

Original Article

Food distribution influences social organization and population growth in a small rodent

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In polygynous mammals, the spatial clumping and predictability of food should influence spacing behavior of females whose reproductive success depends to a great extent on food availability, which would in turn affect male spacing behavior. Changes in the social and mating systems can then influence individual fitness and population dynamics. To test these hypotheses, we manipulated food distribution and predictability in enclosed populations of bank voles (*Myodes glareolus*) and monitored spacing behavior, survival, and reproduction of adult females and males over 3 months. Food was either spread out (dispersed treatment), spatially clumped and highly predictable (clumped treatment) or spatially clumped but less predictable (variable treatment). We found that females in the clumped treatment were more aggregated and had more overlapping home ranges compared with females in the dispersed and variable treatments. Male spacing behavior followed the same patterns. Despite different social organizations between treatments, no differences in home range size and mating systems were found in females and males. In addition, we found that females in the clumped food treatment had a higher probability of successfully producing weaned offspring, likely due to lower infanticide rates. This led to higher population growth compared with the other 2 treatments. These results suggest a tight relationship between the spatiotemporal distribution of food, social organization, and population dynamics.

Key words: demography, food distribution, intrasexual interactions, reproductive success, space use. [*Behav Ecol*]

INTRODUCTION

The distribution and the predictability of food resources are important ecological factors explaining variability in social and mating systems among and within species (Macdonald 1983; Davies and Lundberg 1984; Lott 1991; Ebensperger 2001; Streatfeild et al. 2011). According to the classical model of a polygynous mating system in mammals, energetic demands of female reproduction are high and female reproductive success is more limited by access to food than to mates, whereas the opposite pattern occurs in males (Trivers 1972). Thus, spatiotemporal availability of food should influence the spatial distribution and social organization of females, including their investment in territoriality defined as the proportion of the home range exclusively used and defended by an individual (Ims 1987; Ostfeld 1990; Wauters and Dhondt 1992; Streatfeild

et al. 2011). Social organization of females could in turn have an effect on male reproductive strategies and space use (Emlen and Oring 1977; Ims 1988; Cudworth and Koprowski 2010).

Females are expected to aggregate around the food source and display less pronounced intrasexual territoriality when food is highly spatially clumped, as the costs of excluding female competitors from the food source would be too high (Maher and Lott 2000). As a result, male competition for access to mates should increase and a more polygynous mating system should be observed (Emlen and Oring 1977). More spatially dispersed but still patchy food sources should decrease interactions among females, reduce the costs of home range defense, and favor a stronger female territoriality (Maher and Lott 2000). In this case, males could either have large overlapping home ranges and adopt a promiscuous mating system (Ostfeld 1990) or could defend a single female territory and mate monogamously (Emlen and Oring 1977; Taber and Macdonald 1992; Streatfeild et al. 2011). In addition, female territoriality

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should be less pronounced when food predictability is low as food resources are not economically defensible (Wauters and Dhondt 1992; Maher and Lott 2000; Verdolin 2009; but see Eide et al. 2004).

Food distribution and predictability are also expected to change individual reproduction and survival, and therefore population growth, through its influence on social organizations. Female competition for territories may limit the density of breeding females (Boonstra and Rodd 1983; Wolff 1997; Sommaro et al. 2010). Moreover, female space use influences the rates of agonistic behavior among females (Scott and Lockard 2006; Stockley and Bro-Jørgensen 2011), the rates of infanticide (Mappes et al. 1995; Jonsson et al. 2002), and cooperative behaviors (Lambin and Krebs 1991). Male competition should also be considered because behaviors resulting from competition among males, such as sexual harassment or infanticide, can alter female reproductive success and population growth (Rankin and Kokko 2007).

Despite numerous studies testing the effects of food distribution on individual behavior, fitness, or demography, to our knowledge, very few studies have analyzed the link from changes in spacing behavior induced by food distribution and predictability to individual fitness and then to demographic trajectories. Two descriptive studies with red squirrels (*Sciurus vulgaris*; Wauters and Dhondt 1992) and prairie voles (*Microtus ochrogaster*; Streatfeild et al. 2011) found differences in female spacing behavior between habitats contrasted for their distribution of prized food resources. Habitats with aggregated food and aggregated females had higher population densities in prairie voles (Streatfeild et al. 2011), but not in red squirrels (Wauters et al. 2004). In addition, Stueck and Barrett (1978) observed that experimental populations of house mice (*Mus musculus*) experiencing a centralized food treatment were smaller at the end of the breeding season than those with a more dispersed food treatment. In the centralized food treatment, male competition for access to aggregated females was so high that impregnation success of females was reduced. Ylönen and Viitala (1991) further demonstrated that female bank voles from populations with a clumped food overlapped more and tended to produce their first litter earlier in spring than females from an evenly distributed food treatment, though this did not translate into differences in population size between treatments in late spring.

