



**Hedmark University College**

Faculty of applied ecology and agriculture

## **BRAGE**

Hedmark University College's Open Research Archive

<http://brage.bibsys.no/hhe/>

This is the author's version of the article published in

### ***Behavioral Ecology***

The article has been peer-reviewed, but does not include the publisher's layout, page numbers and proof-corrections

Citation for the published paper:

Remy, A. M. J., Odden, M., Richard, M., Stene, M. T., Le Galliard, J.-F., & Andreassen, H. P. (2013). Food distribution influences social organization and population growth in a small rodent. *Behavioral Ecology*.

doi: 10.1093/beheco/art029

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

3

4 Alice Rémy<sup>1,2\*</sup>, Morten Odden<sup>1</sup>, Murielle Richard<sup>3</sup>, Marius Tyr Stene<sup>1</sup>, Jean-François Le  
5 Galliard<sup>3,4</sup>, and Harry P. Andreassen<sup>1</sup>

6 <sup>1</sup> Faculty of Applied Ecology and Agricultural Sciences, Hedmark University College, Anne  
7 Evenstadsvei 80, 2480 Koppang, Norway

8 <sup>2</sup> Centre for Ecological and Evolutionary Synthesis, University of Oslo, P.O. Box 1066, Blindern,  
9 Oslo NO-0316, Norway

10 <sup>3</sup> CNRS – UMR 7625, Laboratoire Ecologie-Evolution, Université Pierre et Marie Curie, Case  
11 237, 7 Quai St Bernard, 75005 Paris, France

12 <sup>4</sup> CNRS/ENS UMS 3194, CEREEP – Ecotron IleDeFrance, École Normale Supérieure, 78 rue du  
13 Château, 77140 St-Pierre-lès-Nemours

14

15 \* Correspondence author: Alice Rémy (address: Hedmark University College, Anne  
16 Evenstadsvei 80, 2480 Koppang, Norway; Email: [remy.alice@neuf.fr](mailto:remy.alice@neuf.fr))

17

18

19

20 **Short title:** Small rodent's responses to food distribution

21 **ABSTRACT**

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

39 **Key-words:** demography, food distribution, intra-sexual interactions, reproductive success,  
40 space use

41

## 42 INTRODUCTION

43 The distribution and the predictability of food resources are important ecological factors  
44 explaining variability in social and mating systems among and within species (Macdonald 1983;  
45 Davies and Lundberg 1984; Lott 1991; Ebensperger 2001; Streatfeild, et al. 2011). According to  
46 the classical model of a polygynous mating system in mammals, energetic demands of female  
47 reproduction are high and female reproductive success is more limited by access to food than to  
48 mates, while the opposite pattern occurs in males (Trivers 1972). Thus, spatio-temporal  
49 availability of food should influence the spatial distribution and social organization of females,  
50 including their investment in territoriality defined as the proportion of the home range  
51 exclusively used and defended by an individual (Ims 1987; Ostfeld 1990; Wauters and Dhondt  
52 1992; Streatfeild, et al. 2011). Social organization of females could in turn have an effect on  
53 male reproductive strategies and space use (Emlen and Oring 1977; Ims 1988; Cudworth and  
54 Koprowski 2010).

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

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

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

76 Despite numerous studies testing the effects of food distribution on individual behavior,  
77 fitness, or demography, to our knowledge, very few studies have analyzed the link from changes  
78 in spacing behavior induced by food distribution and predictability to individual fitness and then  
79 to demographic trajectories. Two descriptive studies with red squirrels (*Sciurus vulgaris*;  
80 Wauters and Dhondt 1992) and prairie voles (*Microtus ochrogaster*; Streatfeild, et al. 2011)  
81 found differences in female spacing behavior between habitats contrasted for their distribution of  
82 prized food resources. Habitats with aggregated food and aggregated females had higher  
83 population densities in prairie voles (Streatfeild, et al. 2011), but not in red squirrels (Wauters, et  
84 al. 2004). In addition, Stueck and Barrett (1978) observed that experimental populations of house  
85 mice (*Mus musculus*) experiencing a centralized food treatment were smaller at the end of the  
86 breeding season than those with a more dispersed food treatment. In the centralized food  
87 treatment, male competition for access to aggregated females was so high that impregnation

88 success of females was reduced. Ylönen and Viitala (1991) further demonstrated that female  
89 bank voles from populations with a clumped food overlapped more and tended to produce their  
90 first litter earlier in spring than females from an evenly distributed food treatment, though this  
91 did not translate into differences in population size between treatments in late spring.

92         Here, we studied populations of bank voles, a species where females (but not males) are  
93 usually territorial (Bujalska 1990) and where individuals usually rely on scattered food resources  
94 (Jensen 1982). We manipulated the distribution and predictability of food in experimental plots  
95 during the late breeding season to test effects on spacing behavior of females and males,  
96 individual body mass, survival and reproduction, and population growth. We compared food  
97 treatments with (1) a dispersed distribution, (2) a spatially clumped and predictable distribution,  
98 and (3) a spatially clumped and unpredictable distribution. We predicted that females from a  
99 dispersed food treatment should be territorial, while females from a clumped and predictable  
100 food treatment should aggregate and have less exclusive home ranges. This spatial clumping of  
101 females could reduce female reproduction through decreased offspring survival (Mappes, et al.  
102 1995; Jonsson, et al. 2002) and/or increased mating competition among males (Stueck and  
103 Barrett 1978). Alternatively, spatial clumping could increase familiarity among aggregated  
104 females and enhance juvenile recruitment (Ylönen, et al. 1990, 1997). In a spatially clumped and  
105 unpredictable food treatment, females should have large overlapping home ranges, with negative  
106 effects on juvenile survival and demography because longer time is spent away from the nest for  
107 foraging. We also expected that the distribution of males should map onto that of females, and  
108 that competition among males, and hence the strength of sexual selection, should be higher in the  
109 clumped and predictable food treatment than in the other two treatments. Finally, we expected

110 that these changes in spacing behavior would explain variation in population growth rates  
111 through changes in individual fitness.

## 112 **MATERIALS AND METHODS**

### 113 **STUDY ANIMALS AND EXPERIMENTAL AREA**

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

123 The experiment was carried out at Evenstad Research Station, south-east Norway,  
124 between August and November 2009. This period corresponds to the late breeding season when  
125 the diet of bank voles consists more of seeds and less of green parts of plants (Jensen 1982), and  
126 was thus more appropriate to test potential effects of our food manipulation (see below). The  
127 experimental area had 12 plots (50 × 34 m) fenced with a galvanized, steel sheet fence extending  
128 0.4 m above and 0.6 m below ground. The size of the enclosures was sufficient to analyze  
129 population trajectories (see Results section). To prevent mammalian predation, a fence 1.5 m  
130 high topped with an electric wire surrounded the area. Vegetation cover within the plots  
131 consisted of a dense meadow, except along the fences where the vegetation was mowed on a 2.5

132 m-wide strip prior to the experiment and thereafter every two weeks. All rodents present in the  
133 plots were removed before the experiment.

