-Bianchet M, Jorgenson JT, Strobeck C (2002) Age-dependent sexual selection in bighorn rams. *Proc R Soc Lond B* 269:165–172
- Crawley MJ (2007) The R Book. Wiley, Chichester, UK
- Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223
- Gittleman JL, Thompson SD (1988) Energy allocation in mammalian reproduction. *Am Zool* 28:863–875
- Ims RA (1987) Responses in spatial organization and behavior to manipulation of the food resource in the vole *Clethrionomys rufocanus*. *J Anim Ecol* 56:585–596
- Kalinowski ST, Taper ML, Marshall TM (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol Ecol* 16:1099–1106
- Kappeler PM (1997) Intrasexual selection in *Mirza coquereli*: evidence for scramble competition polygyny in a solitary primate. *Behav Ecol Sociobiol* 41:115–127
- Kawamichi M (1980) Food, food hoarding and seasonal changes of Siberian chipmunks. *Jpn J Ecol* 30:211–220
- Kawamichi M (1989) Nest structure dynamics and seasonal use of nests by Siberian chipmunks *Eutamias sibiricus*. *J Mammal* 70:44–57
- Kawamichi M (1996) Ecological factors affecting annual variation in commencement of hibernation in wild chipmunks *Tamias sibiricus*. *J Mammal* 77:731–744
- 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
- Kawamichi T, Kawamichi M, Kishimoto R (1987) Social organization of solitary mammals. In: Ito Y, Brown JL, Kikkawa J (eds) *Animal societies: theories and facts*. Japan Science Society Press, Tokyo, pp 173–188
- Kingsolver JG, Hoekstra HE, Hoekstra JM, Berrigan D, Vignieri SN, Hill CE, Hoang A, Gibert P, Beerli P (2001) The strength of phenotypic selection in natural populations. *Am Nat* 157:245–261
- Klug H, Heuschele J, Jennions MD, Kokko H (2010) The mismeasurement of sexual selection. *J Evol Biol* 23:447–462
- Kruuk LEB, Slate J, Pemberton JM, Brotherstone S, Guinness F, Clutton-Brock T (2002) Antler size in red deer: heritability and selection but no evolution. *Evolution* 56:1683–1695
- Lande R, Arnold SJ (1983) The measurement of selection on correlated characters. *Evolution* 37:1210–1226
- Lane JE, Boutin S, Gunn MR, Coltman DW (2009) Sexually selected behavior: red squirrel males search for reproductive success. *J Anim Ecol* 78:296–304
- Le Boeuf BJ, Reiter J (1988) Lifetime reproductive success in northern elephant seals. In: Clutton-Brock TH (ed) *Reproductive success: studies of individual variation in contrasting breeding systems*. University of Chicago Press, Chicago, pp 344–362
- Marmet J (2008) Traits d'histoire de vie du Tamia de Sibérie *Tamias sibiricus*, espèce exotique naturalisée dans la forêt de Sénart Essonne : démographie, biologie de la reproduction, occupation de l'espace et dispersion. Dissertation, Muséum National d'Histoire Naturelle
- Marmet J, Pisanu B, Chapuis J-L (2009) Home range, range overlap and site fidelity of introduced Siberian chipmunks in a French suburban forest. *Eur J Wildl Res* 5:497–504
- Marmet J, Pisanu B, Chapuis J-L (2011) Natal dispersal of introduced Siberian chipmunks, *Tamias sibiricus*, in a suburban forest. *J Ethol* 29:23–29
- Mohr CO (1947) Table of equivalent populations of North American small mammals. *Am Midl Nat* 37:223–249
- Moya-Larano J, El-Sayyid MET, Fox CW (2007) Smaller beetles are better scramble competitors at cooler temperatures. *Biol Lett* 3:475–478
- Murphy CG (1998) Interaction-independent sexual selection and the mechanisms of sexual selection. *Evolution* 52:8–18
- Obolenskaya EV, Lee M-Y, Dokuchaev NE, Oshida T, Lee M-S, Lee H, Lissovsky AA (2009) Diversity of Palaearctic chipmunks (*Tamias*, Sciuridae). *Mammalia* 73:281–298