Here, we studied populations of bank voles, a species where females (but not males) are usually territorial (Bujalska 1990) and where individuals usually rely on scattered food resources (Jensen 1982). We manipulated the distribution and predictability of food in experimental plots during the late breeding season to test effects on spacing behavior of females and males, individual body mass, survival and reproduction, and population growth. We compared food treatments with 1) a dispersed distribution, 2) a spatially clumped and predictable distribution, and 3) a spatially clumped and unpredictable distribution. We predicted that females from a dispersed food treatment should be territorial, whereas females from a clumped and predictable food treatment should aggregate and have less exclusive home ranges. This spatial clumping of females could reduce female reproduction through decreased offspring survival (Mappes et al. 1995; Jonsson et al. 2002) and/or increased mating competition among males (Stueck and Barrett 1978). Alternatively, spatial clumping could increase familiarity among aggregated females and enhance juvenile recruitment (Ylönen et al. 1990, 1997). In a spatially clumped and unpredictable food treatment, females should have large overlapping home ranges, with negative effects on juvenile survival and demography

because longer time is spent away from the nest for foraging. We also expected that the distribution of males should map onto that of females and that competition among males, and hence the strength of sexual selection, should be higher in the clumped and predictable food treatment than in the other 2 treatments. Finally, we expected that these changes in spacing behavior would explain variation in population growth rates through changes in individual fitness.

MATERIALS AND METHODS

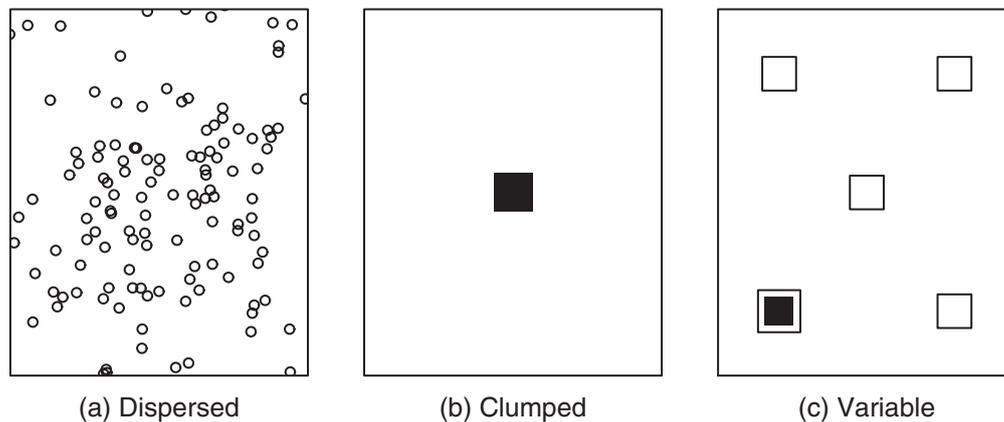
Study animals and experimental area

The bank vole is a small microtine rodent distributed across Europe from mature forests to reforestation areas and meadows (Myllymäki 1977; Mitchell-Jones et al. 1999). Reproduction mainly occurs from late April to October, with females giving birth to up to 4 litters per year, and from 2 to 10 offspring per litter (Koivula et al. 2003). Offspring are weaned before the age of 3 weeks (Oksanen et al. 2001). Individuals used in this experiment were caught in Telemark County (south Norway) in July 2009. They were kept in wire mesh cages (32 × 23 × 20 cm) in an outdoor shelter during the 2 weeks before the start of experiment to ensure that females were not pregnant prior to release. During captivity, animals were fed with carrots, apples, and sunflower seeds and provided with water ad libitum.

The experiment was carried out at Evenstad Research Station, southeast Norway, between August and November 2009. This period corresponds to the late breeding season when the diet of bank voles consists more of seeds and less of green parts of plants (Jensen 1982) and was thus more appropriate to test potential effects of our food manipulation (see below). The experimental area had 12 plots (50 × 34 m) fenced with a galvanized steel sheet fence extending 0.4 m above and 0.6 m below ground. The size of the enclosures was sufficient to analyze population trajectories (see Results). To prevent mammalian predation, a fence 1.5 m high topped with an electric wire surrounded the area. Vegetation cover within the plots consisted of a dense meadow, except along the fences where the vegetation was mowed on a 2.5-m wide strip prior to the experiment and thereafter every 2 weeks (vegetation patch size: 45 × 29 m). All rodents present in the plots were removed before the experiment.

Manipulation of food distribution and predictability

We manipulated food distribution and predictability by supplementing enclosures with a mixture of sunflower and oat seeds in equal proportion; the former being a prized food resource for bank voles (Eccard and Ylönen 2001). In the dispersed treatment, food was manually spread out all over the plot (Figure 1a). In the other 2 treatments, food was placed in a food hopper, providing food on the ground, and covered by a galvanized metal sheet chimney. Food hoppers were located 5 m away from the closest trap. In the clumped and predictable treatment, hereafter named “clumped” treatment, the position of the food was fixed throughout the experiment and located in the center of the plot (Figure 1b). In the clumped and unpredictable treatment, hereafter named “variable” treatment, the position of the food was changed twice a week by randomly placing the food hopper in 1 of the 5 preset sites (Figure 1c). Those 5 sites were far enough from each other (ca. 20 m) such that there were on average only 1.4 ± 0.2 (standard error [SE]) food sites within a female home range. Each of the 3 food

**Figure 1**

Experimental design. (a) Dispersed treatment: food was manually spread all over the plot. (b) Clumped treatment: food was placed in a food hopper (black square), permanently located in the center of the plot. (c) Variable treatment: food was placed in a food hopper (black square) and was randomly moved to 1 of the 5 preset sites (white squares) twice a week.

treatments was replicated in 4 randomly chosen plots. We initially supplied each plot with 5 kg of seed mixture and then supplied additional food when two-thirds of the seed stores were depleted. On average, we added 2 kg of seeds every 3 weeks. The same amount of food was supplied to all plots. In total, approximately 13 kg of seeds were added to each plot throughout the experiment.