#### 134 MANIPULATION OF FOOD DISTRIBUTION AND PREDICTABILITY

135 We manipulated food distribution and predictability by supplementing enclosures with a mixture  
136 of sunflower and oat seeds in equal proportion; the former being a prized food resource for bank  
137 voles (Eccard and Ylönen 2001). In the dispersed treatment, food was manually spread out all  
138 over the plot (Figure 1a). In the other two treatments, food was placed in a food hopper,  
139 providing food on the ground, and covered by a galvanized metal sheet chimney. Food hoppers  
140 were located 5 m away from the closest trap. In the clumped and predictable treatment, hereafter  
141 named “clumped” treatment, the position of the food was fixed throughout the experiment and  
142 located in the center of the plot (Figure 1b). In the clumped and unpredictable treatment,  
143 hereafter named “variable” treatment, the position of the food was changed twice a week by  
144 randomly placing the food hopper in one of the five pre-set sites (Figure 1c). Those five sites  
145 were far enough from each other (ca. 20 m) such that there were on average only  $1.4 \pm 0.2$  (SE)  
146 food sites within a female home range. Each of the three food treatments was replicated in four,  
147 randomly chosen plots. We initially supplied each plot with 5 kg of seed mixture and then  
148 supplied additional food when two thirds of the seeds’ stores were depleted. On average, we  
149 added 2 kg of seeds every three weeks. The same amount of food was supplied to all plots. In  
150 total, approximately 13 kg of seeds were added to each plot throughout the experiment.

#### 151 RELEASE AND LIVE TRAPPING

152 Before release, all individuals were sexed, weighed to the nearest 0.1 g, and individually marked  
153 by toe-clipping (two toes) for future identification. Toes were fixed with 98% ethanol in order to  
154 run genetic analyses (see below). On August 6, four females and four males were released from



155 their cages in the middle of each plot. All animals were sexually mature and of similar age.  
156 Individuals of each sex were randomly allocated to treatments, making sure that the initial body  
157 mass was standardized between plots. The initial density (61 animals per ha) matched the early  
158 summer density during peak years and was therefore high enough to induce competition for  
159 territories (Ylönen, et al. 1988). Animals were left undisturbed for a ten-day period during which  
160 they could establish a social system (Koskela, et al. 1997). Thereafter, populations were  
161 monitored by live trapping every two weeks until early October and an additional final trapping  
162 session was conducted in early November, encompassing then two cohorts of newborns. A grid  
163 of 4 × 5 Ugglan special live traps (Grahnb, Marieholm, Sweden) was set in each plot, with a  
164 distance of 10 m between traps (Koskela, et al. 1997). Each trapping session consisted of two  
165 trap checks per day during four days. Traps were baited with carrots, sunflower and oat seeds,  
166 which were removed after each trapping session to avoid food supplementation. For each  
167 capture, we recorded identity, sex, body mass, trap location and reproductive status for females  
168 (pregnant or lactating). Field-born offspring were individually marked by toe-clipping when first  
169 captured (most often at weaning age), and their toes were also fixed with 98% ethanol.

#### 170 PARENTAGE ASSESSMENT

171 To assess maternity and paternity, all adults and field-born offspring were genotyped at nine  
172 polymorphic microsatellite loci: MSCg-4, MSCg-7, MSCg-9 (Gockel, et al. 1997; Gerlach and  
173 Musolf 2000) and Cg13B8, Cg16A3, Cg1F11, Cg2A4, Cg3A8, Cg5E8 (Rikalainen, et al. 2008).  
174 Genomic DNA was extracted from toe tissue with the proteinase K / NaCl method, and purified  
175 with a QIAquick 96 PCR Purification Kit (QIAGEN, USA). Microsatellites were amplified with  
176 a Taq DNA Polymerase 5U/μl (MP Biomedicals Europe, France) in three multiplexes using a  
177 GeneAmp PCR System 9700 thermocycler (Applied Biosystems, California, USA). Samples

178 were then run on an ABI 310 automated sequencer (Applied Biosystems). Allelic size was  
179 determined using GENESCAN software v. 3.7 by reference to the GENESCAN ROX 400HD  
180 size standard. We used the software Cervus 3.0.3 ([www.fieldgenetics.com](http://www.fieldgenetics.com); Kalinowski, et al.  
181 2007) to assign parentage at 99% confidence.

## 182 DATA ANALYSES

183 We analyzed the effects of food treatments on space use, body mass, survival and reproduction  
184 of adult females and males, as well as on population sizes, using statistical procedures available  
185 in R 2.8.0 (<http://cran.r-project.org/>). Our general models included the fixed effect of the food  
186 treatment and a random effect identifying the populations. We tested main effects with an  
187 ANOVA procedure and selected the most parsimonious model by a backward elimination of  
188 non-significant terms. Results are given as mean  $\pm$  SE unless otherwise stated. We chose to split  
189 the trapping data into two periods when analyzing spacing behavior, body mass, and  
190 reproduction: (1) the first three trapping sessions, which corresponded to the establishment  
191 period and the production and weaning of a first litter ( $N_f = 40$  released females and  $N_m = 35$   
192 released males that survived after release), and (2) the last three trapping sessions, which  
193 corresponded to the appearance of the weaned first cohort and the production and weaning of a  
194 second litter ( $N_f = 40$  females = 36 released females + 4 weaned offspring observed pregnant;  $N_m$   
195 = 23 released males). We included in our models a factor “period” to account for changes  
196 between these two periods, as well as a random effect “individual identity” to account for  
197 multiple observations of individuals.

198 We inferred spacing behavior in females and males from trapping locations (trapability  
199 did not differ between food treatments; Anova:  $F_{2,86} = 0.09$ ,  $P = 0.941$ ). Trapping locations  
200 provide only crude estimations of space use relative to more sophisticated methods, such as radio

201 tracking. However, the aim of our study was to quantify effects of food treatments on indexes of  
202 home range size and overlap, and we did not need to analyze absolute values of space use  
203 variables. So we believe that using trapping locations was sufficient to test our question. For  
204 each individual, we calculated the mean squared distance from the center of activity to obtain an  
205 index of home range sizes, less biased with regard to sample size than those estimated from the  
206 Minimum Convex Polygon method (Slade and Russell 1998). We used at least three locations  
207 per individual per period for calculations. These distances differed greatly between sexes (males:  
208  $294 \pm 42 \text{ m}^2$ ; females:  $92 \pm 9 \text{ m}^2$ ; Wilcoxon test:  $W = 390$ ,  $P < 0.001$ ). Furthermore, for each  
209 time period, we described social interactions within each sex by calculating (i) the proportion of  
210 traps shared with same-sex conspecifics (i.e., the number of shared traps divided by the total  
211 number of traps used), which we considered as an index of home range overlap, (ii) the number  
212 of overlapping same-sex individuals, i.e., the number of same-sex conspecifics that used the  
213 same traps, and (iii) the distance to the nearest same-sex neighbor, calculated as the distance  
214 between activity centers of same-sex conspecifics (Clark and Evans 1954). We ran a Principal  
215 Component Analysis (PCA) with these four space use variables to obtain two uncorrelated  
216 variables, for females and for males. The first two principal components (PC1 and PC2,  
217 respectively) accounted for 80.7 % and for 74.3 % of the total variance for females and males,  
218 respectively. In both sexes, PC1 was positively correlated to the proportion of traps shared with  
219 same-sex individuals and the number of overlapping same-sex individuals, and negatively  
220 correlated to the distance to the nearest same-sex neighbor (Table 1). PC1 therefore described a  
221 “territorial-social” axis, with high scores representing spatial aggregation and overlapping  
222 ranges, and low scores representing territoriality. PC2 was positively correlated to the mean  
223 squared distance from the center of activity in both sexes, and to the distance to the nearest

224 neighbor for males (Table 1). PC2 therefore described home range size. We tested the effects of  
225 food treatment on PC1 and PC2 separately with a linear mixed model (LMM). For each sex, we  
226 included a linear effect of the density of same-sex individuals and of individual body mass, and  
227 the interaction between the latter variable and food treatment.

