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Male space use and mating strategies
in relation to the spatial distribution of
females in bank voles
(*Myodes glareolus*)

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Abstract

The spatial and temporal distribution of females is affected by the distribution of food and other resources such as nest sites, whereas spacing behavior of males is suggested to be determined by the distribution of females. When females are aggregated, the males should display territorial behavior in order to monopolize this defensible resource, while territorial, more dispersed females should lead males to have large, overlapping home ranges. However, previous studies found contrasting results. In the present study, we thus investigated how males' space use and mating strategies are affected by females' distribution in bank vole *Myodes glareolus*. We manipulated the distribution and predictability of food in order to influence the spatial distribution of females: the food was either dispersed (treatment "spread"), spatially clumped and predictable (treatment "fixed"), or spatially clumped but unpredictable (treatment "unpredictable"). This food manipulation successfully generated different spatial distribution of females, and we investigated (i) space use patterns in males, estimated from trapping data, and (ii) their mating and reproductive success through paternity analyses.

Our results showed that males' home range size and overlap did not differ between the treatments, but they decreased through time, likely because of the increasing overall density. The weight of males had an effect on their reproductive success (number of offspring), but the distribution of females did not. The weight also had an effect on the mating success (number of partners), in interaction with the treatment. In both Fixed and Unpredictable treatments, the number of partners increased with the weight of males, but in the Spread treatments there was not such a relationship. In the Fixed and Unpredictable treatments, males might have been organized in social hierarchies, with bigger, dominant males having more chances to get partners and offspring. Further research is needed to investigate dominance relationships among males, and to test whether having a greater body mass benefit individuals during direct aggressive conflicts, or during sperm competition.

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1 Introduction

Females in estrous are determinant resources for males' fitness (Ims, 1987a). Different mating systems in mammals arise from the probability for males of acquiring females, which is determined by the variation in female home range size, group size and movements (Krebs & Davies, 1993). In a monogamous system, a male and a female form a pair bond and the couple usually shares an exclusive territory (Krebs & Davies, 1993). This may arise in populations where female home ranges are large and males are only able to defend one female. However, the monogamous system is rare in mammals because the male usually mate with the female and then leaves her to copulate with other females (Krebs & Davies, 1993; Luque-Larena, Lopez, & Gosalbez, 2004). In polygynous systems, males mate with several females, whereas females mate only with one male. Either males have exclusive (non-overlapping) home ranges that are defended against other males, which is defined as territoriality, or the males are organized in dominance hierarchies through intrasexual competition (Clutton-Brock, 1989). In both cases, several females are included within their ranges. Polyandrous systems can be seen as the opposite of polygyny, in that females mate with several males (Clutton-Brock, 1989; Krebs & Davies, 1993; Ostfeld, 1990). In promiscuous systems, individuals of both sexes may mate with several partners (Krebs & Davies, 1993; Luque-Larena, et al., 2004). These mating behaviors may vary in time and space within the same species or population as a consequence of changes in their social and ecological environments (Clutton-Brock, 1989).

It has been suggested that the spatial and temporal distribution of females is affected by the distribution of food and other resources such as nest sites, whereas the spacing behavior of males is determined by the distribution of females (Gipps, 1985; Ims, 1988; Jonsson, Hartikainen, Koskela, & Mappes, 2002; Ostfeld, 1985, 1990). Empirical studies have shown that both sexes respond rapidly to a change in distribution of their main resource. Females tend to aggregate and have overlapping home ranges when food is clumped (Ims, 1987b; Ostfeld, Lidicker, & Heske, 1985; Ostfeld, 1986). Contrary to the assumption that aggregated females with small overlapping home ranges should induce territorial behavior in males (Ostfeld, 1990), Ims (1988) observed space sharing among male grey-sided voles *Clethrionomy rufocanus* with a clumped distribution of females. The author suggested that competition with many other males might have been too strong for individual males to monopolize females. Maher and Lott (2000) also reported contrasting results regarding territoriality and distribution of key-resources.

To date, some studies have investigated the influence of resource distribution on the spacing behavior and the reproductive success of females (Ims, 1987a; Jonsson, et al., 2002; Ostfeld, et al., 1985), but very few studies have studied the effects on the mating strategies and reproductive success of males. Stueck and Barrett (1978) examined the social organization and population growth of house mice *Mus musculus* by distributing the food either in a centralized food depot, or in four dispersed food depots. In the former treatment, females aggregated around the food station, and males were organized in dominance hierarchies. From the reduced number of pregnant females, they inferred that these males were less successful at impregnating females due to a strong intrasexual competition. They did not, however, study individual variation in mating strategies and reproductive success.