Release and live trapping

Before release, all individuals were sexed, weighed to the nearest 0.1 g, and individually marked by toe-clipping (2 toes) for future identification. Toes were fixed with 98% ethanol in order to run genetic analyses (see below). On 6 August, 4 females and 4 males were released from their cages in the middle of each plot (in total, 48 individuals of each sex were released). All animals were sexually mature and of similar age. Individuals of each sex were randomly allocated to treatments, making sure that the initial body mass was standardized between plots. The initial density (61 animals per hectare) matched the early summer density during peak years and was therefore high enough to induce competition for territories (Ylönen et al. 1988). Animals were left undisturbed for a 10-day period during which they could establish a social system (Koskela et al. 1997). Thereafter, populations were monitored by live trapping every 2 weeks until early October and an additional final trapping session was conducted in early November, encompassing then 2 cohorts of newborns. A grid of 4 × 5 Uggulan special live traps (Grahnb, Marieholm, Sweden) was set in each plot, with a distance of 10 m between traps (Koskela et al. 1997). Each trapping session consisted of 2 trap checks per day during 4 days. Traps were baited with carrots, sunflower and oat seeds, which were removed after each trapping session to avoid food supplementation. For each capture, we recorded identity, sex, body mass, trap location, and reproductive status for females (pregnant or lactating). Field-born offspring were individually marked by toe-clipping when first captured (most often at weaning age), and their toes were also fixed with 98% ethanol.

Parentage assessment

To assess maternity and paternity, all adults and field-born offspring were genotyped at 9 polymorphic microsatellite loci: MSCg-4, MSCg-7, and MSCg-9 (Gockel et al. 1997; Gerlach and Musolf 2000) and Cg13B8, Cg16A3, Cg1F11, Cg2A4, Cg3A8, and Cg5E8 (Rikalainen et al. 2008). Genomic DNA was extracted

from toe tissue with the proteinase K/NaCl method and purified with a QIAquick 96 PCR Purification Kit (Qiagen, Valencia, CA). Microsatellites were amplified with a Taq DNA Polymerase 5 U/μl (MP Biomedicals Europe, France) in 3 multiplexes using a GeneAmp PCR System 9700 thermocycler (Applied Biosystems, Foster City, CA). Samples were then run on an ABI 310 automated sequencer (Applied Biosystems). Allelic size was determined using GENESCAN software v. 3.7 by reference to the GENESCAN ROX 400HD size standard. We used the software Cervus 3.0.3 (www.fieldgenetics.com; Kalinowski et al. 2007) to assign parentage at 99% confidence.

Data analyses

We analyzed the effects of food treatments on space use, body mass, survival, and reproduction of adult females and males, as well as on population sizes, using statistical procedures available in R 2.8.0 (<http://cran.r-project.org/>). Our general models included the fixed effect of the food treatment and a random effect identifying the 12 populations. We tested main effects with an Anova procedure and selected the most parsimonious model by a backward elimination of nonsignificant terms. Results are given as mean ± SE unless otherwise stated. We chose to split the trapping data into 2 periods when analyzing spacing behavior, body mass, and reproduction: 1) the first 3 trapping sessions, which corresponded to the establishment period and the production and weaning of a first litter ($N_f = 40$ released females and $N_m = 35$ released males that survived after release) and 2) the last 3 trapping sessions, which corresponded to the appearance of the weaned first cohort and the production and weaning of a second litter ($N_f = 40$ females = 36 released females + 4 weaned offspring observed pregnant, and $N_m = 23$ released males). We included in our models a factor “period” to account for changes between these 2 periods, as well as a random effect “individual identity” to account for multiple observations of individuals.

We inferred spacing behavior in females and males from trapping locations (trapability did not differ between food treatments; Anova: $F_{2,86} = 0.09$, $P = 0.941$). Trapping locations provide only crude estimations of space use relative to more sophisticated methods, such as radio tracking. However, the aim of our study was to quantify effects of food treatments on indexes of home range size and overlap, and we did not need to analyze absolute values of

space use variables. So we believe that using trapping locations was sufficient to test our question. For each individual, we calculated the mean squared distance from the center of activity to obtain an index of home range sizes, less biased with regard to sample size than those estimated from the Minimum Convex Polygon method (Slade and Russell 1998). We used at least 3 locations per individual per period for calculations. These distances differed greatly between sexes (males: 294 ± 42 m²; females: 92 ± 9 m²; Wilcoxon test: $W = 390$, $P < 0.001$). Furthermore, for each time period, we described social interactions within each sex by calculating 1) the proportion of traps shared with same-sex conspecifics (i.e., the number of shared traps divided by the total number of traps used), which we considered as an index of home range overlap, 2) the number of overlapping same-sex individuals, that is, the number of same-sex conspecifics that used the same traps, and 3) the distance to the nearest same-sex neighbor, calculated as the distance between activity centers of same-sex conspecifics (Clark and Evans 1954). We ran a principal component analysis with these 4 space use variables to obtain 2 uncorrelated variables, the first 2 principal components (PC1 and PC2, respectively), for each of the 2 sexes. PC1 and PC2 accounted for 80.7% and 74.3% of the total variance for females and males, respectively. In both sexes, PC1 was positively correlated to the proportion of traps shared with same-sex individuals and the number of overlapping same-sex individuals and negatively correlated to the distance to the nearest same-sex neighbor (Table 1). Therefore, PC1 described a “territorial–social” axis, with high scores representing spatial aggregation and overlapping ranges and low scores representing territoriality. PC2 was positively correlated to the mean squared distance from the center of activity in both sexes and to the distance to the nearest neighbor for males (Table 1). Therefore, PC2 described home range size. We tested the effects of food treatment on PC1 and PC2 separately with a linear mixed model (LMM). For each sex, we included a linear effect of the density of same-sex individuals and of individual body mass, and the interaction between the latter variable and food treatment.