228         We further analyzed the effect of food treatment, sex and their interaction on body mass  
229 and survival. Mean adult body mass per period was analyzed with a LMM; for females, we  
230 censored mass data during pregnancy. Mortality rates of released females and males ( $n = 96$ )  
231 were analyzed with a binomial generalized linear mixed model (GLMM) including the trapping  
232 sessions as a covariate. For female reproduction, we analyzed (i) the probability that a female  
233 successfully produced at least one weaned offspring per period with a binomial GLMM ( $N = 71$ ;  
234 we removed from the analyses the females that prematurely died so that observation of  
235 pregnancy was not possible), and (ii) the number of weaned offspring per period, calculated  
236 among the successful breeding females ( $N = 58$ ) with a Poisson GLMM. For these two analyses,  
237 we included effects of female body mass and its interaction with food treatment, and a linear  
238 effect of adult female density. We also checked whether the food treatment experienced by the  
239 mother influenced offspring body mass at weaning ( $n = 181$ ; not all offspring have been caught  
240 at weaning age) and offspring survival after weaning, using recapture data ( $n = 225$ ). We used a  
241 LMM and a binomial GLMM respectively, including offspring sex as a covariate and the mother  
242 identity as a random factor for both analyses, and the offspring identity for the latter analysis.

243         We also checked food treatment effects (i) on the variance in male mating success  
244 (number of genetic mates) and in male reproductive success (number of weaned offspring)  
245 within populations by calculating the opportunity of sexual selection and the opportunity of  
246 selection, respectively, and (ii) on sexual selection on body mass by estimating standardized

247 directional selection gradients (see Klemme, et al. 2007 for calculations and references). We  
248 chose male body mass since it could be correlated with dominance status (Horne and Ylonen  
249 1998) and male mating and reproductive success (Klemme, et al. 2007). For these analyses, we  
250 used LMMs including as a covariate the operational sex ratio of populations (OSR), defined as  
251 the ratio of sexually active males to fertilizable females. We further analyzed whether the  
252 proportion of females mating with one male (monoandry) versus females mating with several  
253 males (polyandry) differed between food treatments with a binomial GLMM, including female  
254 body mass and OSR as covariates. Average values ( $\pm$  SE) for individual variables related to  
255 spacing behavior, body mass and reproduction are provided in Table A1 in Supplementary  
256 material.

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

## 261 **RESULTS**

### 262 SPACING BEHAVIOR

263 Regarding females, scores on the PC1 (“territorial-social”) axis differed between treatments:  
264 females from the clumped treatment were more aggregated and had more overlapping ranges  
265 than females from the two other treatments (Figure 2a, Table 2). Scores on the PC1 axis also  
266 increased with adult female density, indicating stronger overlap with increasing number of  
267 females, but those were not affected by female body mass, time period and second-order  
268 interactions (Table 2). Scores on the PC2 axis (“home range size”) were not affected by the food

269 treatment (Figure 2a) or by any of the other variables (Table 2). For males, scores on the PC1  
270 axis only tended to differ between treatments (Likelihood Ratio tests:  $LR = 4.82$ ,  $df = 2$ ,  $P =$   
271  $0.090$ ), and increased with adult male density ( $LR = 13.8$ ,  $df = 1$ ,  $P = 0.0002$ ). Individuals from  
272 the clumped treatment tended to have more overlapping ranges (Figure 2b). The other variables  
273 did not significantly affect PC1 scores (all  $P > 0.136$ ). Scores on the PC2 axis decreased with  
274 adult male density ( $LR = 10.9$ ,  $df = 1$ ,  $P = 0.001$ ), but neither the food treatment (Figure 2b) nor  
275 the other variables had a significant effect (all  $P > 0.124$ ).

#### 276 BODY MASS, SURVIVAL

277 We found no significant effect of food treatments ( $LR = 0.29$ ,  $df = 2$ ,  $P = 0.865$ ), sex ( $LR = 0.25$ ,  
278  $df = 1$ ,  $P = 0.617$ ), time period ( $LR = 0.08$ ,  $df = 1$ ,  $P = 0.774$ ) and their second-order interactions  
279 (all  $P > 0.227$ ) on adult body mass. The mortality rate of released adults tended to be higher for  
280 males than for females (contrast males =  $0.74 \pm 0.38$ ,  $Z = 1.92$ ,  $P = 0.054$ ), but was not affected  
281 by food treatments (treatment:  $LR = 1.54$ ,  $df = 2$ ,  $P = 0.464$ ; treatment  $\times$  sex:  $LR = 0.23$ ,  $df = 2$ ,  $P$   
282 =  $0.893$ ).

#### 283 REPRODUCTION

284 For females, the probability of successfully producing at least one weaned offspring was higher  
285 in the clumped treatment than in the variable and dispersed treatments (Table 3; treatment effect:  
286  $LR = 5.81$ ,  $df = 2$ ,  $P = 0.055$ ). This probability was not significantly correlated with female body  
287 mass or the time period (Table 3), but tended to decrease with increasing adult female density  
288 ( $LR = 3.28$ ,  $df = 1$ ,  $P = 0.070$ ). In addition, among successful females ( $N = 58$ ), there was a  
289 significant interaction of the food treatment and time period on the number of weaned offspring  
290 per female ( $LR = 8.19$ ,  $df = 2$ ,  $P = 0.017$ ). For the dispersed treatment, the number of weaned  
291 offspring dropped during the second part of the experiment from an average of  $4.7 \pm 0.5$  weaned

292 offspring per female to  $2.9 \pm 0.4$ . In clumped and variable plots, the number of weaned offspring  
293 per female increased through time (clumped treatment: from  $3.6 \pm 0.5$  to  $4.8 \pm 0.6$ ; variable  
294 treatment: from  $3.0 \pm 0.3$  to  $4.9 \pm 0.4$ ). The number of weaned offspring per female was not  
295 affected by adult female density ( $LR = 0.33$ ,  $df = 1$ ,  $P = 0.563$ ), or female body mass ( $LR = 1.47$ ,  
296  $df = 1$ ,  $P = 0.226$ ). Regarding indexes of offspring quality, offspring body mass at weaning was  
297 not affected by the food treatment (treatment:  $LR = 2.56$ ,  $df = 2$ ,  $P = 0.277$ ; treatment  $\times$  sex:  $LR$   
298  $= 0.92$ ,  $df = 2$ ,  $P = 0.632$ ) and sex ( $LR = 0.05$ ,  $df = 1$ ,  $P = 0.830$ ). Similar results were obtained  
299 for the survival of weaned offspring (treatment:  $LR = 1.58$ ,  $df = 2$ ,  $P = 0.453$ ; sex:  $LR = 0.09$ ,  $df$   
300  $= 1$ ,  $P = 0.765$ ; treatment  $\times$  sex:  $LR = 0.04$ ,  $df = 2$ ,  $P = 0.979$ ).

301 For males, the opportunity of sexual selection (variance in standardized mating success)  
302 was positively correlated with the OSR (estimate =  $1.41 \pm 0.69$ ,  $t_8 = 2.37$ ,  $P = 0.045$ ), but it was  
303 not affected by food treatments or time period (treatment:  $LR = 1.71$ ,  $df = 2$ ,  $P = 0.426$ ; period:  
304  $LR = 2.69$ ,  $df = 1$ ,  $P = 0.101$ ; treatment  $\times$  period:  $LR = 1.10$ ,  $df = 2$ ,  $P = 0.576$ ). Similar results  
305 were found for the opportunity of selection (variance in standardized reproductive success; OSR:  
306 estimate =  $1.71 \pm 0.59$ ,  $t_8 = 2.89$ ,  $P = 0.020$ ; others variables:  $P > 0.080$ ). The directional  
307 selection gradient on body mass for mating success was positive (mean  $\pm$  SE =  $0.40 + 0.19$ ),  
308 implying that heavier males mated and fertilized more females than lighter males. This gradient  
309 tended to decrease during the second half of the experiment (contrast =  $-0.49 \pm 0.21$ ,  $t_8 = -2.28$ ,  $P$   
310  $= 0.052$ ), but was not influenced by food treatment (treatment:  $LR = 3.24$ ,  $df = 2$ ,  $P = 0.197$ ;  
311 treatment  $\times$  period:  $LR = 3.78$ ,  $df = 2$ ,  $P = 0.151$ ) or by OSR ( $LR = 0.03$ ,  $df = 1$ ,  $P = 0.861$ ).  
312 Similar results were obtained when selection gradient was calculated for reproductive success  
313 (mean  $\pm$  SE =  $0.40 + 0.21$ ; time period: contrast “period 2” =  $-0.50 \pm 0.22$ ,  $t_8 = -2.28$ ,  $P = 0.052$ ;  
314 other variables:  $P > 0.171$ ). Finally, the proportion of females mating with one male

