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Research article

Effects of competition and season on survival and maturation of young bank vole females

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Abstract. In territorial microtines intra-specific density dependent processes can limit the maturation of individuals during the summer of their birth. This may have demographic consequences by affecting the number and the age distribution of breeding individuals in the population. Little is known about this process on a community level, though populations of many northern microtine species fluctuate in synchrony and are known to interfere socially with each other. We experimentally studied the influence of the field vole *Microtus agrestis* on maturation, breeding, space use and survival of weanling bank voles, *Clethrionomys glareolus*. Two additive competition experiments on bank vole populations were conducted in large outdoor enclosures, half of them additionally housing a field vole population. In a mid-summer experiment low population density and absence of older breeding females minimised intra-specific competition. Survival was not affected by the presence of field voles. Season had a significant effect on both the probability of maturation and breeding of the weanlings. Competition with field voles significantly delayed breeding, and coupled with seasonal effects decreased the probability of breeding. In a late-summer experiment breeding and survival of bank vole weanlings were studied for three weeks as part of a high density breeding bank vole population. Weanlings did not mature at all nor were their space use and survival affected by the presence of field voles. Our results show that competition with other species can also have an impact on breeding of immatures. In an extreme seasonal environment, even a short delay of breeding may decrease survival chances of offspring. Seasonal and competition effects together may thus limit the contribution of year born females to reproductive output of the population. Other studies have shown that adult breeding bank voles suffer lower survival in the presence of field voles, but this study showed no survival effects on the weanlings. Thus it might be beneficial for weanlings to stay immature especially in the end of the breeding season and postpone reproduction to the next breeding season if densities of competing species are high.

Key words: *Clethrionomys*, competition, maturation, *Microtus*, survival

Introduction

Population demography in many species is regulated by intra-specific density-dependent interactions but individuals of other species may also have an effect if actors utilise common resources like food or space (Connell, 1983; Schoener, 1983; Gurevitch *et al.*, 1992). In small mammals populations growth rate and habitat use can be influenced other species (Viitala, 1977; Hansson, 1983; Löfgren, 1995). However, the mechanisms through which inter-specific competition can influence the fitness of the individuals of competing species are poorly understood, and only few studies have investigated the individual fitness costs of inter-specific competition in small mammals (Gliwicz, 1981; Eccard and Ylönen, 2002a, b).

In territorial *Clethrionomys* voles, density-dependent intra-specific social interactions are a powerful tool for regulating the number of breeders through breeding suppression. Maturation and breeding of young females is limited by the numbers of adult females of the same species (Bujalska, 1985; Bondrup-Nielsen and Ims, 1986) but can also be limited by the numbers of females of other *Clethrionomys* species (Löfgren, 1995; Prevot-Julliard *et al.*, 1999). Since all breeding *Clethrionomys* females are territorial (Bujalska, 1985) limitations might be due to lack of available breeding territories. Females either breed in the summer of their birth or delay their first reproduction into the next breeding season (Tkadlec and Zejda, 1998; Prevot-Julliard *et al.*, 1999). Delayed breeding into the next season may be seen as an optimal decision (Mappes and Ylönen, 1997; Kaitala *et al.*, 1997) or a social constraint (Prevot-Julliard *et al.*, 1999; Eccard and Ylönen, 2001). The bimodal distribution of age at first reproduction leads to a bimodal age pattern of breeders in late breeding season when both overwintered and year born females can breed. Differences in the age distribution of breeders between years may partly be responsible for generating differences in population growth patterns and population fluctuations between years (Boonstra, 1994; Tkadlec and Zejda, 1998).

Clethrionomys in many northern habitats interact with voles of the genus *Microtus*. Experiments have shown competitive exclusion of *Clethrionomys* voles by *Microtus* voles (Grant, 1969, 1970; Iverson and Turner, 1972). In fragmented landscapes of Fennoscandia, the bank vole *Clethrionomys glareolus* and the field vole *Microtus agrestis* display considerable habitat overlap especially when densities of both species are high (Viitala, 1977; Henttonen and Hansson, 1984; Löfgren, 1995). Presence of field voles can reduce survival of breeding bank voles, especially of year born mature breeders (Eccard and Ylönen, 2002b), through direct interference (Eccard and Ylönen, 2002a). The effects of inter-specific interference competition on maturation, breeding and survival of weanlings (year born immatures, shortly after weaning) has not been studied before. If inter-specific competition would could influence survival of juveniles, or influence their breeding patterns of immature bank voles like intra-specific competition does, this could have consequences to the population demography and density fluctuations.