We further analyzed the effect of food treatment, sex, and their interaction on body mass and survival. Mean adult body mass per period was analyzed with a LMM; for females, we censored mass data during pregnancy. Mortality rates of released females and males ($N = 96$) were analyzed with a binomial generalized linear mixed model (GLMM) including the trapping sessions as a

covariate. For female reproduction, we analyzed 1) the probability that a female successfully produced at least 1 weaned offspring per period with a binomial GLMM ($N = 71$ female periods; we removed from the analyses the females that prematurely died so that observation of pregnancy was not possible) and 2) the number of weaned offspring per period, calculated among the successful breeding females ($N = 58$ female periods) with a Poisson GLMM. For these 2 analyses, we included effects of female body mass and its interaction with food treatment, and a linear effect of adult female density. We also checked whether the food treatment experienced by the mother influenced offspring body mass at weaning ($N = 181$; not all offspring have been caught at weaning age) and offspring survival after weaning, using recapture data ($N = 225$). We used a LMM and a binomial GLMM, respectively, including offspring sex as a covariate and the mother identity as a random factor for both analyses, and the offspring identity for the latter analysis.

We also checked food treatment effects 1) on the variance in male mating success (number of genetic mates) and in male reproductive success (number of weaned offspring) within populations by calculating the opportunity of sexual selection and the opportunity of selection, respectively, and 2) on sexual selection on body mass by estimating standardized directional selection gradients (see Klemme et al. 2007 for calculations and references). We chose male body mass because it could be correlated with dominance status (Horne and Ylonen 1998) and male mating and reproductive success (Klemme et al. 2007). For these analyses, we used LMMs including as a covariate the operational sex ratio (OSR) of populations, defined as the ratio of sexually active males to fertilizable females. We further analyzed whether the proportion of females mating with 1 male (monandry) versus females mating with several males (polyandry) differed between food treatments with a binomial GLMM, including female body mass and OSR as covariates. Average values (\pm SE) for individual variables related to spacing behavior, body mass, and reproduction are provided in Supplementary Table A1.

Finally, we tested whether food treatment had an impact on population growth through time (number of days after release). We analyzed population sizes, estimated as the minimum number of animals known to be alive, after the trapping session 3 (i.e., 21 days after release) with a LMM.

RESULTS

Spacing behavior

Regarding females, scores on the PC1 (“territorial–social”) axis differed between treatments: females from the clumped treatment were more aggregated and had more overlapping ranges than females from the other 2 treatments (Figure 2a and Table 2). Scores on the PC1 axis also increased with adult female density, indicating stronger overlap with increasing number of females, but those were not affected by female body mass, time period, and second-order interactions (Table 2). Scores on the PC2 axis (“home range size”) were not affected by the food treatment (Figure 2a) or by any of the other variables (Table 2). For males, scores on the PC1 axis only tended to differ between treatments (likelihood ratio tests: $LR = 4.82$, $df = 2$, $P = 0.090$) and increased with adult male density ($LR = 13.8$, $df = 1$, $P = 0.0002$). Individuals from the clumped treatment tended to have more overlapping ranges (Figure 2b). The other variables did not significantly affect PC1 scores (all $P > 0.136$). Scores on the PC2 axis decreased with adult male density ($LR = 10.9$, $df = 1$, $P = 0.001$), but neither the food treatment (Figure 2b) nor the other variables had a significant effect (all $P > 0.124$).

Table 1
Principal component analysis on individual space use descriptors

Space use descriptors	PC1	PC2
Females		
Mean squared distance	−0.118	0.983
Proportion of traps shared with females	0.887	−0.149
Number of overlapping females	0.872	0.291
Distance to the nearest female neighbor	− 0.771	0.007
Males		
Mean squared distance	0.408	0.808
Proportion of traps shared with males	0.787	−0.311
Number of overlapping males	0.821	0.305
Distance to the nearest male neighbor	− 0.584	0.574

The table presents factor loadings of the space use descriptors on the first 2 principal components. Variables that loaded strongly to 1 of the 2 principal components (absolute values greater than 0.5) are bold typed.