315 (monoandry) to females mating with several males (polyandry) did not differ between food  
316 treatments (treatment:  $LR = 0.07$ ,  $df = 2$ ,  $P = 0.964$ ; treatment  $\times$  period:  $LR = 1.90$ ,  $df = 2$ ,  $P =$   
317  $0.386$ ), and was not affected by time period ( $LR = 1.17$ ,  $df = 1$ ,  $P = 0.279$ ), OSR ( $LR = 1.16$ ,  $df =$   
318  $1$ ,  $P = 0.281$ ) or female body mass ( $LR = 1.63$ ,  $df = 1$ ,  $P = 0.202$ ).

#### 319 POPULATION GROWTH

320 The increase in population size through time was higher in clumped plots than in variable plots  
321 (Figure 3; contrast =  $-0.09 \pm 0.04$ ,  $t_{45} = -2.06$ ,  $P = 0.045$ ). The population growth in dispersed  
322 plots was intermediate between, and not significantly different of, the growth of the two other  
323 treatments (contrast clumped =  $0.05 \pm 0.04$ ,  $t_{45} = 1.12$ ,  $P = 0.267$ ; contrast variable =  $-0.04 \pm$   
324  $0.04$ ,  $t_{45} = -0.94$ ,  $P = 0.354$ ).

#### 325 DISCUSSION

326 Our experiment demonstrates that the territorial behavior usually observed in female bank voles  
327 is a flexible strategy, confirming the key influence of food distribution and predictability on  
328 spacing systems in small mammals (Ostfeld 1990; Lott 1991). We further found that changes in  
329 female spacing behavior likely affected female reproductive success and population growth.  
330 Females from the clumped and predictable food treatment overlapped more and had a higher  
331 breeding success (with regard to the probability of producing weaned offspring) in comparison  
332 with females from the other two treatments, where populations had a lower growth rate during  
333 the late summer. Food treatments had no detectable effects on female and offspring body mass,  
334 while we would have expected females from the dispersed and variable plots to have access to  
335 lower quantities of food given the similarities in home range size between treatments. If we  
336 assume a straightforward relationship between food acquisition and body mass, these results  
337 suggest that acquisition of food resources was similar between treatments, and that the observed



338 differences in fitness and demography between treatments were most likely caused by some  
339 indirect effects of social interactions between females rather than by direct effects of the energy  
340 provided by food. Finally, we observed no significant effect of food distribution and  
341 predictability on mating systems, which runs against some theoretical predictions from sexual  
342 selection theory and the results of previous studies (Emlen and Oring 1977; Davies and  
343 Lundberg 1984; Ostfeld 1990; Streatfeild, et al. 2011). Davies and Hartley (1996) argued that  
344 mating systems are affected by individual conflicts of interest, and could be more strongly  
345 influenced by the number of competitors and mates than by food distribution. The observed  
346 influence of the OSR on the variance in male mating and reproductive success confirms this idea  
347 (see Klemme, et al. 2007 for similar results).

#### 348 HOME RANGE SIZE

349 The descriptor of home range size (PC2) was not affected by the treatment in neither sex (see  
350 Ylönen and Viitala 1991 for similar results). These results are not consistent with the predictions  
351 of the resource dispersion hypothesis, which states that home range size increases with  
352 increasing food dispersion in order to meet individuals' metabolic needs (Macdonald 1983;  
353 empirical studies: Kruuk and Parish 1982; Eide, et al. 2004; Verdolin 2009). In addition, home  
354 range size should increase with decreasing spatial predictability of food (Wauters and Dhondt  
355 1992; Eide, et al. 2004). It might be that the presence of fences and the high densities of adult  
356 females and males in our study constrained their home range. Indeed, male density had negative  
357 effects on male home range size, which is consistent with previous results on rodents (Erlinge, et  
358 al. 1990; Priotto, et al. 2002). Another possibility is that our estimates from trapping data lumped  
359 in two periods may be too coarse to detect minor effects of food treatments on home range size.  
360 We should therefore be cautious about the interpretation of these results.

361 SOCIAL SYSTEM

362 In accordance with our predictions and with previous studies (Rogers 1987; Ylönen and Viitala  
363 1991; Verdolin 2009), females were aggregated and less territorial when the food was clumped  
364 and predictable, whereas females were more spaced out and reduced their overlap when the food  
365 was dispersed. Food distribution is therefore an important determinant of the female spacing  
366 behavior in bank voles. However, these results do not imply that female territoriality evolves  
367 solely to defend food. Indeed, breeding female bank voles may overlap in their foraging areas  
368 (Bujalska 1991), but still secure an exclusive area around the nest site to protect pups against  
369 infanticidal individuals (Bujalska 1991; Wolff 1993; Koskela, et al. 1997). Regarding the  
370 variable food treatment, our results were not consistent with our predictions since females were  
371 just as territorial in this treatment as in the dispersed food treatment. The occurrence of a  
372 territorial behavior in an unpredictable environment may be explained by a food hoarding  
373 strategy (Maher and Lott 2000), as bank voles can store seeds in caches and in their nest  
374 (Pulliainen and Keränen 1979; Hansson 1986; Mappes 1998). In an unpredictable environment,  
375 hoarding behavior reduces the costs of foraging and provides continuous food source, and  
376 territoriality might be a strategy to secure food caches (Vander Wall 1990). If this interpretation  
377 is confirmed, our results suggest that spatio-temporal predictability of food can initiate food  
378 hoarding behavior in bank voles.

379 We found similar spacing patterns for males than for females, with higher overlaps  
380 between home ranges in the clumped treatment than in the dispersed and variable treatments.  
381 Yet, differences in male spacing systems among food treatments were weaker than in females. It  
382 is likely that male spacing behavior was more influenced by the distribution of females than by  
383 distribution of food *per se* (Ims 1988; Ostfeld 1990). However, additional experiments are

384 needed to disentangle the direct effects of food distribution on male social systems and the  
385 indirect ones via changes in female distribution.

#### 386 INDIVIDUAL FITNESS TRAITS

387 Food distribution and predictability had no detectable effects on individual body mass and  
388 mortality, contrary to what was observed by Stueck & Barrett (1978) with house mice. Previous  
389 studies also showed that spatial clumping of resources can lead to differential allocation of  
390 resources among individuals (e.g. Monaghan and Metcalfe 1985; Murray, et al. 2006) and can  
391 increase agonistic interactions when resources can be monopolized by a few individuals at a time  
392 (e.g. Boccia, et al. 1988; Scott and Lockard 2006). However, monopolization of food resources is  
393 less likely to occur with our experimental design and our study species. Indeed, Lopucki  
394 (Lopucki 2007) observed that individual visits of bank voles at feeding stations were short (less  
395 than one minute in most cases) and resulted in few direct social interactions, consisting mainly of  
396 avoidance. Previous behavioral studies in other microtine species even found that clumped food  
397 can increase familiarity and reduce aggressive interactions among females using regularly the  
398 same feeding station (Ims 1987; Ferkin 1988).

