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Intra- and interspecific density dependence in the survival and recruitment of grey-sided (*Clethrinomys rufocanus*) and bank voles (*C. glareolus*)

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Habitat use patterns by sympatric bank (*Clethrionomys glareolus*) and grey-sided (*Clethrionomys rufocanus*) voles indicate interspecific competition between the two species, with grey-sided voles being the superior competitor. Data from a four-year study of two populations of bank and grey-sided voles were analysed with capture-recapture models to investigate the effects of competition on winter and summer demographic parameters. In summer survival of bank voles was positively correlated with bank vole density, whereas recruitment was negatively correlated to bank vole density. No evidence was found for intraspecific density-dependence in the demographic parameters of grey-sided voles, although there was a tendency towards a negative intraspecific effect on winter survival. There were no detected effects of interspecific competition on the demography of either vole species.

Introduction

Mathematical modelling has shown that interspecific competition, together with mustelid predation, can be important in shaping microtine population dynamics (Hanski & Henttonen 1996). However, very few empirical studies (but *see* Prévot-Julliard *et al*. 1999) have explored the effect of interspecific competition on microtine demographic parameters, such as survival and recruitment.

Here I present results from a four-year capture-recapture study on the demography of two *microtine* species, *C. glareolus* and *C. rufocanus* in a Norwegian subalpine forest habitat. Of the two species, the larger grey-sided vole is believed to be dominant, and studies have shown that grey-sided voles exclude bank voles from certain habitat types (Løfgren 1995a,b), limit maturation of juvenile bank voles (Løfgren 1995b), and behave dominantly in dyadic behavioural tests (Johannesen *et al*. 2002, *see* McPhee 1984 and Viitala 1984 for other two species *Clethrionomys* studies). These studies on interspecific relationships have been undertaken during the summer. As habitat segregation between the two species can change seasonally (Johannesen & Mauritzen 1998), the importance of interspecific competition (Rosenzweig 1981, Hanski 1995) might differ between seasons. This possibility is highlighted by the increasing attention recently devoted towards seasonality in vole population dynamics (e.g. Stenseth *et al.* 1998, Hansen *et al.* 1999a, 1999b, Yoccoz *et al.* 2001).

Summer and winter demography is influenced by different biological processes. Survival is the most important demographic parameter during winter, since winter breeding in *Clethrionomys* is uncommon (Bujalska 1995). Little is known of the exact causes of mortality of microtines during winter, but there is evidence of the importance of acquiring an overwintering location with favourable microclimatic conditions (Karlsson 1988, Sharpe & Millar 1991, Hambäck *et al.* 1998). There might be both intra- and interspecific competition for this resource. Nonetheless, there are potential benefits of aggregation for conspecifics as subadult bank voles have been found to overwinter in groups (Karlsson 1988), most likely to help with thermoregulation. In summer, the mechanisms governing population growth rate are more complex. The most important proximate cause of summer microtine mortality has been found to be predation (Steen *et al.* 1997, Steen 1995, Wilson *et al.* 1999). Predation probability is likely to vary between habitat types, setting the stage for interspecific competition. In addition, since breeding females of both species require territories that are both intra- and interspecific exclusive (Løfgren 1995), it is likely that competition for this resource will be very important during the summer.

Here, the importance of intraspecific and interspecific density on summer and winter demography of grey-sided and bank voles is evaluated by analysing variation in demographic parameters over a four-year period in two sympatric populations. Based on previous observations (Løfgren 1995a, 1995b, Johannesen & Mauritzen 1998, Johannesen *et al.* 2002) I predicted that grey-sided voles would have a stronger negative impact on the demographic parameters of bank voles than *vice versa*. I also predicted that the interspecific effects would be strongest during winter since, within the study area, the two species select more similar habitat types towards autumn than in the peak of the breeding season (Johannesen & Mauritzen 1998).

Material and methods

Area description

The study area was situated in Arabygdi, Telemark county, in southern Norway, 59°44´N, 7°43´E about 700 m a.s.l. In this area, the first snow fall is usually in early October, and the snow cover disappears in May. Trapping was conducted on two plots 1 km apart on the steep north-facing and south-facing slopes of a narrow valley. The 1.89 ha north-facing plot had 84 Ugglan multiple-capture live-traps and the 3.51 ha south-facing plot had 156 traps. The traps were placed 15 m apart in both plots. To reduce plot edge effects due to only partially re-trappable animals on the borders of the plots, the trapping grids were located so that they bordered unsuitable habitat for *Clethrionomys*. The north-facing plot was bounded by a bog and a small creek, whereas a road and a big boulder field with no vegetation delimited the south-facing plot (trapping was conducted 45 m into the barren boulder field the first trapping sessions, but no voles were trapped there).