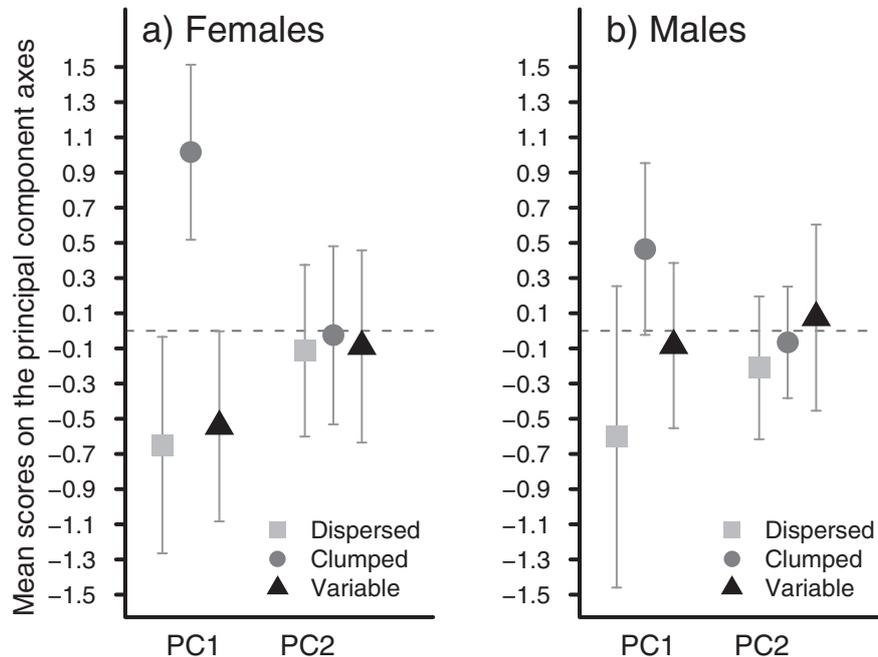


Figure 2

Average scores on the principal component axes (\pm SE) for the “dispersed” (light gray squares), “clumped” (dark gray circles), and “variable” (black triangles) food treatments in adult females (a) and adult males (b). PC1 represents a “territorial–social” axis, where high scores indicate extensive home range overlaps and short neighboring distances with same-sex individuals. PC2 is positively correlated to home range size.

Table 2

Results of model selection from a full model describing the effects of food treatments, time period, adult female density, and female body mass on the principal components' scores

Response variable	Factors	Estimate \pm SE	df	Statistics	<i>P</i>
Scores on PC1	Intercept	-2.34 ± 0.66			
	Adult female density	0.77 ± 0.15	1	LR = 23.0	<0.0001
	Food treatments	Dispersed: -0.89 ± 0.34 ; variable: -0.72 ± 0.34	2	LR = 6.15	0.046
	Body mass	0.08 ± 0.05	1	LR = 2.20	0.138
	Period	Period 2: -0.21 ± 0.22	1	LR = 0.87	0.350
	Food treatments \times period	Dispersed:period 2: -0.10 ± 0.59 ; variable:period 2: 0.19 ± 0.56	2	LR = 0.26	0.878
	Food treatments \times body mass	Dispersed:mass: 0.05 ± 0.12 ; variable:mass: 0.06 ± 0.13	2	LR = 0.24	0.885
	Individual identity	$\sigma^2 = 0.14$	1	LR = 0.31	0.580
	Plot identity	$\sigma^2 < 0.0001$	1	LR < 0.001	0.999
Scores on PC2	Intercept	-0.02 ± 0.12			
	Body mass	0.07 ± 0.05	1	LR = 2.15	0.143
	Period	Period 2: 0.03 ± 0.21	1	LR = 0.02	0.880
	Adult female density	0.02 ± 0.12	1	LR = 0.02	0.881
	Food treatments	Dispersed: -0.12 ± 0.33 ; variable: -0.11 ± 0.32	2	LR = 0.16	0.922
	Food treatments \times period	Dispersed:period 2: -0.42 ± 0.58 ; variable:period 2: -0.80 ± 0.54	2	LR = 2.16	0.340
	Food treatments \times body mass	Dispersed:mass: 0.06 ± 0.12 ; variable:mass: -0.16 ± 0.13	2	LR = 2.79	0.248
	Individual identity	$\sigma^2 = 0.14$	1	LR = 0.43	0.513
	Plot identity	$\sigma^2 < 0.0001$	1	LR < 0.001	0.999

Decreasing scores on PC1 indicate a more exclusive use of the home range and longer distance between females. PC2 is positively related to home range size (see Table 1). $N = 80$ female periods. LR, likelihood ratio.

Body mass and survival

We found no significant effect of food treatments (LR = 0.29, $df = 2$, $P = 0.865$), sex (LR = 0.25, $df = 1$, $P = 0.617$), time period (LR = 0.08, $df = 1$, $P = 0.774$), and their second-order interactions (all $P > 0.227$) on adult body mass. The mortality rate of released adults tended to be higher for males than for females (contrast males = 0.74 ± 0.38 , $\chi = 1.92$, $P = 0.054$), but was not affected by

food treatments (treatment: LR = 1.54, $df = 2$, $P = 0.464$; treatment \times sex: LR = 0.23, $df = 2$, $P = 0.893$).

Reproduction

For females, the probability of successfully producing at least 1 weaned offspring was higher in the clumped treatment than in the variable and dispersed treatments (Table 3; treatment effect:

Table 3

Results of model selection from a full model describing variation in the probability for females to successfully produce weaned offspring according to food treatments, body mass, adult female density, and time period

Factors	Estimate \pm SE	df	Statistics	<i>P</i>
Intercept	6.24 \pm 2.70			
Food treatments	Dispersed: -2.01 \pm 1.14 Variable: -2.51 \pm 1.19		$\zeta = -1.77$ $\zeta = -2.10$	0.077 0.036
Adult female density	-0.91 \pm 0.56		$\zeta = -1.63$	0.103
Period	Period 2: -0.94 \pm 0.72	1	LR = 1.80	0.179
Body mass	0.05 \pm 0.15	1	LR = 0.12	0.730
Food treatments \times body mass	Dispersed:mass: 0.72 \pm 0.43 Variable:mass: 0.18 \pm 0.35	2	LR = 3.26	0.196
Individual identity	$\sigma^2 < 0.0001$	1	LR < 0.0001	0.999
Plot identity	$\sigma^2 < 0.0001$	1	LR < 0.0001	0.999

The interaction between the food treatment and the period could not be fitted in the model. $N = 71$ female periods.