The aim of the present study is to investigate male mating strategies in bank vole *Myodes glareolus*, whose social system is usually characterized by female territoriality and space sharing in males (Bujalska, 1973; Ostfeld, 1985), and the mating system has been described as promiscuous (Klemme, Ylonen, & Eccard, 2007; Kozakiewicz, Choluj, Kozakiewicz, & Sokol, 2009). Our study was based on an experiment conducted by Rémy et al. (unpublished manuscript), where food distribution and predictability was manipulated in order to affect the spatial distribution of females. They found that females inhabiting plots with clumped and predictable food were more aggregated and social than females from plots with dispersed food, or from plots with clumped but unpredictable food (those females were territorial and dispersed). Social aggregation of females in the former treatment resulted in increased juvenile recruitment and in higher population sizes by the end of the experiment. In our study, we investigated how the contrasting female social organization affected space use and reproductive success of males. We predicted a higher individual variation in mating success (number of partners) and reproductive success (number of offspring) between males where females were aggregated, due to a strong intrasexual competition. Furthermore, where females were more spatially dispersed and territorial, we predicted that males would search widely for receptive females, resulting in larger home range sizes compared to the former case, and greater overlap between males' home ranges (Emlen & Oring, 1977; Ostfeld, 1985). This would lead to multimale- mating and a more even reproductive success among males.

3 Methods

3.1 Study area

The field work was performed at Evenstad Research Station in Hedmark County, southeastern Norway (61°25'N, 11°04'E; Figure 1). The Research Station was built in the late 80^{ies} to study issues related to landscape ecology within the framework of experimental model systems (Wiens, Stenseth, Vanhorne, & Ims, 1993). This system is used to explore empirically hypotheses at a relatively small spatial and temporal scale (Andreassen, Stenseth, & Ims, 2002). The experimental area consists of twelve plots (50*34m), each of them with steel sheet fences (extending 0.4 m above and 0.6 m below ground) to prevent dispersal between the plots and intrusion of individuals from the surroundings. The Research Station is surrounded by an electric wire which prevents mammalian predation. Vegetation cover within the enclosures (plots) consists of a meadow dominated by Poaceae spp. (mainly *Alopecurus pratensis*, *Elymus caninus* and *Deschampsia* spp.), Fabaceae spp. (mainly *Trifolium pretense*), some Asteraceae spp. (*Cirsium arvense* and *Tanacetum vulgare*) and *Epilobium angustifolium* (Onagraceae spp.).



Figure 1: Evenstad Research Station on Hedmark University College: this picture shows both the campus of Evenstad and the experimental area, copyright: Karen Marie Mathisen.

3.2 Study animal

Bank vole (Figure 2) is a small microtine which is widespread in Europe and parts of Asia (Hansson, Jedrzejewska, & Jedrzejewski, 2000; Stenersen & Syvertsen, 2004). Despite the fact that this animal is most common in deciduous or coniferous forests, it can occupy rich ground vegetation in meadows, around marshes or in harvested areas (Stenersen & Syvertsen, 2004). In some places bank voles can be found up to 1400 m above sea level (Stenseth, Gustafsson, Hansson, & Ugland, 1985). Ostfeld (1985) described the species of the genus

Myodes as omnivores. The diet includes herbs, seeds, heather, fungi, insects such as caterpillars and earthworms, but little grass (Frislid & Semb- Johansson, 1982; Hansson, 1971; Hjeljord, 2008). However, the northern populations replace the large seeds and herbs with berry bushes and small seeds from conifers (Hansson, et al., 2000).



Figure 2: Bank vole *Myodes glareolus*, with its stocky body and blunt nose, short ears and short tail (Ostfeld, 1990), copyright: Romain Bouilly.

Reproduction lasts from February to October, but this may vary depending on the geographic location. If the food is not limited during fall, reproduction can persist through the winter (Larsson, Hansson, & Nyholm, 1973). Females are pregnant for approximately 18 days, and give birth to between 3 and 8 pups, and have 2-4 litters per year (Ylonen & Viitala, 1985).

The individuals used in the experiment were caught in Telemark County, south Norway in July 2009.

3.3 Food- manipulation

Food supplementation consisted of a mixture of sunflower and oat seeds in equal proportion. We distributed the food in three different ways (Figure 3): in the treatment “Spread” the food was distributed randomly all over the plot. In the two other treatments, the food was placed in a bucket with openings in the bottom and covered by a metal sheet chimney to protect it against precipitations. In the treatment “Fixed”, the bucket was placed in the middle of the plot (spatially clumped), whereas in the treatment “Unpredictable” the bucket was moved randomly twice a week (spatially clumped but unpredictable). Unlike Ims (1988), who manipulated the distribution of caged females to study the spacing behavior of males, our

design cannot totally exclude the possibility that males' distribution was also partly affected by the food distribution itself, and not only by the females' distribution. But as stated previously, we believe that the latter influences more strongly male reproductive strategies.