399 In addition, we did not observe a higher variance in mating and reproductive success  
400 among males as a consequence of a stronger competition for access to females in the clumped  
401 treatment than in the other two treatments. The potential for monopolization of several mates and  
402 polygyny was likely weak in our experiment since female voles bred synchronously (see also  
403 Emlen and Oring 1977; Poikonen, et al. 2008). The slight benefit for males of being heavier, in  
404 terms of mating and reproductive success, might not be then explained by their ability to  
405 efficiently guard their mates, but rather by their ability to impregnate more females. Indeed, as  
406 male body mass and testes size are correlated in bank voles (Ylönen, et al. 2004; Lemaître, et al.

407 2012) and as the operational sex ratio was intermediate or female-biased in most populations  
408 studied here, it could have been easier for larger males to produce sperm at sufficient quantity or  
409 rates to successfully fertilize several females as suggested by Klemme, et al. (2007).

410 Differences in female reproductive success between food treatments were not caused by  
411 differences in the quantity or the quality of offspring, for which our proxies were body mass at  
412 weaning and survival. We cannot exclude that other indexes of quality, such as offspring's  
413 reproduction, differed between the treatments (Klemme, et al. 2008; Stockley and Bro-Jørgensen  
414 2011). Instead, we observed that variation in female reproductive success between food  
415 treatments was due to the probability of successfully producing weaned offspring. All but two  
416 females that failed to produce weaned offspring were observed at the latest stage of pregnancy or  
417 of lactation. Hence, they lost their litter after birth, which indicates the occurrence of infanticides  
418 and/or a mortality of low condition pups. However, we favor the former hypothesis, as  
419 infanticides are more likely to wipe out the whole litter (Heise and Lippke 1997), while a poor  
420 condition would result in lower litter sizes at weaning. Infanticide can result from female  
421 competition (Stockley and Bro-Jørgensen 2011) or from male attempts to increase reproductive  
422 opportunities (Ebensperger 1998). The higher probability of producing weaned offspring for  
423 females in the clumped plots might be due to less time spent away from the nest for foraging and  
424 patrolling (Gray, et al. 2002), resulting in a better protection of pups in the nest (Ylönen and  
425 Horne 2002). In addition, increased familiarity among aggregated females may reduce the  
426 propensity of neighboring females to commit infanticide (Ylönen, et al. 1997) and increase their  
427 success at repelling infanticidal males (Ebensperger 1998). Another explanation could be that  
428 females from the clumped plots used more often a multiple male mating strategy to confuse  
429 paternity of the offspring among males and decrease the frequency of male infanticide

430 (Ebensperger 1998). However, our results did not show any differences between treatments  
431 regarding female genetic mating strategy. This should be interpreted with some caution because  
432 the behavioral mating strategy of females could greatly differ from their genetic mating strategy.

#### 433 DEMOGRAPHIC RESPONSES

434 Food distribution and predictability influenced population growth during the late breeding  
435 season. A clumped food treatment enhanced population growth, contrary to what has previously  
436 been observed in small mammals (Stueck and Barrett 1978; Ylönen and Viitala 1991). As for  
437 many other short-lived mammal species (Wauters and Lens 1995; Heppell, et al. 2000), the main  
438 demographic factor explaining the variation in population growth between treatments was the  
439 different rates of breeding failure of females, likely mediated by different degree of familiarity  
440 among females and different infanticide rates (Ylönen, et al. 1990, 1995).

441         The relaxation of female territoriality when food resources are clumped can have both  
442 proximate and ultimate implications for population dynamics. First, when populations receive  
443 clumped supplemental food, either for management purposes or under more natural conditions,  
444 such as during seed masting, we can expect that the synergetic effects of the increasing energy  
445 input provided by food and the relaxation of territoriality may lead to remarkably high  
446 population growth and even population outbreaks (Jensen 1982). Second, we can expect that  
447 food distribution and predictability would affect the mechanisms of regulation of populations, as  
448 observed by Wauters and Lens (1995). Populations relying on more dispersed food resources  
449 would be more importantly regulated by intrinsic factors, such as female territoriality which  
450 limits the density of breeding females (Wolff 1997). On the other hand, regulation of populations  
451 relying on spatially clumped food resources would be more importantly influenced by extrinsic  
452 factors, such as the variation in food availability. Whenever clumped food is predictable,

453 relaxation of territoriality and familiarity among females would lead to high population growth,  
454 while less predictability in food supply or other factors affecting social organizations of clumped  
455 females, such as dispersal (Andreassen and Gundersen 2006) or predation (Ims, et al. 1993),  
456 would slow down this growth.

#### 457 CONCLUSION

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

#### 468 SUPPLEMENTARY MATERIAL

469 Supplementary Table A1 can be found at <http://www.beheco.oxfordjournals.org>.

#### 470 REFERENCES

- 471 Andreassen HP, Glorvigen P, Rémy A, Ims RA. 2013. New views on how population-intrinsic  
472 and community-extrinsic processes interact during the vole population cycles. *Oikos*.  
473 DOI: 10.1111/j.1600-0706.2012.00238.x.
- 474 Andreassen HP, Gundersen G. 2006. Male turnover reduces population growth: an enclosure  
475 experiment on voles. *Ecology*. 87:88-94.

476 Boccia ML, Laudenslager M, Reite M. 1988. Food distribution, dominance, and aggressive  
477 behaviors in bonnet macaques. *American Journal of Primatology*. 16:123-130.

478 Boonstra R, Rodd FH. 1983. Regulation of breeding density in *Microtus pennsylvanicus*. *Journal*  
479 *of Animal Ecology*. 52:757-780.

480 Bujalska G. 1990. Social system of the bank vole, *Clethrionomys glareolus*. In: Tamarin RH,  
481 Ostfeld RS, Pugh SR, Bujalska G, editors. *Social systems and population cycles in voles*.  
482 Basel: Birkhauser Verlag. p. 155-167.

483 Bujalska G. 1991. The ecology of territoriality in bank voles. *Trends in Ecology & Evolution*.  
484 6:300-301.

485 Clark PJ, Evans FC. 1954. Distance to nearest neighbor as a measure of spatial relationships in  
486 populations. *Ecology*. 35:445-453.

487 Cudworth NL, Koprowski JL. 2010. Influences of mating strategy on space use of Arizona gray  
488 squirrels. *Journal of Mammalogy*. 91:1235-1241.

489 Davies NB, Hartley IR. 1996. Food patchiness, territory overlap and social systems: an  
490 experiment with dunnocks *Prunella modularis*. *Journal of Animal Ecology*. 65:837-846.

491 Davies NB, Lundberg A. 1984. Food distribution and a variable mating system in the dunnock,  
492 *Prunella modularis*. *Journal of Animal Ecology*. 53:895-912.

493 Ebensperger L. 2001. A review of the evolutionary causes of rodent group-living. *Acta*  
494 *Theriologica*. 46:115-144.

495 Ebensperger LA. 1998. Strategies and counterstrategies to infanticide in mammals. *Biological*  
496 *Reviews*. 73:321-346.

497 Eccard JA, Ylönen H. 2001. Initiation of breeding after winter in bank voles: effects of food and  
498 population density. *Canadian Journal of Zoology*. 79:1743-1753.

499 Eide NE, Jepsen JU, Prestrud P. 2004. Spatial organization of reproductive Arctic foxes *Alopex*  
500 *lagopus*: responses to changes in spatial and temporal availability of prey. *Journal of*  
501 *Animal Ecology*. 73:1056-1068.

502 Emlen ST, Oring LW. 1977. Ecology, sexual selection, and the evolution of mating systems.  
503 *Science*. 197:215-223.

504 Erlinge S, Hoogenboom I, Agrell J, Nelson J, Sandell M. 1990. Density-related home range size  
505 and overlap in adult field voles (*Microtus agrestis*) in southern Sweden. *Journal of*  
506 *Mammalogy*. 71:597-603.