With this study we experimentally investigated the influence of the field vole *M. agrestis* on maturation, breeding and survival of weanling bank vole females *C. glareolus* in large outdoor enclosures. We generated inter-specific competition by adding and maintaining a stable, controlled field vole population in half of the enclosures. The experiments were carried out in the latter part of the breeding season, when the weanlings have two 'options' – to mature and breed during their birth year, or to postpone breeding until next summer. The progression of the season was taken into account in the analysis. Effects of field vole presence on the reproductive parameters, as well as survival of the young bank vole females were studied both under circumstances where intra-specific interactions with older, breeding females were excluded, as well as under more natural circumstances, as a part of a breeding population. A process like maturation can only be observed in the field through sudden, external changes (in females the opening of the vagina), therefore animals have to be followed very closely. We studied maturation in a short-term set up over 7–10 days with an intensive monitoring schedule of bank vole weanlings in low density. In a second experiment survival and space use of weanlings as a part of a breeding bank vole population were observed in over a 3-week period.

Material and methods

Study site

Experiments were carried out in eight 0.25 ha enclosures in a for over 20 years abandoned field with tall grasses and bushy thickets at Konnevesi Research Station, Central Finland (62°37′ N, 26°20′ E). The enclosures were fenced with 1.5-m high metal sheets dug into the ground and each enclosure was equipped with 25 trap locations in a 5 × 5 grid with 10 m distance. Each location held one multiple-capture Ugglan trap, sheltered by a metal chimney. One experiment was conducted in mid breeding season (early July–early August 2000), called mid-summer experiment later on, and the other experiment in late breeding season of a different year (late July to early September 1998) called late-summer experiment. Breeding season of bank voles in our latitudes extends from May into September (Kaikusalo, 1972).

Both experiments were designed as additive competition experiments. In this classical set up, responses of populations of species A without competitors are compared with similar populations of species A in the presence of a second species. The total densities in the presence of the second species are thus higher. The design is useful to detect the occurrence of competition or to rule out any effects of competition. If an effect is detected, its interpretation is however open to a second explanation, that the same effect would have been observed in high densities of species A on its own ('Type 1 experiment, Occurrence of inter-specific competition' – Connell, 1983; 'additive experiment' – Begon *et al.*, 1996). We decided to use this design in order to test, whether the life history variables in question (age at maturity, age at first reproduction, survival as immature) are affected by competition.

An alternative experimental design would use constant a constant density and change the proportion of species A to species B ('reciprocal design, replacement series' – Connell, 1983; 'substitutive experiment' – Begon *et al.*, 1996) to be able to distinguish the relative strength of inter-specific versus intra-specific competition. The design however is difficult to adopt for vertebrates with highly complex social structures. Different densities (individuals, biomass, breeders) may be chosen to be keep constant, depending on the life history trait and the functional cohort investigated. The design furthermore has the disadvantage, that if no significant differences are found in the response to mixed versus single-species treatments at the same total density, it is impossible to decide whether any competition occurs at all (Connell, 1983).

Mid-summer experiment with low density of weanlings

The weanling bank vole females, used as the experimental animals, were bred in captivity and were separated from their mother at the age of 18–20 days. The weanlings were ear-tagged and released to enclosures at the age of 19–25 days (in average 22 days) weighing 10–15 g (average 12.4 g). All females were checked for sexual maturity and only immature animals (closed vagina) were selected for the experiment. Sisters from the same litter were always assigned to different enclosures. Average age and average weight per enclosure were equally distributed between one-species and two-species enclosures and over the season (ANCOVA: age: $F_{\text{factor comp } 1,17} = 0.1$, $p = 0.786$; $F_{\text{covariate date of replicate } 1,17} = 0.6$, $P = 0.433$; weight: $F_{\text{factor comp } 1,17} = 0.8$, $P = 0.392$; $F_{\text{covariate date of replicate } 1,17} = 0.1$, $P = 0.797$).

Each experimental population consisted of four weanling bank vole females and two adult, fertile bank vole males. Half of the populations were confronted with a field vole population of 11–14 adult field voles, half males half females. During the experiment field vole numbers were monitored and kept constant by adding new animals from the laboratory and removing pregnant females. The experimental set up is explained in Table 1.