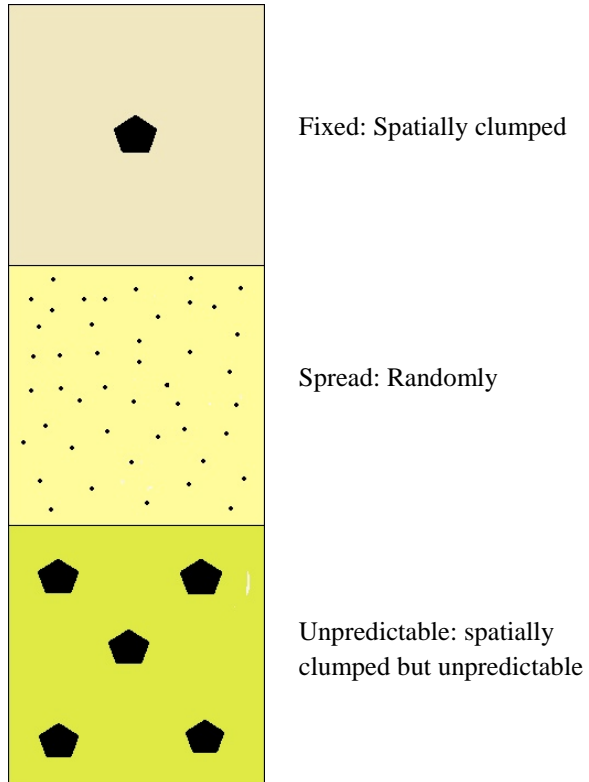


Figure 3: The three different treatments in the experimental area.



Figure 4: Ugglan special live trap. These traps were placed in a 4*5 grid manner in each plot, copyright: Bénédicte Chalaye

3.4 Live trapping

The experiment was performed between August and November 2009. Four females and four males, all sexually mature and marked by toe clipping, were released in each plot. The trapping started ten days after the release, and at this point the Operational Sex Ratio (OSR, i.e. the ratio of fertile males to receptive females (Emlen & Oring, 1977)) was biased towards females (2:1). The traps used during the experiment were Ugglan special live traps (Grahnbab, Marieholm, Sweden; Figure 4). In each plot, 20 traps were placed in a 4*5 grid manner, with a distance of 10 m between each other. We used sunflower-seeds, oat and carrot as trap baits, and we sometimes placed sawdust into the traps when the weather was cold and/or wet.

We conducted 4-days trapping sessions every two weeks until early October. A last trapping session was also conducted in early November. The trapping was organized with one check in the morning and one check in the afternoon, with the capture- mark- recapture- method (CMR). For each individual, we recorded identity, sex, weight, reproductive status for females if they were pregnant or lactating, and trap location. When new individuals (juveniles) were caught, we marked them by toe clipping. Toes of both released animals and recruits were fixed with 98% ethanol in order to run genetic analysis. This marking technique is widely used for small vertebrates (Gundersen & Andreassen, 1998), and harmful effects of this technique on the health or breeding performance of voles has never been observed.

Finally, at the end of each trapping session, we emptied the traps and left them open.

3.5 Genetic analysis

Paternity of all field-born offspring was determined using 9 microsatellite markers: MSCg-4, MSCg-7, MSCg-9 (Gerlach & Musolf, 2000; Gockel et al., 1997) and Cg13B8, Cg16A3, Cg1F11, Cg2A4, Cg3A8, Cg5E8 (Rikalainen, Grapputo, Knott, Koskela, & Mappes, 2008). Genomic DNA was extracted from toes tissue with the proteinase K / NaCl method, and purified with a QIAquick 96 PCR Purification Kit (QIAGEN, USA). Microsatellites were amplified with a *Taq* DNA Polymerase 5U/μl (MP Biomedicals Europe, France). After migration by electrophoresis, products of polymerase chain reaction were identified with GeneMapper (Applied Biosystems, California, USA). We used the software Cervus 3.0.3 (www.fieldgenetics.com) to assign parentage. (A. Rémy, personal communication).

3.6 Data analysis

We analyzed how female spatial distribution affected the space use and mating strategy of males with statistical analysis in R (Team, 2009), R commander (Rcmdr) package and Excel. The most parsimonious models were selected by backward elimination of non-significant terms, with an ANOVA procedure.

We grouped the trapping sessions due to the small number of capture positions per individual within each trapping session. This resulted in two Group Sessions: (1) we grouped the first 3 trapping sessions, which corresponded to the establishment period and the production of the first litter, and (2) we grouped the last 3 trapping sessions, which corresponded to the appearance of field-born offspring and the production of a second litter.

We first checked whether the number of adult males, adult females and the total number of voles (including juveniles) changed from the first to the second Group Session, by using a paired t-test.