LR = 5.81, df = 2, $P = 0.055$). This probability was not significantly correlated with female body mass or the time period (Table 3), but tended to decrease with increasing adult female density (LR = 3.28, df = 1, $P = 0.070$). In addition, among successful females ($N = 58$ female periods), there was a significant interaction of the food treatment and time period on the number of weaned offspring per female (LR = 8.19, df = 2, $P = 0.017$). For the dispersed treatment, the number of weaned offspring dropped during the second part of the experiment from an average of 4.7 ± 0.5 weaned offspring per female to 2.9 ± 0.4 . In clumped and variable plots, the number of weaned offspring per female increased through time (clumped treatment: from 3.6 ± 0.5 to 4.8 ± 0.6 ; variable treatment: from 3.0 ± 0.3 to 4.9 ± 0.4). The number of weaned offspring per female was not affected by adult female density (LR = 0.33, df = 1, $P = 0.563$) or female body mass (LR = 1.47, df = 1, $P = 0.226$). Regarding indexes of offspring quality, offspring body mass at weaning was not affected by the food treatment (treatment: LR = 2.56, df = 2, $P = 0.277$; treatment \times sex: LR = 0.92, df = 2, $P = 0.632$) and sex (LR = 0.05, df = 1, $P = 0.830$). Similar results were obtained for the survival of weaned offspring (treatment: LR = 1.58, df = 2, $P = 0.453$; sex: LR = 0.09, df = 1, $P = 0.765$; treatment \times sex: LR = 0.04, df = 2, $P = 0.979$).

For males, the opportunity of sexual selection (variance in standardized mating success) was positively correlated with the OSR (estimate = 1.41 ± 0.69 , $t_8 = 2.37$, $P = 0.045$), but it was not affected by food treatments or time period (treatment: LR = 1.71, df = 2, $P = 0.426$; period: LR = 2.69, df = 1, $P = 0.101$; treatment \times period: LR = 1.10, df = 2, $P = 0.576$). Similar results were found for the opportunity of selection (variance in standardized reproductive success; OSR: estimate = 1.71 ± 0.59 , $t_8 = 2.89$, $P = 0.020$; other variables: $P > 0.080$). The directional selection gradient on body mass for mating success was positive (mean \pm SE = 0.40 ± 0.19), implying that heavier males mated and fertilized more females than lighter males. This gradient tended to decrease during the second half of the experiment (contrast = -0.49 ± 0.21 , $t_8 = -2.28$, $P = 0.052$), but was not influenced by food treatment (treatment: LR = 3.24, df = 2, $P = 0.197$; treatment \times period: LR = 3.78, df = 2, $P = 0.151$) or by OSR (LR = 0.03, df = 1, $P = 0.861$). Similar results were obtained when the selection gradient was calculated for reproductive success (mean \pm SE = 0.40 ± 0.21 ; time period: contrast "period 2" = -0.50 ± 0.22 , $t_8 = -2.28$, $P = 0.052$; other variables: $P > 0.171$). Finally, the proportion of females mating with 1 male (monandry) to females mating with several males (polyandry) did not differ between food treatments (treatment: LR = 0.07, df = 2, $P = 0.964$; treatment \times period: LR = 1.90, df = 2, $P = 0.386$) and was not affected by

time period (LR = 1.17, df = 1, $P = 0.279$), OSR (LR = 1.16, df = 1, $P = 0.281$), or female body mass (LR = 1.63, df = 1, $P = 0.202$).

Population growth

The increase in population size through time was significantly higher in clumped plots than in variable plots (Figure 3; contrast = -0.09 ± 0.04 , $t_{45} = -2.06$, $P = 0.045$). The population growth in dispersed plots was intermediate between, and not significantly different from, the growth of the other 2 treatments (contrast clumped = 0.05 ± 0.04 , $t_{45} = 1.12$, $P = 0.267$; contrast variable = -0.04 ± 0.04 , $t_{45} = -0.94$, $P = 0.354$).

DISCUSSION

Our experiment demonstrates that the territorial behavior usually observed in female bank voles is a flexible strategy, confirming the key influence of food distribution and predictability on spacing systems in small mammals (Ostfeld 1990; Lott 1991). We further found that changes in female spacing behavior likely affected female reproductive success and population growth. Females from the clumped and predictable food treatment overlapped more and had a higher breeding success (with regard to the probability of producing weaned offspring) in comparison with females from the other 2 treatments, where populations had a lower growth rate during the late summer. Food treatments had no detectable effects on female and offspring body mass, while we would have expected females from the dispersed and variable plots to have access to lower quantities of food given the similarities in home range size between treatments. If we assume a straightforward relationship between food acquisition and body mass, these results suggest that acquisition of food resources was similar between treatments and that the observed differences in fitness and demography between treatments were most likely caused by some indirect effects of social interactions between females rather than by direct effects of the energy provided by food. Finally, we observed no significant effect of food distribution and predictability on mating systems, which runs against some theoretical predictions from sexual selection theory and the results of previous studies (Emlen and Oring 1977; Davies and Lundberg 1984; Ostfeld 1990; Streatfield et al. 2011). Davies and Hartley (1996) argued that mating systems are affected by individual conflicts of interest and could be more strongly influenced by the number of competitors and mates than by food distribution. The observed influence of the OSR on the variance in male