Growth, maturation, breeding and survival of bank vole weanlings were monitored daily after 2–3 days of habituation to the field. We tried to limit the mobility of animals as little as possible. During a 48-h period, traps were set in the afternoon, controlled in the evening, and controlled and opened in the morning of the next day (16-h set traps). Traps were then open (not set) during the rest of the day and the following night (32-h open traps) until set again in

Table 1. Experimental set up of the two experiments on the effects of inter-specific competition on fitness variables of juvenile bank vole females (numbers per 0.25 hectare enclosures)

	Maturation experiment			Survival experiment
Season and year	July 2000			July–September 1998
Duration (days)				
Field	10 (7)			20
Laboratory	25			25
Enclosures				
One-species	9			6
Two-species	11			6
	No. of replicates	No. of enclosures	Starting date (duration in days)	First replicate 28 July–13 August, Second replicate 18 August–3 September
	1	4	4/7 (10)	
	2	2	7/7 (10)	
	3	2	10/7 (10)	
	4	3	13/7 (10)	
	5	1	15/7 (10)	
	6	2	19/7 (10)	
	7	2	21/7 (10)	
	8	4	25/7 (10)	
Number of bank voles in each enclosure				
Weanlings	4			6
Adult females	–			5
Nestling litters	–			2–3
Adult males	2			3
Age of weanlings (days)	19–25, immature			25–35
Number of field voles	11–14			5–12
Vole individuals/hectare at start of experiment (excluding nestling litters)	24 Bank voles + 44–56 field voles			44 Bank voles + 20–48 field voles
Trapping	Daily			3 Days, 10 times at end of experiment
Variables investigated	Growth, maturation, breeding, survival			Space use, breeding survival

the afternoon. Intervals between ‘days’ thus vary between 12 and 36 h, which limits the accuracy of daily observations to ±1.5 days. Animals were weighed with an electrical scale to the nearest 0.01 g. For each weanling, we recorded daily weight development, survival, the date of maturation in the enclosures, and date of parturition and litter size in the laboratory. The median date between the last capture with closed vagina and the first capture with open vagina was used as the maturation date.

After 10 days the weanlings were removed from the field and kept singly in laboratory cages until parturition. A new group of weanlings and males were then released to the enclosures. Replicates were started in groups of 1–4 enclosures at a time (Table 1), depending on the availability of weanlings. The first sixteen enclosures, in replicates 1–7, were run for 10 days, but the last four enclosures in replicate 8 had to be finished after 7 days for logistic reasons. The starting dates, and the number of enclosures for all eight replicates are given in Table 1. In each replicate there were both one-species and two-species enclosures, except for replicate 5 that consisted of only one enclosure.

Continuous data (days until maturation, days until breeding, weight development, litter sizes) were averaged for each enclosure. Replicate 8 was left out of this analysis, since there was little maturation and no breeding. Enclosures were compared with an ANCOVA model using competition treatment (single-species enclosures, two-species enclosures) as factor and the starting date of the replicate as a covariate. Interactions were never significant ($P > 0.1$) and all models were re-run without interaction.

When comparing the proportion of weanlings surviving, maturing or breeding in each replicate, we used events occurring until the 7th day of the replicate in all cases in order to be able to include the last four populations in replicate 8 in the analysis. We have also tested proportions over 10 days leaving out the last replicate and report them if they were different. Proportional data was derived from binary data obtained from individuals (alive or dead, mature or immature, breeding or not breeding) and their variation was investigated with a binary logistic regression model. We used the stepwise backward regression procedure in SPSS (2001, Release 10.1.3). The log-likelihood χ^2-statistic provided a measure index of goodness-of-fit of the model and served to determine, whether the removal of a parameter significantly changed the model. At the first step, a constant and the following covariates were included in the model: competition treatment (categorial, single-species enclosure vs. two-species enclosure), experimental replicate (starting date, continuous), and their two-way interactions. Covariates were removed from the model if their removal did not change the model significantly.

Late-summer experiment in high-density, age-structured populations of bank voles

The late-summer experiment consisted of two subsequent replicates, each lasting for three weeks. The experimental animals were weanling bank vole females that were 25–35 days of age and had been raised by their mothers in outdoor enclosures. Maturation status of weanlings was not considered, since we did not monitor their development in detail during the trial. In this experiment the weanlings were part of age structured populations consisting also of five adult, unrelated, reproductive females, two or three of which nursing a litter, and three adult males. Half of the populations were confronted with a population of 5–12 adult field voles.