Next, we analyzed the effects of the treatment and Group Session on male space use. More specifically, we studied the number of different traps used, which provided an estimate of home range size, as well as the number of traps shared with other males, which was an index of home range overlap between males. We also analyzed the effects of the treatment and Group Session on the number of females within the males' territories. We used Generalized Linear Models (GLM) with a Poisson distribution. A factor "plot" was included in all analyses to account the non-independence of males present in the same plot. When studying the number of traps shared, we controlled for the number of traps used (home range size).

We calculated the Coefficient of Variation ($CV=100 \times 1 \text{ SD}/\text{mean}$) (Jacquemyn, Brys, & Hermy, 2002) among males for their numbers of partners and their numbers of offspring in each Group Session and in each Treatment. We investigated the mating success (number of partners) and the reproductive success (number of offspring) of males using Quasi- Poisson GLMs for the effects of the Treatment, Group Session, male weight, overlap (ratio of the number of traps shared to the number of traps used), and the interactions between the latter three variables and the Treatment variable.

4 Results

4.1 Population densities

The number of voles (the overall density, including juveniles) increased from the first to the second Group Session ($t_{11}=5.91$, $P < 0.001$; Table 1), but there were no differences in the number of adult males ($t_{11}=0.41$, $P=0.687$; Table 1) and adult females ($t_{11}=1.75$, $P=0.108$; Table 1).

Table 1: Average \pm 2SE number of juveniles, males and females per plot in Group Session 1 and Group Session 2.

	Group Session 1	Group Session 2
Number of juveniles	1.14 \pm 0.45	17.36 \pm 3.20
Number of Males	3.71 \pm 0.67	4.64 \pm 0.86
Number of females	2.69 \pm 0.54	3.89 \pm 0.51

4.2 Space use

The number of traps used per male (home range size estimate) decreased from the first (5.23 \pm 1.00 2SE) to the second Group Session (3.75 \pm 0.83 2SE; $F=2.75$, $P=0.006$). However, neither the treatment ($\chi^2=0.08$, $df=2$, $P=0.962$), nor the interaction between treatment and Group Session ($\chi^2=0.49$, $df=2$, $P=0.781$) had an effect on the number of traps used.

The number of traps shared (overlap estimate) decreased from the first (3.37 \pm 0.78) to the second Group Session (1.56 \pm 0.48; $F=2.10$, $P=0.036$). However, neither the treatment ($\chi^2=2.64$, $df=2$, $P=0.267$), nor the interaction between treatment and Group Session ($\chi^2=0.71$, $df=2$, $P=0.700$) had an effect on the number of traps shared.

4.3 Reproduction

The number of females within male home ranges decreased from the first (2.97 \pm 0.71) to the second Group Session (1.61 \pm 0.45; $F=3.57$, $P < 0.001$). However, neither the treatment ($\chi^2=0.39$, $df=2$, $P=0.822$), nor the interaction between treatment and Group Session ($\chi^2=0.18$, $df=2$, $P=0.914$) had an effect on the number of females within the male home ranges.

The coefficients of variation (CV) for both the number of partners and the number of offspring (Tables 2 and 3) suggested that males in the “Spread” treatment had more equal

chances to get partners and offspring, while a higher proportion of males failed to reproduce in the other two treatments. Figures 5 and 6 show the skewed distribution of the number of offspring and partners per male in the “Fixed” and “Unpredictable” treatments, especially during the second Group Session.

Analyses with GLMs showed that the number of partners was influenced by the weight of males ($F=5.80$, $df=1$, $P=0.020$) and the interaction between the treatment and the weight ($F=3.80$, $df=2$, $P=0.028$). More specifically, for both fixed and unpredictable treatments, the number of partners increased with the weight of males. But when the food was spread, there was not such a relationship between the number of partners and the weight of the males (Figure 7). However, no significant effects were found for the treatment ($F =0.80$, $df=2$, $P=0.453$), the interaction between treatment and Group Session ($F =0.62$, $df=2$, $P=0.542$), overlap among male home ranges ($F =0.16$, $df=1$, $P=0.694$), or Group Session ($F =0.42$, $df=1$, $P=0.518$).

Male weight also had a significant effect on the number of offspring ($t_{2,28}$, $df=63$, $P=0.026$; Figure 8). But no significant effects on the number of offspring were observed for the treatment ($F =0.01$, $df=2$, $P=0.993$), the interaction between treatment and Group Session ($F =0.28$, $df= 2$, $P= 0.76$), the home range overlap ($F =0.06$, $df= 1$, $P= 0.815$), the Group Session ($F =0.35$, $df= 2$, $P=0.560$), or the interaction between treatment and weight ($F =2.13$, $df= 2$, $P= 0.128$).

Table 2: Coefficients of variation ($CV=100\times 1\text{ SD}/\text{mean}$) and the median for the number of offspring and partners in Session Group 1 in treatments Fixed, Spread and Unpredictable.

