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

2 **small rodent**

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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

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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, while the opposite pattern occurs in males (Trivers 1972). Thus, spatio-temporal 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 intra-sexual 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 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

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, while 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 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.

MATERIALS AND METHODS

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

6

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 ± 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 (Grahnab, 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

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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; 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 ± 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 ± 42 m^2; females: 92 ± 9 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

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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 (± 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 × 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 ± 0.5 weaned

292   offspring per female to 2.9 ± 0.4. In clumped and variable plots, the number of weaned offspring

293   per female increased through time (clumped treatment: from 3.6 ± 0.5 to 4.8 ± 0.6; variable

294   treatment: from 3.0 ± 0.3 to 4.9 ± 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 × 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 × 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 $= 1.41 ± 0.69$, $t_8 = 2.37$, $P = 0.045$), 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 x 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 $= 1.71 ± 0.59$, $t_8 = 2.89$, $P = 0.020$; others variables: $P > 0.080$). The directional

307   selection gradient on body mass for mating success was positive (mean ± 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 $= -0.49 ± 0.21$, $t_8 = -2.28$, P

310   $= 0.052$), but was not influenced by food treatment (treatment: $LR = 3.24$, $df = 2$, $P = 0.197$;

311   treatment x 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 ± SE $= 0.40 + 0.21$; time period: contrast "period 2" $= -0.50 ± 0.22$, $t_8 = -2.28$, $P = 0.052$;

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 × 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 ± 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 ± 0.04, $t_{45} = 1.12$, $P = 0.267$; contrast variable = -0.04 ±

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

15

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

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.

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FIGURE LEGENDS

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 one of the five pre-set sites (white squares) twice a week.

Figure 2. Average scores on the principal component axes ($\pm$ SE) for the "dispersed" (light grey squares), "clumped" (dark grey 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.

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.

TABLES AND TABLE LEGENDS

666   **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**

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 ± SE	df	Statistics	P
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	2	$LR = 6.15$	0.046
		Variable: -0.72 ± 0.34			
	Body mass	0.08 ± 0.05	1	$LR = 2.20$	0.138
	Period	Period2: -0.21 ± 0.22	1	$LR = 0.87$	0.350
	Food treatments × period	Dispersed:Period2: -0.10 ± 0.59	2	$LR = 0.26$	0.878
		Variable:Period2: 0.19 ± 0.56			
	Food treatments × body mass	Dispersed:Mass: 0.05 ± 0.12	2	$LR = 0.24$	0.885
		Variable:Mass: 0.06 ± 0.13			
	Individual identity	$\sigma^2 = 0.14$	1	$LR = 0.31$	0.580
	Plot identity	$\sigma^2 < .0001$	1	$LR < .001$	0.999
Scores on PC2	Intercept	-0.02 ± 0.12			
	Body mass	0.07 ± 0.05	1	$LR = 2.15$	0.143
	Period	Period2: 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	2	$LR = 0.16$	0.922
		Variable: -0.11 ± 0.32			
	Food treatments × period	Dispersed:Period2: -0.42 ± 0.58	2	$LR = 2.16$	0.340
		Variable:Period2: -0.80 ± 0.54			
	Food treatments × body mass	Dispersed:Mass: 0.06 ± 0.12	2	$LR = 2.79$	0.248
		Variable:Mass: -0.16 ± 0.13			
	Individual identity	$\sigma^2 = 0.14$	1	$LR = 0.43$	0.513
	Plot identity	$\sigma^2 < .0001$	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.

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32

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.

| Factors	Estimate ± SE	*df*	Statistics	*P*
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			
Individual identity	$\sigma^2 < .0001$	1	$LR < .0001$	0.999
Plot identity	$\sigma^2 < .0001$	1	$LR < .0001$	0.999

679 The interaction between the food treatment and the period could not be fitted in the model. $N =$
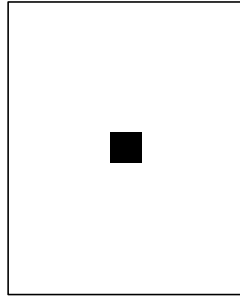
680 71.

681

682 **FIGURES**

683 **Figure 1**
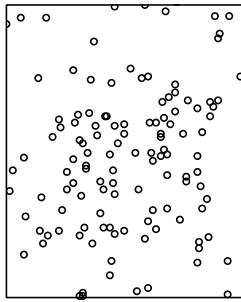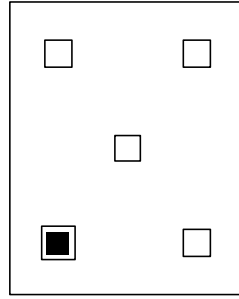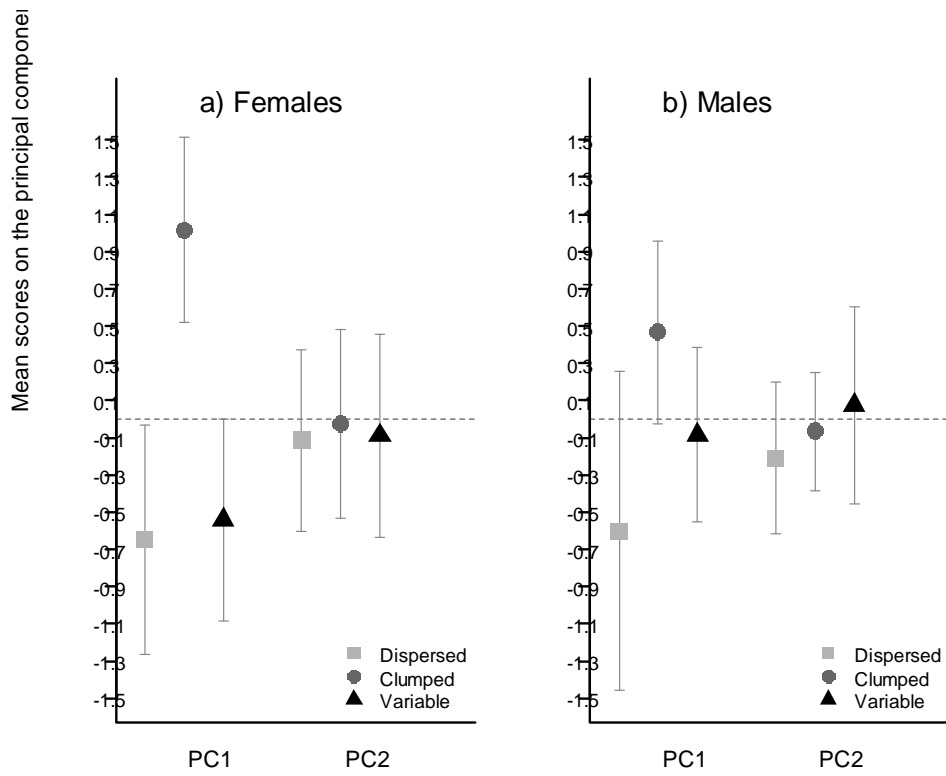

(a) Dispersed   (b) Clumped   (c) Variable

684

685

Figure 2

Figure 3

(a) Dispersed   (b) Clumped   (c) Variable

Number of days after release