The adult females were released to the enclosures first and were given 3 days to habituate to the enclosures, find nesting sites for their litters and establish territories before the weanlings, males and field voles were introduced to the enclosures simultaneously. Adult females were breeding during both runs of the trial (Eccard and Ylönen, 2002a). Live trapping was started 2 weeks after the weanlings had been released to the enclosures and it consisted of ten trappings carried out during three days. After the live trapping all voles were removed from the enclosures.

Survival, breeding and space use data of the weanlings were averaged for each enclosure, and the enclosures were then compared using analysis of covariance with the competition treatment (one-species enclosure, two-species enclosure) and the experimental run (first run, second run) as factors. Factor interactions were removed from the model if not significant ($P > 0.1$), and the model was re-run without factor interaction. Trapping data were processed using RANGES V software (Kenward and Hodder, 1997) and home range sizes (100% convex polygons) and the home range overlap with other juveniles and adult bank vole females were calculated.

Results

Mid-summer experiment

In the mid-summer experiment the proportion of bank vole weanlings surviving the experiment (first 7 days) was 96 ± 5% (mean ± standard devia-

Table 2. Binary logistic regression models of survival, maturation and breeding of weanling bank vole females during a 7-day enclosure experiment on competition with field voles during progressing breeding season. Covariates: competition treatment (single-species or two-species enclosure), starting date of replicate (continuous), and their interaction were entered to the model at step 1 and removed from the model in a backward stepwise regression procedure if their removal did not change the model ($P < 0.1$). The change of log likelihood $\Delta(-2LL)$ of the model follows the χ^2-statistics

Dependent	Model includes a constant			Model if term removed		
	Females	Model-2LL	Covariates in the model	Δ(−2LL) if covariate removed	df	*P*
Survival	80	22.3	Date of replicate	2.3	1	0.070
Maturation	72	61.4	Date of replicate	12.2	1	< 0.001
Pregnancy	74	84.9	Date of replicate	5.5	1	0.019
			Competition × Date repl.	4.5	1	0.033

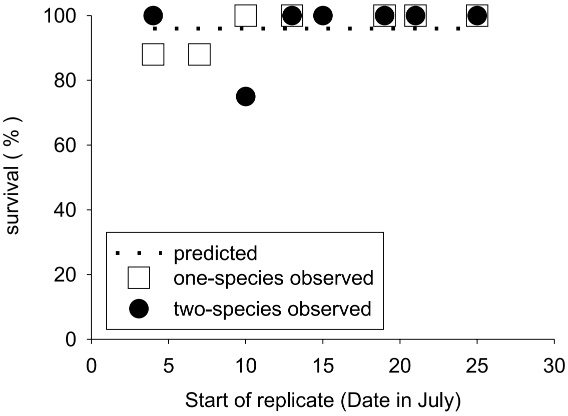

Figure 1. Proportion of females alive after 7 days was not explained by competition treatment (□: one-species enclosures, ●: two-species enclosures) or the date of starting a replicate. Binary logistic regression lines (predicted values) superimposed on experimental data (observed values).

tion, $n = 8$ replicates). Survival was not explained by any of the covariates: competition treatment (one-species vs. two-species enclosures) was removed from the binary regression model and the effect of the starting date of the replicate was not significant (logistic regression, $\Delta(-2\text{LL}) = 3.3$, $P = 0.070$; Table 2). Daily weight gain of weanlings, averaged over the enclosure, was 0.43 ± 0.18 g, and did not differ between treatments or with season (ANCOVA: $F_{\text{comp } 1,17} = 0.0$, $P = 0.908$; $F_{\text{date of replicate } 1,17} = 0.1$, $P = 0.808$).

Most of the weanlings had matured (94% ± 8%) during the first week of the experiment in all earlier replicates (1–7), while in the last, eighth replicate, the proportion of mature weanlings had dropped to 40% (Fig. 1). The proportion of mature weanlings was significantly explained by the starting date of the replicate (logistic regression: $\Delta(-2\text{LL}) = 12.2$, $P < 0.001$; Table 2, Fig. 1), but not by the competition treatment. Mean maturation date of individual weanlings was 3.9 days (range 2–10 days) after the start of the experiment.