	Fixed		Spread		Unpredictable	
	Nb Offspring	Nb Partners	Nb Offspring	Nb Partners	Nb Offspring	Nb Partners
CV	1.0897	0.9520	0.7612	0.5416	1.2246	1.1821
Median	7.0	1.0	7.5	2.5	1.5	1.0

Table 3: Coefficients of variation ($CV=100\times 1\text{ SD}/\text{mean}$) and the median for the number of offspring and partners in Session Group 2 in treatments Fixed, Spread and Unpredictable.

	Fixed		Spread		Unpredictable	
	Nb Offspring	Nb Partners	Nb Offspring	Nb Partners	Nb Offspring	Nb Partners
CV	1.3397	1.18778	0.9981	0.8528	1.2071	1.2103
Median	0.5	0.5	6.0	2.5	1.5	1.0

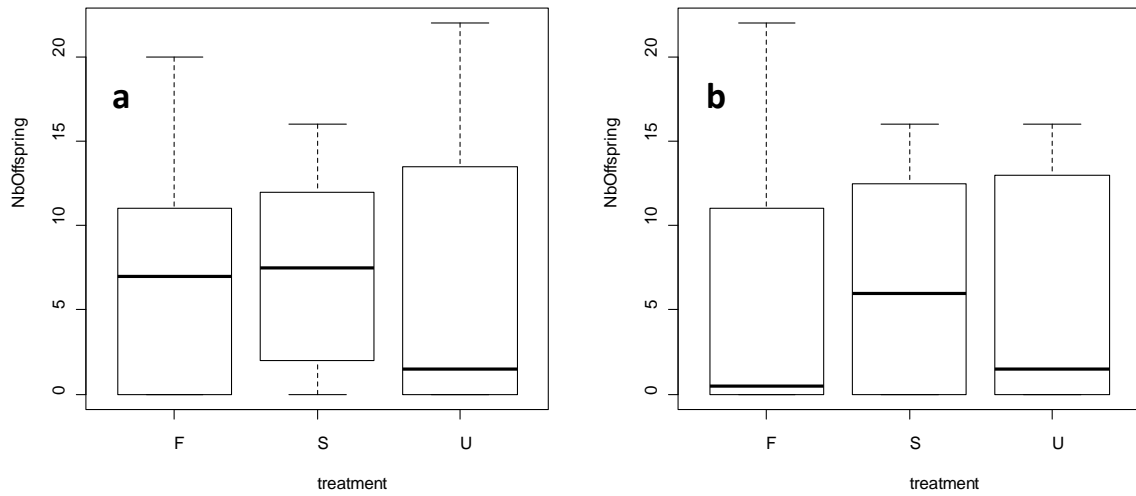


Figure 5: Box plots showing the distribution of the number of offspring per male Bank vole in Group Session 1 (a) and Group Session 2 (b) for the treatments Fixed (F), Spread (S) and Unpredictable (U). In the treatment Fixed the food was spatially clumped, in treatment Spread the food was distributed randomly all over the plot, and in treatment Unpredictable the food was spatially clumped but unpredictable, where the food was moved randomly twice a week within the plot. The line inside the box represents the median value.