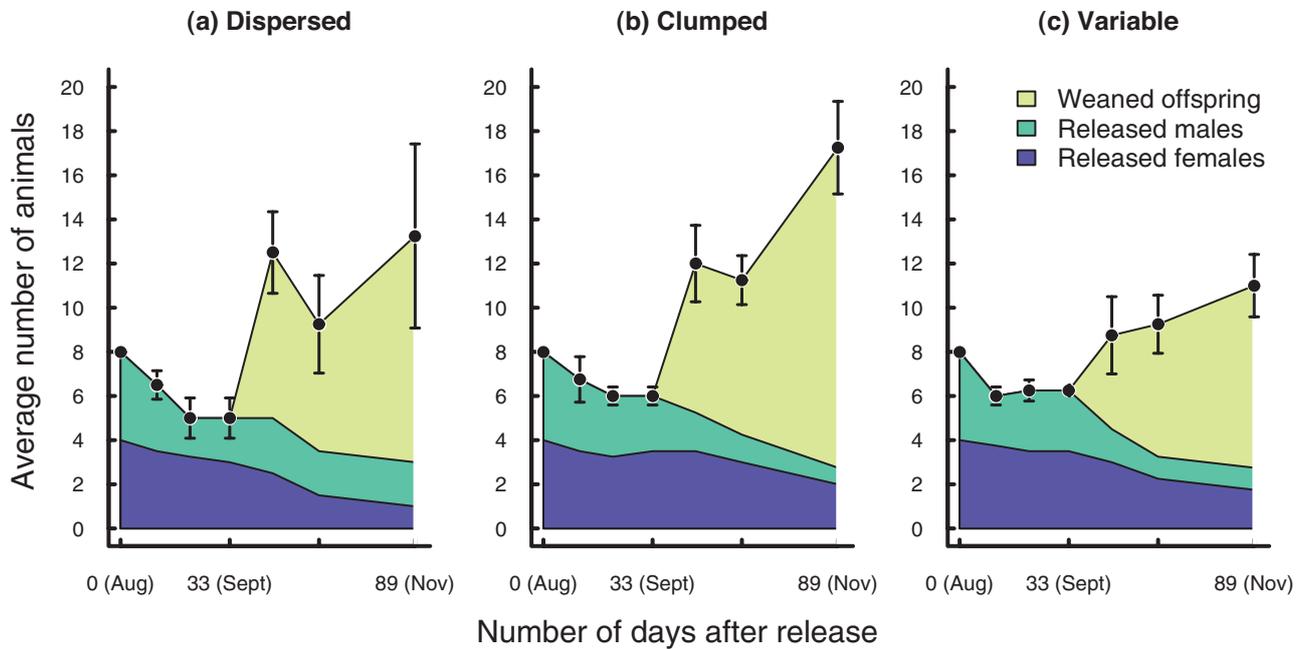


Figure 3

Average number of individuals (black dots, \pm SE) and population structure in the (a) “dispersed”, (b) “clumped” and (c) “variable” food treatment throughout the duration of the experiment. Mean numbers of weaned offspring, released males and females are indicated for each treatment.

mating and reproductive success confirms this idea (see Klemme et al. 2007 for similar results).

Home range size

The descriptor of home range size (PC2) was not affected by the treatment in neither sex (see Ylönen and Viitala 1991 for similar results). These results are not consistent with the predictions of the resource dispersion hypothesis, which states that home range size increases with increasing food dispersion in order to meet individuals’ metabolic needs (Macdonald 1983; empirical studies: Kruuk and Parish 1982; Eide et al. 2004; Verdolin 2009). In addition, home range size should increase with decreasing spatial predictability of food (Wauters and Dhondt 1992; Eide et al. 2004). It might be that the presence of fences and the high densities of adult females and males in our study constrained their home range. Indeed, male density had negative effects on male home range size, which is consistent with previous results on rodents (Erlinge et al. 1990; Priotto et al. 2002). Another possibility is that our estimates from trapping data lumped in 2 periods may be too coarse to detect minor effects of food treatments on home range size. We should, therefore, be cautious about the interpretation of these results.

Social system

In accordance with our predictions and with previous studies (Rogers 1987; Ylönen and Viitala 1991; Verdolin 2009), females were aggregated and less territorial when the food was clumped and predictable, whereas females were more spaced out and reduced their overlap when the food was dispersed. Food distribution is, therefore, an important determinant of the female spacing behavior in bank voles. However, these results do not imply that female territoriality evolves solely to defend food. Indeed, breeding female bank voles may overlap in their foraging areas (Bujalska 1991), but still secure an exclusive area around the nest site to protect pups

against infanticidal individuals (Bujalska 1991; Wolff 1993; Koskela et al. 1997). Regarding the variable food treatment, our results were not consistent with our predictions because females were just as territorial in this treatment as in the dispersed food treatment. The occurrence of a territorial behavior in an unpredictable environment may be explained by a food hoarding strategy (Maher and Lott 2000), as bank voles can store seeds in caches and in their nest (Pulliainen and Keränen 1979; Hansson 1986; Mappes 1998). In an unpredictable environment, hoarding behavior reduces the costs of foraging and provides continuous food source, and territoriality might be a strategy to secure food caches (Vander Wall 1990). If this interpretation is confirmed, our results suggest that spatiotemporal predictability of food can initiate food hoarding behavior in bank voles.

We found similar spacing patterns for males than for females, with higher overlaps between home ranges in the clumped treatment than in the dispersed and variable treatments. Yet, differences in male spacing systems among food treatments were weaker than in females. It is likely that male spacing behavior was more influenced by the distribution of females than by distribution of food per se (Ims 1988; Ostfeld 1990). However, additional experiments are needed to disentangle the direct effects of food distribution on male social systems and the indirect ones via changes in female distribution.