- Patterson LD, Schulte-Hostedde AI (2011) Behavioural correlates of parasitism and reproductive success in male eastern chipmunks, *Tamias striatus*. *Anim Behav* 81:1129–1137
- Payne RB (1979) Sexual selection and intersexual differences in variance of breeding success. *Am Nat* 114:447–452
- Peters M, Glenn J, Svete P, Svete P, Hagen C, Tsyusko O, Decoursey P, Lieutenant-Gosselin M, Garant D, Glenn T (2007) Development and characterization of microsatellite loci in the eastern chipmunk *Tamias striatus*. *Mol Ecol Notes* 7:877–879
- 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
- R Development Core Team (2011) R: A language and environment for statistical computing, version 2.14.1. R Foundation for Statistical Computing, Vienna, Austria
- Robinson MR, Pilkington JG, Clutton-Brock TH, Pemberton JM, Kruuk LEB (2006) Live fast, die young: trade-offs between fitness components and sexually antagonistic selection on weaponry in Soay sheep. *Evolution* 60:2168–2181
- Schulte-Hostedde AI, Gibbs HL, Millar JS (2000) Microsatellite DNA loci suitable for parentage analysis in the yellow-pine chipmunk (*Tamias amoenus*). *Mol Ecol* 9:2180–2181
- Schulte-Hostedde AI, Millar JS, Gibbs HL (2004) Sexual selection and mating patterns in a mammal with female-biased sexual size dimorphism. *Behav Ecol* 15:351–356
- Schwagmeyer PL (1988) Scramble-competition polygyny in an asocial mammal: male mobility and mating success. *Am Nat* 131:885–892
- Schwagmeyer PL, Parker GA (1987) Queuing for mates in thirteen-lined ground squirrels. *Anim Behav* 35:1015–1025

- Schwagmeyer PL, Woontner SJ (1986) Scramble competition polygyny in thirteen-lined ground squirrels: the relative contributions of overt conflict and competitive mate searching. *Behav Ecol Sociobiol* 19:359–364
- Schwagmeyer PL, Parker GA, Mock DW (1998) Information asymmetries among males: implications for fertilization success in the thirteen-lined ground squirrel. *Proc R Soc Lond B* 265:1861–1865
- Shuster SM, Wade MJ (2003) Mating systems and mating strategies. Princeton University Press, Princeton, N.J
- Siegel S, Castellan NJ Jr (1988) Nonparametric statistics for the behavioral sciences, 2nd edn. McGraw-Hill, New York
- Sokal RR, Rohlf FJ (1995) Biometry: the principles and practice of statistics in biological research, 3rd edn. W. H. Freeman and Co, New York
- Spritzer MD, Solomon NG, Meikle DB (2005) Influence of scramble competition for mates upon the spatial ability of male meadow voles. *Anim Behav* 69:375–386
- Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. *Behav Ecol Sociobiol* 41:291–309
- Stockley P, Bro-Jorgensen J (2011) Female competition and its evolutionary consequences in mammals. *Biol Rev* 86:341–366
- Symonds MRE, Moussali A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's Information Criterion. *Behav Ecol Sociobiol* 65:13–21
- Sztatecsny M, Jehle R, Burke R, Hoedl W (2006) Female polyandry under male harassment: the case of the common toad (*Bufo bufo*). *J Zool* 270:517–522
- Thornhill R, Alcock J (1983) The evolution of insect mating systems. University Press, Cambridge, Massachusetts, USA
- Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man, 1871–1971. Heinemann, London, pp 136–179
- Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer, New York
- Waterman J (2007) Male mating strategies in rodents. In: Sherman PW, Wolff JO (eds) Rodent societies: an ecological and evolutionary perspectives. University of Chicago Press, Chicago, pp 27–41
- Zuur A, Ieno E, Walker N, Saveliev A, Smith G (2009) Mixed effect models and extensions in ecology with R. Springer, New York
- Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol* 1:3–14