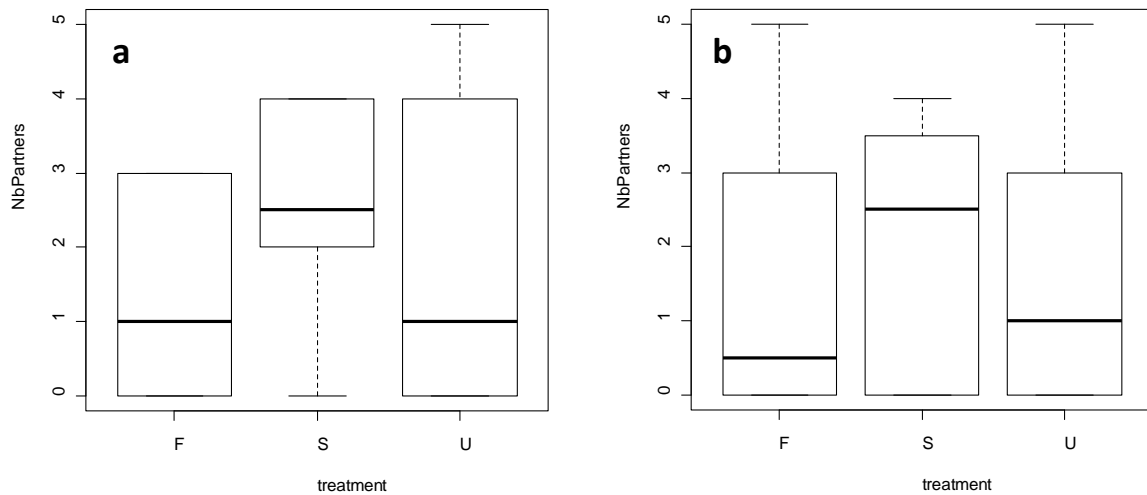


Figure 6: Box plots showing the distribution of the number of partners per male Bank vole in Group Session 1 (a) and Group Session 2 (b) for the treatments Fixed (F), Spread (S) and Unpredictable (U). In the treatment Fixed the food was spatially clumped, in treatment Spread the food was distributed randomly all over the plot, and in treatment Unpredictable the food was spatially clumped but unpredictable, where the food was moved randomly twice a week within the plot. The line inside the box represents the median value.

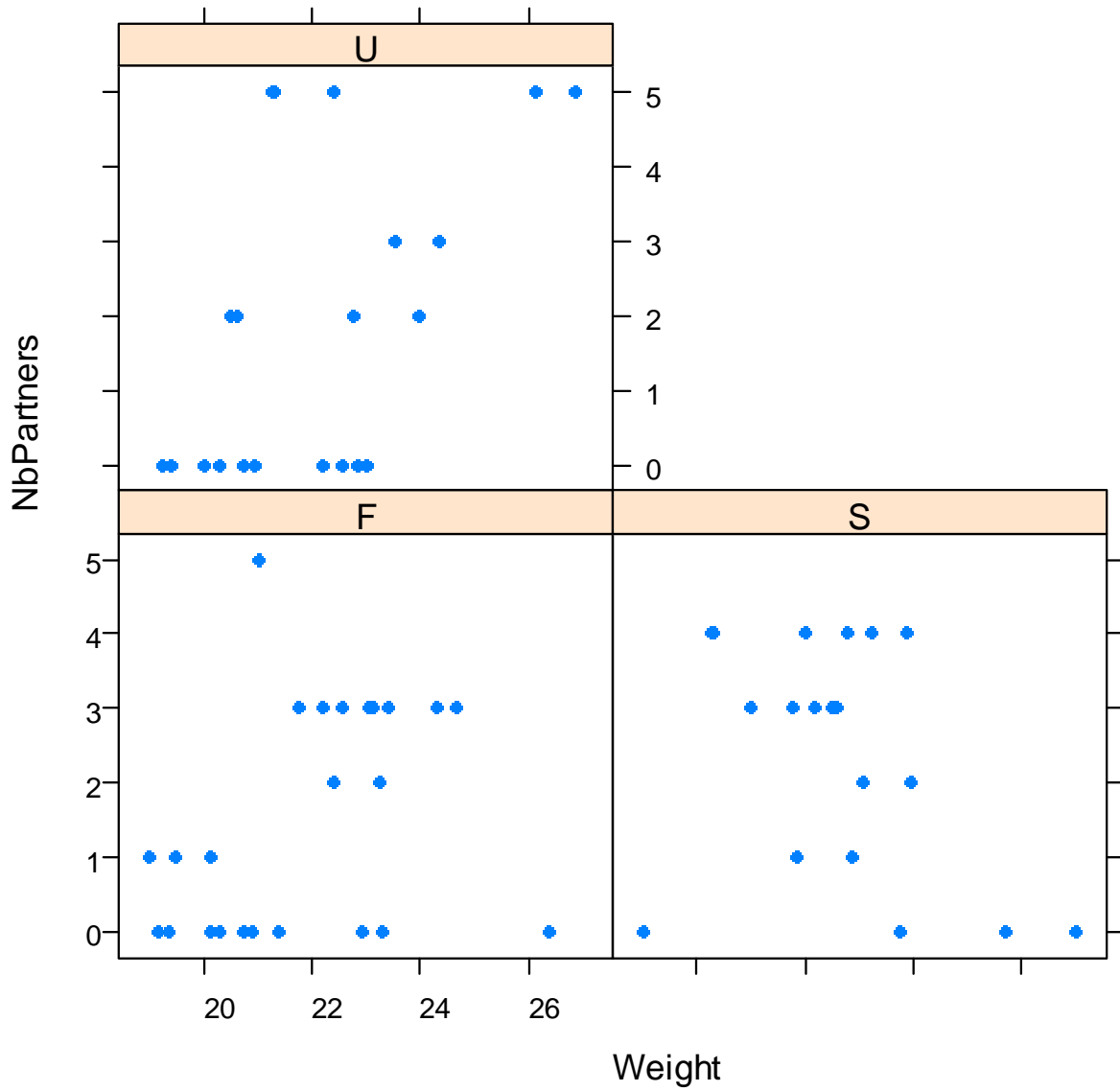


Figure 7: The relationship between male weight and the number of partners, for treatments Fixed (F), Spread (S) and Unpredictable (U). In the treatment Fixed the food was spatially clumped, in treatment Spread the food was distributed randomly all over the plot, and in treatment Unpredictable the food was spatially clumped but unpredictable, where the food was moved randomly twice a week within the plot.