507 Ferkin MH. 1988. The effect of familiarity on social interactions in meadow voles, *Microtus*  
508 *pennsylvanicus*: a laboratory and field-study. *Animal Behaviour*. 36:1816-1822.

509 Gerlach G, Musolf K. 2000. Fragmentation of landscape as a cause for genetic subdivision in  
510 bank voles. *Conservation Biology*. 14:1066-1074.

511 Gockel J, Harr B, Schlotterer C, Arnold W, Gerlach G, Tautz D. 1997. Isolation and  
512 characterization of microsatellite loci from *Apodemus flavicollis* (Rodentia, Muridae) and  
513 *Clethrionomys glareolus* (Rodentia, Cricetidae). *Molecular Ecology*. 6:597-599.

514 Gray SJ, Jensen SP, Hurst JL. 2002. Effects of resource distribution on activity and territory  
515 defence in house mice, *Mus domesticus*. *Animal Behaviour*. 63:531-539.

516 Hansson L. 1986. Geographic differences in the sociability of voles in relation to cyclicity.  
517 *Animal Behaviour*. 34:1215-1221.

518 Heise S, Lippke J. 1997. Role of female aggression in prevention of infanticidal behavior in male  
519 common voles, *Microtus arvalis* (Pallas, 1779). *Aggressive Behavior*. 23:293-298.

520 Heppell SS, Caswell H, Crowder LB. 2000. Life histories and elasticity patterns: Perturbation  
521 analysis for species with minimal demographic data. *Ecology*. 81:654-665.



522 Horne TJ, Ylonen H. 1998. Heritabilities of dominance-related traits in male bank voles  
523 (*Clethrionomys glareolus*). *Evolution*. 52:894-899.

524 Ims RA. 1987. Responses in spatial organization and behavior to manipulations of the food  
525 resource in the vole *Clethrionomys rufocanus*. *Journal of Animal Ecology*. 56:585-596.

526 Ims RA. 1988. Spatial clumping of sexually receptive females induces space sharing among  
527 male voles. *Nature*. 335:541-543.

528 Ims RA, Rolstad J, Wegge P. 1993. Predicting space use responses to habitat fragmentation: Can  
529 voles *Microtus oeconomus* serve as an experimental-model system (EMS) for capercaillie  
530 grouse *Tetrao urogallus* in boreal forest. *Biological Conservation*. 63:261-268.

531 Jensen TS. 1982. Seed production and outbreaks of non-cyclic rodent populations in deciduous  
532 forests. *Oecologia*. 54:184-192.

533 Jonsson P, Hartikainen T, Koskela E, Mappes T. 2002. Determinants of reproductive success in  
534 voles: space use in relation to food and litter size manipulation. *Evolutionary Ecology*.  
535 16:455-467.

536 Kalinowski ST, Taper ML, Marshall TC. 2007. Revising how the computer program CERVUS  
537 accommodates genotyping error increases success in paternity assignment. *Molecular*  
538 *Ecology*. 16:1099-1106.

539 Klemme I, Ylönen H, Eccard J. 2007. Reproductive success of male bank voles (*Clethrionomys*  
540 *glareolus*): the effect of operational sex ratio and body size. *Behavioral Ecology and*  
541 *Sociobiology*. 61:1911-1918.

542 Klemme I, Ylönen H, Eccard JA. 2008. Long-term fitness benefits of polyandry in a small  
543 mammal, the bank vole *Clethrionomys glareolus*. *Proceedings of the Royal Society B:*  
544 *Biological Sciences*. 275:1095-1100.

545 Koivula M, Koskela E, Mappes T, Oksanen TA. 2003. Cost of reproduction in the wild:  
546 manipulation of reproductive effort in the bank vole. *Ecology*. 84:398-405.

547 Koskela E, Mappes T, Ylönen H. 1997. Territorial behaviour and reproductive success of bank  
548 vole *Clethrionomys glareolus* females. *Journal of Animal Ecology*. 66:341-349.

549 Kruuk H, Parish T. 1982. Factors affecting population density, group size and territory size of  
550 the european badger, *Meles meles*. *Journal of Zoology*. 196:31-39.

551 Lambin X, Krebs CJ. 1991. Can changes in female relatedness influence microtine population  
552 dynamics? *Oikos*. 61:126-132.

553 Lemaître J-F, Ramm S, Jennings N, Stockley P. 2012. Genital morphology linked to social status  
554 in the bank vole (*Myodes glareolus*). *Behavioral Ecology and Sociobiology*. 66:97-105.

555 Lopucki R. 2007. Social relationships in a bank vole *Clethrionomys glareolus* (Schreber, 1780)  
556 population: video monitoring under field conditions. *Polish Journal of Ecology*. 55:543-  
557 558.

558 Lott DF. 1991. Intraspecific variation in the social systems of wild vertebrates. Cambridge:  
559 Cambridge University Press.

560 Macdonald DW. 1983. The ecology of carnivore social behavior. *Nature*. 301:379-384.

561 Maher CR, Lott DF. 2000. A review of ecological determinants of territoriality within vertebrate  
562 species. *American Midland Naturalist*. 143:1-29.

563 Mappes T. 1998. High population density in bank voles stimulates food hoarding after breeding.  
564 *Animal Behaviour*. 55:1483-1487.

565 Mappes T, Ylönen H, Viitala J. 1995. Higher reproductive success among kin groups of bank  
566 voles (*Clethrionomys glareolus*). *Ecology*. 76:1276-1282.

567 Mitchell-Jones AJ, Amori G, Bogdanowicz W, Kryštufek B, Reijnders PJH, Spitzenberger F,  
568 Stubbe M, Thissen JBM, Vohralík V, Zima J. 1999. The Atlas of European Mammals.  
569 London: Academic Press.

570 Monaghan P, Metcalfe NB. 1985. Group foraging in wild brown hares: effects of resource  
571 distribution and social status. *Animal Behaviour*. 33:993-999.

572 Murray CM, Eberly LE, Pusey AE. 2006. Foraging strategies as a function of season and rank  
573 among wild female chimpanzees (*Pan troglodytes*). *Behavioral Ecology*. 17:1020-1028.

574 Myllymäki A. 1977. Interactions between field vole *Microtus agrestis* and its microtine  
575 competitors in Central Scandinavian populations. *Oikos*. 29:570-580.

576 Oksanen TA, Jonsson P, Koskela E, Mappes T. 2001. Optimal allocation of reproductive effort:  
577 manipulation of offspring number and size in the bank vole. *Proceedings of the Royal  
578 Society of London Series B-Biological Sciences*. 268:661-666.

579 Ostfeld RS. 1990. The ecology of territoriality in small mammals. *Trends in Ecology &  
580 Evolution*. 5:411-415.

581 Poikonen T, Koskela E, Mappes T, Mills SC. 2008. Infanticide in the evolution of reproductive  
582 synchrony: effects on reproductive success. *Evolution*. 62:612-621.

583 Priotto J, Steinmann A, Polop J. 2002. Factors affecting home range size and overlap in *Calomys  
584 venustus* (Muridae: Sigmodontinae) in Argentine agroecosystems. *Mammalian Biology*.  
585 67:97-104.

586 Pulliainen E, Keränen J. 1979. Composition and function of beard lichen stores accumulated by  
587 bank voles, *Clethrionomys glareolus*. *Aquilo Ser Zool*. 19:73-76.

588 Rankin DJ, Kokko H. 2007. Do males matter? The role of males in population dynamics. *Oikos*.  
589 116:335-348.

590 Rikalainen K, Grapputo A, Knott E, Koskela E, Mappes T. 2008. A large panel of novel  
591 microsatellite markers for the bank vole (*Myodes glareolus*). *Molecular Ecology*  
592 *Resources*. 8:1164-1168.