Individual fitness traits

Food distribution and predictability had no detectable effects on individual body mass and mortality, contrary to what was observed by Stueck and Barrett (1978) with house mice. Previous studies also showed that spatial clumping of resources can lead to differential allocation of resources among individuals (e.g., Monaghan and Metcalfe 1985; Murray et al. 2006) and can increase agonistic interactions when resources can be monopolized by a few individuals at a time (e.g., Boccia et al. 1988; Scott and Lockard 2006). However,

monopolization of food resources is less likely to occur with our experimental design and our study species. Indeed, Lopucki (2007) observed that individual visits of bank voles at feeding stations were short (less than 1 min in most cases) and resulted in few direct social interactions, consisting mainly of avoidance. Previous behavioral studies in other microtine species even found that clumped food can increase familiarity and reduce aggressive interactions among females using regularly the same feeding station (Ims 1987; Ferkin 1988).

In addition, we did not observe a higher variance in mating and reproductive success among males as a consequence of a stronger competition for access to females in the clumped treatment than in the other 2 treatments. The potential for monopolization of several mates and polygyny was likely weak in our experiment because female voles bred synchronously (see Emlen and Oring 1977; Poikonen et al. 2008). The slight benefit for males of being heavier, in terms of mating and reproductive success, might not be then explained by their ability to efficiently guard their mates, but rather by their ability to impregnate more females. Indeed, as male body mass and testes size are correlated in bank voles (Ylönen et al. 2004; Lemaître et al. 2012) and as the operational sex ratio was intermediate or female biased in most populations studied here, it could have been easier for larger males to produce sperm at sufficient quantity or rates to successfully fertilize several females as suggested by Klemme et al. (2007).

Differences in female reproductive success between food treatments were not caused by differences in the quantity or the quality of offspring, for which our proxies were body mass at weaning and survival. We cannot exclude that other indexes of quality, such as offspring's reproduction, differed between the treatments (Klemme et al. 2008; Stockley and Bro-Jørgensen 2011). Instead, we observed that variation in female reproductive success between food treatments was due to the probability of successfully producing weaned offspring. All but 2 females that failed to produce weaned offspring were observed at the latest stage of pregnancy or of lactation. Hence, they lost their litter after birth, which indicates the occurrence of infanticides and/or a mortality of low-condition pups. However, we favor the former hypothesis, as infanticides are more likely to wipe out the whole litter (Heise and Lippke 1997), whereas a poor condition would result in lower litter sizes at weaning. Infanticide can result from female competition (Stockley and Bro-Jørgensen 2011) or from male attempts to increase reproductive opportunities (Ebensperger 1998). The higher probability of producing weaned offspring for females in the clumped plots might be due to less time spent away from the nest for foraging and patrolling (Gray et al. 2002), resulting in a better protection of pups in the nest (Ylönen and Horne 2002). In addition, increased familiarity among aggregated females may reduce the propensity of neighboring females to commit infanticide (Ylönen et al. 1997) and increase their success at repelling infanticidal males (Ebensperger 1998). Another explanation could be that females from the clumped plots used more often a multiple male mating strategy to confuse paternity of the offspring among males and decrease the frequency of male infanticide (Ebensperger 1998). However, our results did not show any differences between treatments regarding female genetic mating strategy. This should be interpreted with some caution because the behavioral mating strategy of females could greatly differ from their genetic mating strategy.

Demographic responses

Food distribution and predictability influenced population growth during the late breeding season. A clumped food treatment enhanced population growth, contrary to what has previously been observed in small mammals (Stueck and Barrett 1978;

Ylönen and Viitala 1991). As for many other short-lived mammal species (Wauters and Lens 1995; Heppell et al. 2000), the main demographic factor explaining the variation in population growth between treatments was the different rates of breeding failure of females, likely mediated by different degree of familiarity among females and different infanticide rates (Ylönen et al. 1990, 1995).

The relaxation of female territoriality when food resources are clumped can have both proximate and ultimate implications for population dynamics. First, when populations receive clumped supplemental food, either for management purposes or under more natural conditions, such as during seed masting, we can expect that the synergetic effects of the increasing energy input provided by food and the relaxation of territoriality may lead to remarkably high population growth and even population outbreaks (Jensen 1982). Second, we can expect that food distribution and predictability would affect the mechanisms of regulation of populations, as observed by Wauters and Lens (1995). Populations relying on more dispersed food resources would be more importantly regulated by intrinsic factors, such as female territoriality, which limits the density of breeding females (Wolff 1997). On the other hand, regulation of populations relying on spatially clumped food resources would be more importantly influenced by extrinsic factors, such as the variation in food availability. Whenever clumped food is predictable, relaxation of territoriality and familiarity among females would lead to high population growth, whereas less predictability in food supply or other factors affecting social organizations of clumped females, such as dispersal (Andreassen and Gundersen 2006) or predation (Ims et al. 1993), would slow down this growth.

CONCLUSION

By manipulating food distribution and predictability, we showed that flexible spacing behavior influences population dynamics. In bank voles, the distribution and predictability of prized food resources and social organization are critical determinants of the late summer population increase. In general, flexibility of social behaviors is an important individual attribute to respond to changes in the environment, especially in short-lived species like voles, and differences in flexibility of social behaviors between species might explain differences in their population dynamics (Andreassen et al. 2013). Yet, we did not observe a straightforward causal relationship between changes in social organization of females and males, and the genetic mating systems. The generality of this decoupling between population dynamics and mating systems remains to be tested in other species.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org>.

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