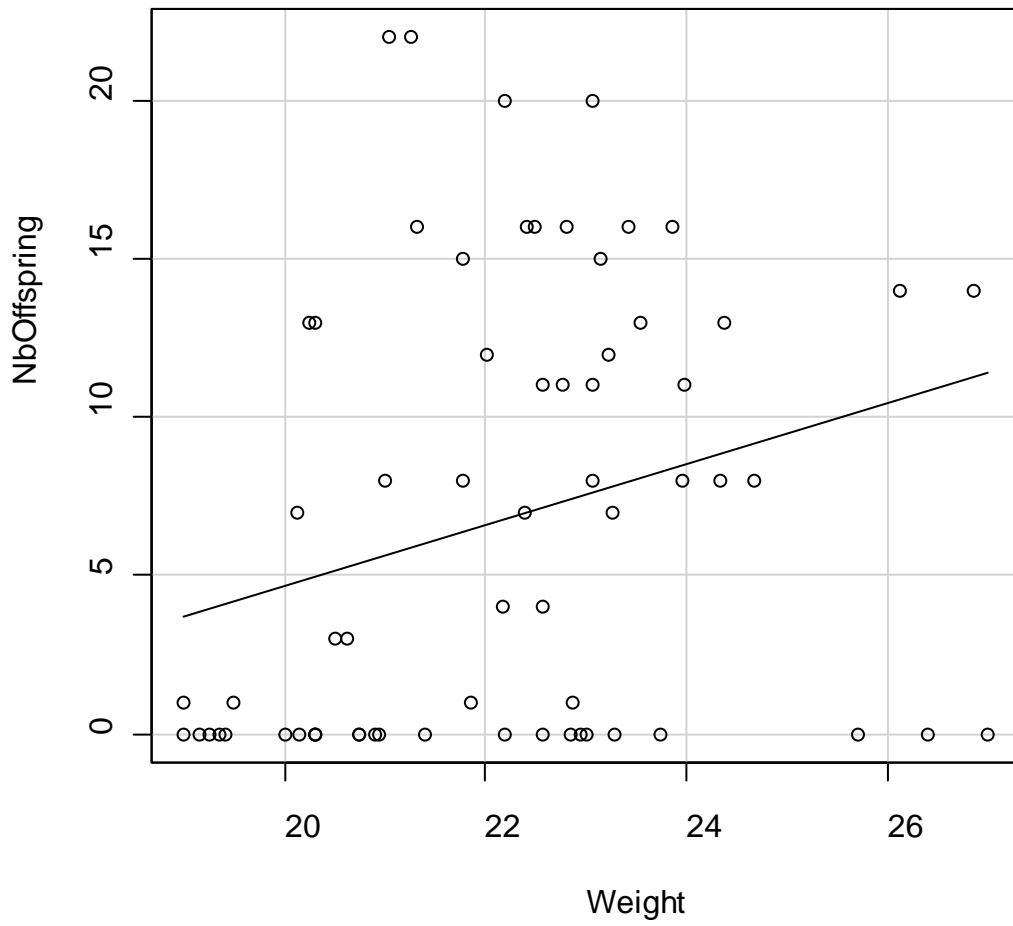


Figure 8: The relationship between male body weight and the number of offspring.

5 Discussion

5.1 Space use

In this experiment, we manipulated the distribution of female bank voles in order to investigate space use and mating strategies of males. Our results showed that males' home range size and overlap decreased over time, but we observed no differences between the experimental treatments. This contradicts our hypothesis and existing studies (Emlen & Oring, 1977; Ostfeld, et al., 1985) suggesting that the males change their space use from smaller, exclusive home ranges when the females are clumped (as in the Fixed treatment), to larger, overlapping home ranges when the females are territorial and dispersed (as in the Spread and Unpredictable treatments). On the contrary, Ims (1988) showed an increase in space sharing among males when the females were aggregated.

The degree of breeding synchrony of females may also have an effect on males' space use (Ostfeld, 1990). When females enter in estrous synchronously, a male may defend a territory including several receptive females. Males are expected to have a smaller home range and evict male competitors from females either by defending a territory, or through social dominance. On the other hand, when females breed asynchronously, males would be unable to monopolize several females and instead they should search widely for receptive females. Thus, they would have bigger home range size and higher overlap (Emlen & Oring, 1977; Ostfeld, 1990). However, in our study it did not seem that the degree of breeding synchrony differed between treatments (A. Rémy, personal communication), which could explain why we did not observe a treatment effect on males' home range size and overlap.