Trapping

The trapping grids were established in early summer 1995 (a post peak year for cyclic small mammals in south-central Norway, Framstad *et al.* 1997) and trapping was conducted until snowfall. The traps were left out over winter and trapping was continued in the summers of 1996, 1997 and 1998, and in the spring of 1999. The live-trapping protocol followed the robust design of Pollock *et al.* (1990). During summer, primary trapping sessions were spaced two to three weeks apart (*see* Table 1 for trapping dates). Each primary trapping session consisted of three secondary trapping sessions where the traps were set in the evening and checked the following morning. All caught animals were individually marked with toe cutting, weighed with a pesola spring scale, sexed, and their sexual condition recorded. The traps were baited with oats, carrots and apples.

Analyses

Estimation of population density

Population density of the two species was estimated in both plots for all primary trapping sessions using closed capture-recapture models using the program CAPTURE (Rexstad & Burnham 1991). The model assumed a constant capture rate for all three secondary capture sessions associated with each primary session. This model was selected as the best model for most of the primary trapping sessions according to the model selection criteria of the CAPTURE package.

Estimation of survival and recruitment probabilities

The summer period was taken as the period from the first primary capture session in the spring, until the last primary capture session in the autumn (Table 1). Since trapping started comparably earlier in 1997 and 1998 (i.e. the May primary trapping session, Table 1), the three weeks from the first to the second primary trapping sessions in these years were included in the winter period. The demographic parameters in both winter and summer were scaled into 4-week rates.

Survival probability and recruitment probability were modelled using open capture-recapture models (e.g. Lebreton *et al*. 1992) implemented by the software MARK (White & Burnham 1999). Capture histories, including all primary capture session for all years and pooling secondary sessions within each primary session, were used. The two species were treated separately. The nuisance parameter in these models, (i.e. recapture probability), was modelled most parsimoniously by letting the recapture probability differ between 1995 and the other years and with an additive effect of plot (bank vole recapture probability north-facing plot, 1995: 0.68 ± 0.06, 1996–1999: 0.87 ± 0.02, south-facing plot, 1995: 0.79 ± 0.03, 1996–1999: 0.92 ± 0.01, grey-sided vole recapture probability north-facing plot, 1995: 0.79 ± 0.04, 1996–1999: 0.87 ± 0.03, south-facing plot, 1995: 0.90 ± 0.03, 1996–1999: 0.94 ± 0.02).

Recruitment was estimated with the method developed by Pradel (1996) by reading the capture histories backwards. The probability of surviving between two primary trapping sessions then becomes equivalent to the probability of being already present in the population between two primary trapping sessions. This probability has been termed ‘seniority probability’ and the probability that an animal was recruited into the population between two trapping sessions is equal to 1-seniority probability (*see* Pradel 1996).

Table 1. Trapping dates. In 1997 and 1998 the interval between the first and second trapping sessions were included in the winter period. In 1997, only the south-facing plot was trapped in May, because of a 1 m snow cover on the north-facing plot.

Trapping dates	1995	1996	1997	1998	1999
May			17–19	23–25	
June			7–9	13–15	5–7
		25–27	28–30		
July	8–10	16–18	19–21	4–6	
	24–26			25–27	
Aug.	7–9	6–8	9–11	15–17	
	21–23	27–29*	30–1 Sep.		
Sep.	4–6	17–19	20–22	6–8**	
	18–20			26–28	
Oct.	2–4	8–10	12–14		

* Only two trap checks in the north-facing plot. ** Only two trap checks both plots.