593 Rogers LL. 1987. Effects of food supply and kinship on social behavior, movements, and  
594 population growth of black bears in Northeastern Minnesota. *Wildlife Monographs*.1-72.

595 Scott J, Lockard J. 2006. Captive female gorilla agonistic relationships with clumped defendable  
596 food resources. *Primates*. 47:199-209.

597 Slade NA, Russell LA. 1998. Distances as indices to movements and home-range size from  
598 trapping records of small mammals. *Journal of Mammalogy*. 79:346-351.

599 Sommaro LV, Steinmann AR, Chiappero MB, Priotto JW. 2010. Effect of high density on the  
600 short term *Calomys musculus* spacing behaviour: a fencing experiment. *Acta*  
601 *Oecologica*. 36:343-348.

602 Stockley P, Bro-Jørgensen J. 2011. Female competition and its evolutionary consequences in  
603 mammals. *Biological Reviews*. 86:341-366.

604 Streatfeild CA, Mabry KE, Keane B, Crist TO, Solomon NG. 2011. Intraspecific variability in  
605 the social and genetic mating systems of prairie voles, *Microtus ochrogaster*. *Animal*  
606 *Behaviour*. 82:1387-1398.

607 Stueck KL, Barrett GW. 1978. Effects of resource partitioning on population dynamics and  
608 energy utilization strategies of feral house mice (*Mus musculus*) populations under  
609 experimental field conditions. *Ecology*. 59:539-551.

610 Taber AB, Macdonald DW. 1992. Spatial organization and monogamy in the mara *Dolichotis*  
611 *patagonum*. *Journal of Zoology*. 227:417-438.

612 Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B, editor. Sexual  
613 Selection and the Descent of Man. Chicago. p. 139-179.

614 Vander Wall SB. 1990. Food hoarding in animals. Chicago: The University of Chicago Press.

615 Verdolin JL. 2009. Gunnison's prairie dog (*Cynomys gunnisoni*): testing the resource dispersion  
616 hypothesis. Behavioral Ecology and Sociobiology. 63:789-799.

617 Wauters LA, Dhondt AA. 1992. Spacing behavior of red squirrels, *Sciurus vulgaris*: variation  
618 between habitats and the sexes. Animal Behaviour. 43:297-311.

619 Wauters LA, Lens L. 1995. Effects of food availability and density on red squirrel (*Sciurus*  
620 *vulgaris*) reproduction. Ecology. 76:2460-2469.

621 Wauters LA, Matthysen E, Adriaensen F, Tosi G. 2004. Within-sex density dependence and  
622 population dynamics of red squirrels *Sciurus vulgaris*. Journal of Animal Ecology. 73:11-  
623 25.

624 Wolff JO. 1993. Why are female small mammals territorial? Oikos. 68:364-370.

625 Wolff JO. 1997. Population regulation in mammals: an evolutionary perspective. Journal of  
626 Animal Ecology. 66:1-13.

627 Ylönen H, Horne T. 2002. Infanticide and effectiveness of pup protection in bank voles: does the  
628 mother recognise a killer? Acta ethologica. 4:97-101.

629 Ylönen H, Horne TJ, Luukkonen M. 2004. Effect of birth and weaning mass on growth, survival  
630 and reproduction in the bank vole. Evolutionary Ecology Research. 6:1-10.

631 Ylönen H, Kojola T, Viitala J. 1988. Changing female spacing behavior and demography in an  
632 enclosed breeding population of *Clethrionomys glareolus*. Holarctic Ecology. 11:286-  
633 292.

634 Ylönen H, Koskela E, Mappes T. 1997. Infanticide in the bank vole (*Clethrionomys glareolus*):  
635 occurrence and the effect of familiarity on female infanticide. *Annales Zoologici Fennici*.  
636 34:259-266.

637 Ylönen H, Mappes T, Viitala J. 1990. Different demography of friends and strangers: an  
638 experiment on the impact of kinship and familiarity in *Clethrionomys glareolus*.  
639 *Oecologia*. 83:333-337.

640 Ylönen H, Pusenius J, Viitala J. 1995. Impact of kinship and familiarity on the annual social-  
641 organization and population-dynamics of *Clethrionomys* and *Microtus* voles. *Annales*  
642 *Zoologici Fennici*. 32:225-232.

643 Ylönen H, Viitala J. 1991. Social overwintering and food distribution in the bank vole  
644 *Clethrionomys glareolus*. *Holarctic Ecology*. 14:131-137.

645

646

647

648 **FIGURE LEGENDS**

649 **Figure 1.** Experimental design. (a) Dispersed treatment: food was manually spread all over the  
650 plot. (b) Clumped treatment: food was placed in a food hopper (black square), permanently  
651 located in the center of the plot. (c) Variable treatment: food was placed in a food hopper (black  
652 square) and was randomly moved to one of the five pre-set sites (white squares) twice a week.

653

654 **Figure 2.** Average scores on the principal component axes ( $\pm$  SE) for the “dispersed” (light grey  
655 squares), “clumped” (dark grey circles), and “variable” (black triangles) food treatments in adult  
656 females (a) and adult males (b). PC1 represents a “territorial-social” axis, where high scores  
657 indicate extensive home range overlaps and short neighboring distances with same-sex  
658 individuals. PC2 is positively correlated to home range size.

659

660 **Figure 3.** Average number of individuals (black dots,  $\pm$  SE) and population structure in the (a)  
661 “dispersed”, (b) “clumped”, and (c) “variable” food treatment throughout the duration of the  
662 experiment. Mean numbers of weaned offspring, released males and females are indicated for  
663 each treatment.

664

665 **TABLES AND TABLE LEGENDS**666 **Table 1.** Principal component analysis on individual space use descriptors.

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

667 The table presents factor loadings of the space use descriptors on the first two principal  
668 components. Variables that loaded strongly to one of the two principal components (values  
669 higher than 0.5) are bold typed.

670



671 **Table 2.** Results of model selection from a full model describing the effects of food treatments,  
 672 time period, adult female density, and female body mass on the principal components' scores.

Response variable	Factors	Estimate $\pm$ SE	df	Statistics	P
Scores on PC1	Intercept	-2.34 $\pm$ 0.66			
	Adult female density	0.77 $\pm$ 0.15	1	LR = 23.0	<0.0001
	Food treatments	Dispersed: -0.89 $\pm$ 0.34 Variable: -0.72 $\pm$ 0.34	2	LR = 6.15	0.046
	Body mass	0.08 $\pm$ 0.05	1	LR = 2.20	0.138
	Period	Period2: -0.21 $\pm$ 0.22	1	LR = 0.87	0.350
	Food treatments $\times$ period	Dispersed:Period2: -0.10 $\pm$ 0.59 Variable:Period2: 0.19 $\pm$ 0.56	2	LR = 0.26	0.878
	Food treatments $\times$ body mass	Dispersed:Mass: 0.05 $\pm$ 0.12 Variable:Mass: 0.06 $\pm$ 0.13	2	LR = 0.24	0.885
	<i>Individual identity</i>	$\sigma^2 = 0.14$	1	LR = 0.31	0.580
	<i>Plot identity</i>	$\sigma^2 < .0001$	1	LR < .001	0.999
	Scores on PC2	Intercept	-0.02 $\pm$ 0.12		
Body mass		0.07 $\pm$ 0.05	1	LR = 2.15	0.143
Period		Period2: 0.03 $\pm$ 0.21	1	LR = 0.02	0.880
Adult female density		0.02 $\pm$ 0.12	1	LR = 0.02	0.881
Food treatments		Dispersed: -0.12 $\pm$ 0.33 Variable: -0.11 $\pm$ 0.32	2	LR = 0.16	0.922
Food treatments $\times$ period		Dispersed:Period2: -0.42 $\pm$ 0.58 Variable:Period2: -0.80 $\pm$ 0.54	2	LR = 2.16	0.340
Food treatments $\times$ body mass		Dispersed:Mass: 0.06 $\pm$ 0.12 Variable:Mass: -0.16 $\pm$ 0.13	2	LR = 2.79	0.248
<i>Individual identity</i>		$\sigma^2 = 0.14$	1	LR = 0.43	0.513
<i>Plot identity</i>		$\sigma^2 < .0001$	1	LR < .001	0.999

673 Decreasing scores on PC1 indicate a more exclusive use of the home range and longer distance between females.

674 PC2 is positively related to home range size (see Table 1). *N* = 80. *LR*, Likelihood Ratio.

676 **Table 3.** Results of model selection from a full model describing variation in the probability for  
 677 females to successfully produce weaned offspring according to food treatments, body mass, adult  
 678 female density, and time period.