Nelson (1995) showed that male home ranges became smaller at high female density, but they were not influenced by the distribution pattern of the females. Ostfeld (1986) also found that males have much bigger home ranges at low than at high density. Hence, in the present study, the decreasing home range size and overlap were probably caused by an increase in the overall density from the first to the second Group session.

5.2 Reproduction

According to our results, the weight had an effect on male reproductive success (number of offspring), but the treatments did not. The weight also had an effect on the mating success (number of partners), in interaction with the treatments. Horne and Ylonen (1998) and

Ylonen, Horne, and Luukkonen (2004) suggested that body size correlates positively with dominance status and testis size in bank voles. In the Spread treatment, where the food was distributed randomly, males were probably unable to monopolize several females (Emlen & Oring, 1977; Ostfeld, 1985), and they tended to have a more equal chance to get partners. In the Fixed and Unpredictable treatments, the number of mating partners increased with males' weight. The results suggest that males were organized in social hierarchies, with bigger, dominant males having more chances to get partners and offspring. The intra- sexual competition between males was higher when the females were aggregated.

Competition between males might also have occurred at a finer scale, other than direct competitive interactions. For example, when females mated with several males, intrasexual competition in the reproductive tract of the female (i.e. sperm-competition) may have occurred (Wolff & Sherman, 2007). Ylonen, et al., (2004) suggested that weight positively correlates with testis size in bank voles. Larger males would then deposit a larger number of sperm, and be more successful during sperm-competition.

At the population level, Rémy et al. (unpublished manuscript) showed that the Clumped treatment led to higher population size by the end of the experiment, following by the populations from Spread treatment, and those from Unpredictable treatment (Figure 9). They explained that the lower reproductive success of females from the Spread and Unpredictable treatments might have been the result of higher infanticidal rates. As both bank vole females and males commit infanticide (Ylonen, Koskela, & Mappes, 1997), these demographic effects of the food treatments can be explained through interactive effects of male and female competition. In the Unpredictable treatment, both female competition and male competition for the access to receptive females seemed high, which might have resulted in a low recruitment rate. Populations from the Spread treatment performed a bit better, probably because of a lower competition between males for the access to mates. Finally, despite the suggested direct competition among males in the Clumped treatment, the populations increased substantially. One explanation can be that aggregation of females and promiscuous mating strategy used by these females might have confused paternity of the offspring among males and decreased the frequency of infanticides performed by them (Ebensperger, 1998).

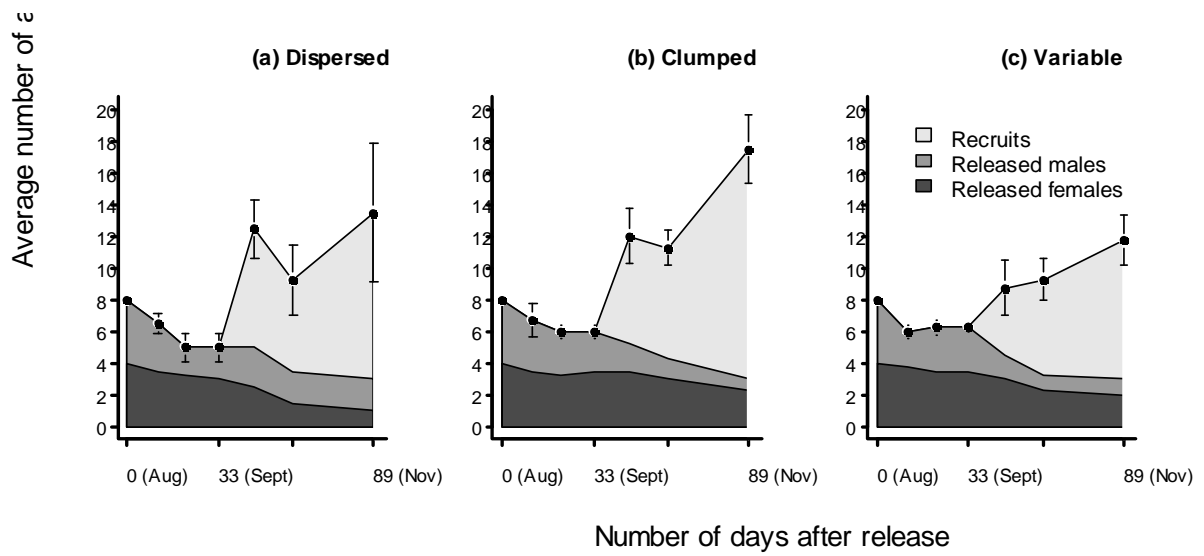


Figure 9: Average sizes (black dots, \pm SE) and structure of the populations in the (a) “Spread”, (b) “Clumped”, or (c) “Unpredictable” food treatment throughout the duration of the experiment. Mean numbers of recruits, released males and females are indicated for each treatment.

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