The probability of breeding was explained significantly by an interaction of competition treatment and the starting date of the replicate (logistic regression: $\Delta(-2\text{LL}) = 4.5$, $P = 0.033$) as well as the date of replicate in itself (logistic regression: $\Delta(-2\text{LL}) = 5.5$, $P < 0.001$; Table 2, Fig. 3). Proportion of breeding weanlings was lower in later replicates in both competition treatments but was generally lower in the two species enclosures (27 ± 26%) than in one-species enclosures (55 ± 30%). While there were no differences in breeding proportion in the early half of July between the competition treatments, breeding had ceased in most of the two-species replicates during the latter half of July, and also in the last of the one-species replicates (Fig. 3). When comparing the total 10 days of the first seven replicates, there was no difference in the proportion of breeders between competition treatments (85% in one species enclosures and 83% in two-species enclosures) nor did the starting date have any effect. The effects of competition on weanling breeding, however, persisted since weanlings from two species enclosures gave birth 3.5 days later than weanlings from one-species enclosures (ANCOVA: $F_{\text{comp } 1,12} = 11.7$, $P = 0.005$; $F_{\text{date of replicate } 1,12} = 2.0$, $P = 0.180$).

Litter size of litters conceived during the experiment (mean 5.6, range 3–7 pups) was not affected by the competition treatment nor the starting date of replicate (ANCOVA: $F_{\text{comp } 1,12} = 0.3$, $P = 0.519$; $F_{\text{date of replicate } 1,12} = 0.5$, $P = 0.578$).

Late-summer experiment

In the late-summer experiment survival was also high (87 ± 18%, $n = 12$ enclosures). Survival did not differ between competition treatments, nor between the first and the second replicate ($F_{\text{comp } 1,9} = 0.1$, $P = 0.810$; $F_{\text{replicate } 1,9} = 0.3$, $P = 0.610$; Fig. 4). Weanling females did not reproduce: Only one weanling female was breeding during the first replicate in a one-species enclosure.

Spatial behaviour of the weanlings did not differ between replicates or treatments (Fig. 5). Home range sizes of weanlings were on average 730 ± 260 m^2 (Two-way ANOVA: $F_{\text{comp } 1,9} = 1.2$; $P = 0.297$; $F_{\text{replicate } 1,9} = 0.8$, $P = 0.402$) and similar to that of adult females (760 ± 140 m^2). Trappability of weanlings was on average 5.3 out of 10 times (Two-way ANOVA: $F_{\text{comp } 1,9} = 0.5$; $P = 0.250$; $F_{\text{replicate } 1,9} = 2.9$, $P = 0.122$). Weanlings were captured in half of the available 25 trap stations of an enclosure (mean 12.4, range 9–24 stations, Two-way ANOVA: $F_{\text{comp } 1,9} = 0.0$, $P = 0.935$; $F_{\text{replicate } 1,9} = 2.3$, $P = 0.158$. The number of weanling home ranges overlapping with home ranges of other bank voles was independent of the survival and the total numbers of bank voles at the end of the experiment (Pearson's correlation: $\rho = 0.43$, $P = 0.156$, $n = 12$).

Discussion

Survival of weanlings was not influenced by in the presence of field voles (Figs. 1 and 4). Proportions of matured and breeding bank vole weanlings were rapidly declined with the progression of the breeding season (Figs. 2 and 3). Weanlings did not mature and breed in August in the late breeding season experiment, even though adult breeding females continued to breed into September. This may have been caused either by late season or the high densities of breeding bank voles. The presence of individuals of a competing species, the field vole, seemed to facilitate the decline of the proportions breeding towards the end mid breeding season (Fig. 3) by delaying breeding shortly but signifi-

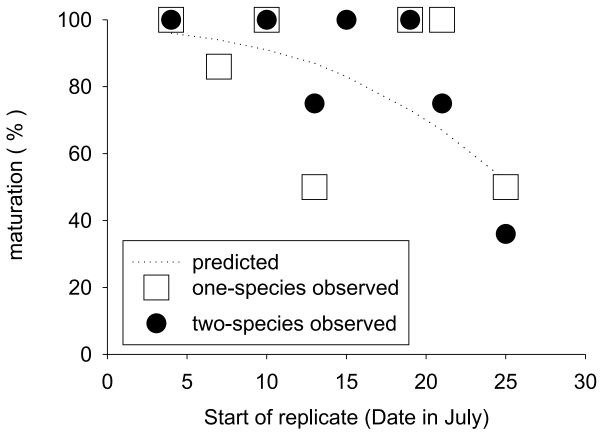

Figure 2. Proportion of matured females over 7 days was explained by the start of the replicate, but not by competition treatment (□: one-species enclosures, ●: two-species enclosures). Proportion of matured females fell sharply in the end of July. Binary logistic regression line (predicted values) superimposed on experimental data (observed values).