<b>Factors</b>	<b>Estimate ± SE</b>	<b>df</b>	<b>Statistics</b>	<b>P</b>
Intercept	6.24 ± 2.70			
Food treatments	Dispersed: -2.01 ± 1.14		Z = -1.77	0.077
	Variable: -2.51 ± 1.19		Z = -2.10	0.036
Adult female density	-0.91 ± 0.56		Z = -1.63	0.103
Period	Period2: -0.94 ± 0.72	1	LR = 1.80	0.179
Body mass	0.05 ± 0.15	1	LR = 0.12	0.730
Food treatments x body mass	Dispersed:Mass: 0.72 ± 0.43	2	LR = 3.26	0.196
	Variable:Mass: 0.18 ± 0.35			
<i>Individual identity</i>	$\sigma^2 < .0001$	1	LR < .0001	0.999
<i>Plot identity</i>	$\sigma^2 < .0001$	1	LR < .0001	0.999

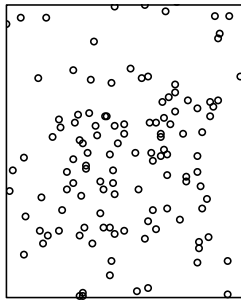
679 The interaction between the food treatment and the period could not be fitted in the model.  $N =$

680 71.

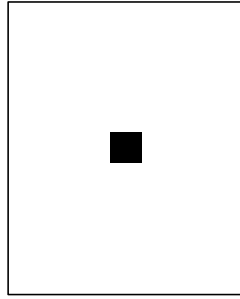
681

682 **FIGURES**

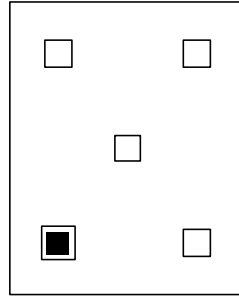
683 **Figure 1**



(a) Dispersed



(b) Clumped

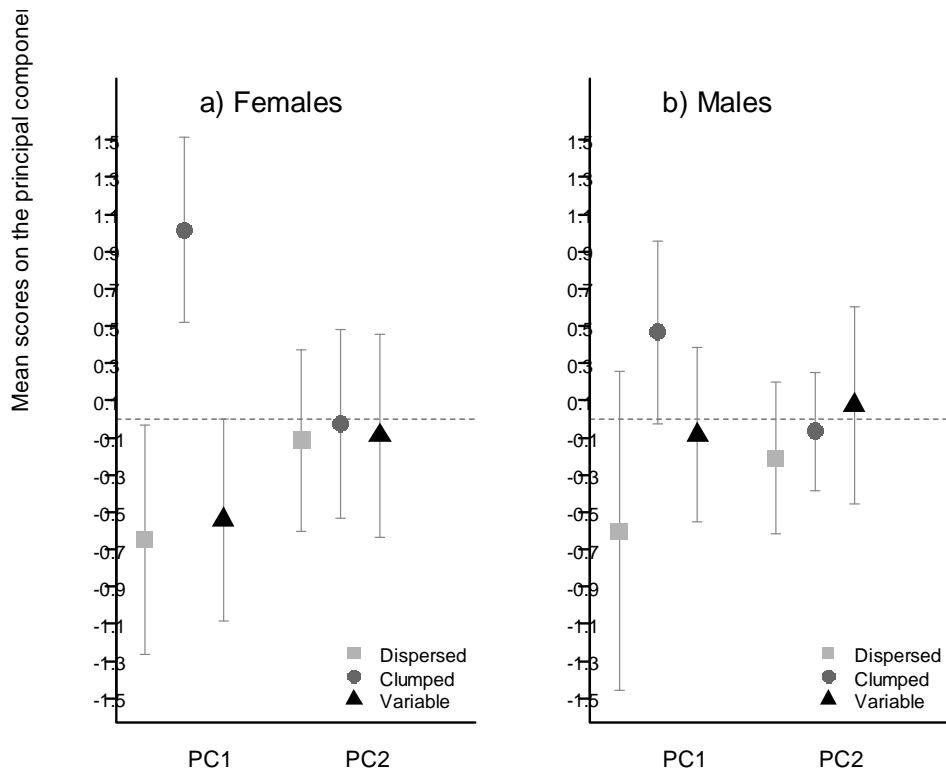


(c) Variable

684

685

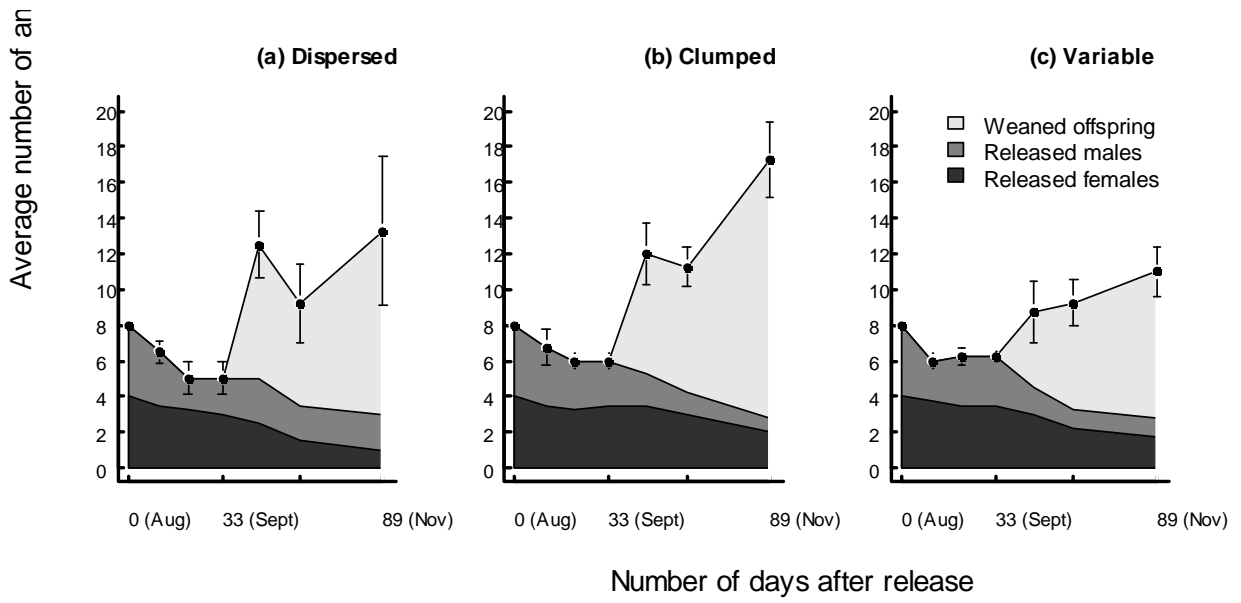
686 **Figure 2**



687

688

689 **Figure 3**



690