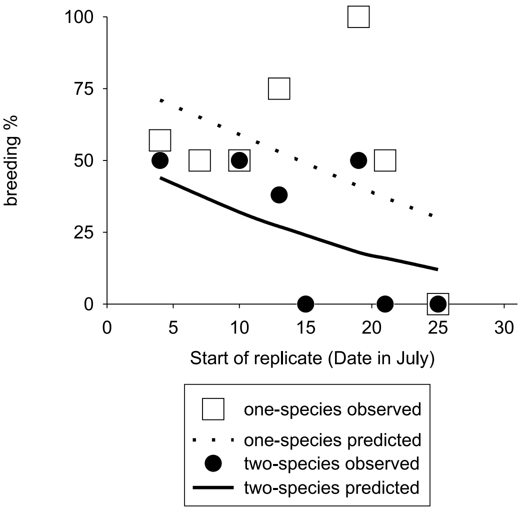

Figure 3. Binary logistic regression lines (predicted values) superimposed on experimental data (observed values). Proportion of bank vole weanlings breeding during seven days of the experiment was explained significantly by the start of the experimental replicate, the competition treatment: one-species enclosures (□) vs. two-species enclosures (●), and their interaction. While proportion of breeders generally dropped with progressing season, weanlings in two-species did not start to breed in many runs of the second half of July, while weanlings in the one-species enclosures still were breeding.

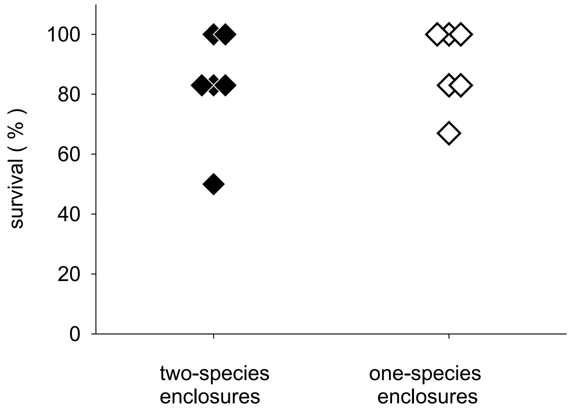

Figure 4. Survival of weanlings did not differ between one-species and two-species enclosures: one-species enclosures (◇) vs. two-species enclosures (◆), values refer to survival percentage per enclosure.

cantly. In the last replicate of the mid summer experiment in late July weanlings did not breed at all, even if there were no field voles or other breeding bank voles that could inhibit maturation of weanlings.

Effects of competition on weanling survival

Breeding bank vole females have lower survival in the presence of field voles (Hansson, 1983; Eccard and Ylönen, 2002a, b). Both our experiments give no evidence that there would be a decrease also in weanlings' survival through interference with field voles (Figs. 1 and 4). Mortality differs for functional groups within a population depending on their spatial and foraging behaviour (Gilbert *et al*., 1986; Bujalska and Grüm, 1989). We suppose, that it is the territorial behaviour of breeding bank vole females that increases their aggressive contact rates with conspecifics and heterospecifics and thus their mortality. Immature bank voles have less metabolic needs than breeding females and need to be less active for foraging. They also do not defend territories or nest sites. The aggressive contact rates weanlings encounter are therefore very low and this might decrease their overall mortality. In the earlier runs of the low-density experiment, many weanlings had started to breed, thus entering the breeding cohort prone to suffer from interference with both conspecifics and field voles. Since the change from immature to mature breeders took place sometime during the short experiment, the time weanlings in breeding condition remained with the field vole must have been very short (few days) and we were not able to measure possible increased mortality. In the high-density experiment, weanlings coexisted with the field vole population for a time period long enough to measure mortality through field voles (Eccard and Ylönen, 2002a, b). However we did not measure increased weanling mortality (Fig. 4) maybe because weanlings did not enter breeding condition and did not undergo behavioural changes associated with breeding that would put them at higher mortality risk.

Effects of competition on reproduction

Maturation and breeding of year born females in bank voles is regulated through density-dependent social interactions with adult conspecific females or territorial females of the same genus (Bujalska, 1985; Bondrup-Nielsen and Ims, 1986). Our study is the first to investigate if competitors from other genera might have similar effects on maturation and breeding of juvenile bank voles. Field voles most probably compete with bank voles on the basis of direct interference competition (Eccard and Ylönen, 2002a, b) but they are not exclusively territorial towards bank voles (Löfgren, 1995; Halle *et al.*, 1999).

Towards the end of weanling bank voles' breeding season we were measuring a negative effect of the presence of field voles on breeding of juvenile bank voles, suggesting combined effects of inter-specific competition and seasonality on breeding of juvenile bank voles (Fig. 3). We found no effects of field voles during early July, at the height of breeding season, and also not in late July when weanlings did not mature and breed any more. In the experimental replicates between however, breeding of juvenile bank voles was delayed only in the presence of field voles. The observed effect is however open to the explanation, that it could have been caused also by an increase of bank vole weanling density alone. Many studies show that breeding of young bank voles is delayed into the next season in high bank vole densities (Bujalska, 1985; Tkadlec and Zejda, 1998; Prevot-Julliard *et al.*, 1999) but in high densities the available breeding territories are occupied by adult bank vole breeders. It is not known however, if high densities of only bank vole weanlings by themselves could cause a similar short-term delay as observed in our study. The spatial data from the survival experiment meanwhile shows, that spatial behaviour of weanlings was not altered in the presence of field voles (Fig. 5). Thus there is no indication of an increased interaction of weanlings with each other, and we argue, that the observed effects are caused by weanlings interaction with field voles.

The observed delay is not comparable to a intra-specific density-dependent delay of breeding into the next season (Tkadlec and Zejda, 1999; Prevot-Julliard, 1999) since after 10 days the proportion of breeders were similar in both competition and control enclosures. Although the measured delay of breeding was rather short – only a few days, it must be considered in the context of an extreme seasonal environment. Unfavourable weather conditions in autumns can decrease offsprings survival chances and thus negatively affect population growth patterns.

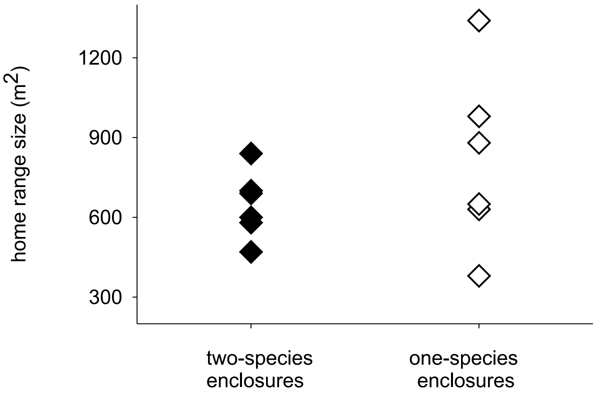

Figure 5. Home range size of immature weanling females in late summer experiment did not differ between competition treatments: one-species enclosures (◇) vs. two-species enclosures (♦), values refer to enclosure averages

Inter-specific competition between bank voles and field voles is probably not through indirect resource competition for food resources, since weanlings' growth, survival, litter size and space use (Fig. 4) were not affected by the presence of field voles. These measures can respond to food addition (Cole and Batzli, 1978; Ostfeld, 1985; Boutin, 1990) and could have therefore responded if food resources were in short supply due to the presence of field voles.

Conclusions

Demographic processes like the age structure of the breeding individuals of the population may play a crucial role in explaining density fluctuations in microtines (Boonstra, 1994; Stenseth *et al.*, 1996). We have shown in this experiment, that breeding of immature weanlings was shortly delayed in the presence of field voles. We know from previous experiments, that inter-specific competition can lower the survival of young breeders, but this study showed no reduced survival of weanlings. It might thus be beneficial for weanlings to stay immature in the end of the breeding season and postpone reproduction to the next breeding season if densities of competing species are high. Thus inter-specific competition may serve as an additional factor explaining density fluctuations in microtines at a community level.

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