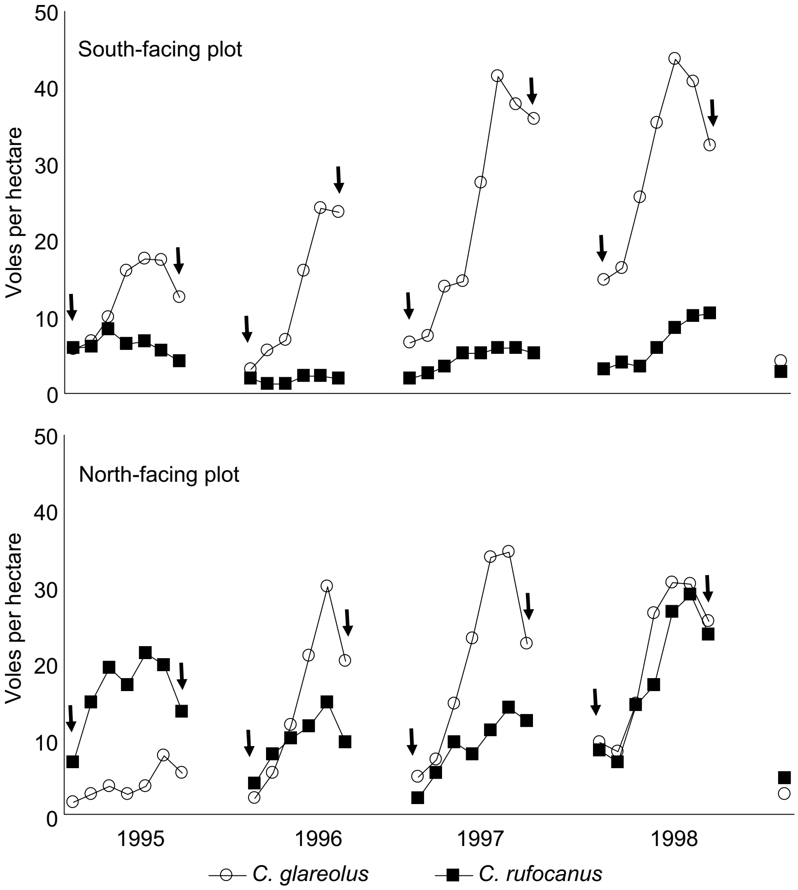

Fig. 1. Population dynamics during the four year study period. Spring and autumn densities used in the analysis are indicated by arrows.

Note that the apparent survival estimated here included both the effects of mortality and permanent emigration, whereas the recruitment parameter included both immigration and reproduction. Furthermore, the more detailed summer data allowed modelling and testing for trends (linear or quadratic) in demographic parameters using capture-recapture models, and these trends were accounted for before testing for density dependence.

Testing for density dependence

The demographic parameters (recruitment and survival for both species) in winter were modelled as dependent on the log transformed autumn densities the preceding autumn. The demographic parameters in summer were modelled as dependent on the log-transformed densities at the beginning of the summer. This is equivalent to testing for direct density dependence using summer and winter periods independently (*see* Hansen *et al.* 1999a, 1999b). The years and plots were treated as independent; hence the sample size for each test was eight (four years and two plots). The assumed independence between years was tested by using models with autocorrelation between the years and comparing them with models treating year as independent. No evidence for temporal autocorrelation was detected (results not shown).

The year and plot specific logit estimate of each parameter was tested for density dependence weighing the estimate with the inverse of the variance estimated from the capture-recapture models. The analysis was performed using S-plus (Venables & Ripley 1999). Three models for each parameter were used: (1) intraspecific density-dependence, (2) interspecific density dependence and (3) intra- and interspecific density dependence combined. Model averaged estimates with confidence intervals (Burnham & Anderson 1998) of density dependence were calculated by weighting the estimates from the difference models according to AIC_c ($AIC_c = -2\log$ Likelihood$/2k + 2k(k + 1)/(n - k - 1)$, where k is the number of parameters in the model). The model with the lowest AIC_c value represents the best compromise between complexity (many parameters, lack of precision) and simplicity (few parameters, bias) of the models used (Burnham & Anderson 1998).

Results

Population Characteristics

There were 3762 captures of 1033 individual bank voles, 480 grey-sided voles and 28 field voles (*Microtus agrestis*, only in 1998). The densities for the primary sessions of both species in the two plots are shown in Fig. 1. The bank voles dominated in the south-facing plot, whereas in the north-facing plot, the species were found in a more equal number (Fig. 1).

Survival probabilities

The average survival rate was higher in the winter than in the summer for both species (bank voles: 76.7% (CI: 74.2–78.7) survival per month in winter and 66.2% (CI: 63.7–68.9) in summer, grey-sided voles: 81.0% (CI: 77.7–83.9) and 57.2% (CI: 53.1–61.1).

Temporal variation in summer survival can be seen from Fig. 2, but the model with constant summer survival with each year and plot was to be preferred according to AIC_c for both species. No calendar date dependent trend for summer survival was detected. Accordingly, including season (quadratic or linear function) as a covariate for summer survival did not improve the fit of the model.

The only significant density-dependence found for survival was in bank vole summer survival (Table 2, Fig. 4). Survival in summers with high bank vole spring density was higher than in summers with low bank vole densities (Table 2, Figs. 1 and 2). There was an indication of a negative effect of grey-sided vole density on bank vole summer survival and indications of negative intraspecific density-dependence in winter survival of both species (Table 2).

Recruitment

The average recruitment probability was higher in summer than in winter when recruitment was attributed to immigration (monthly recruitment probability, bank voles: summer 49.3% (CI: 46.9–51.6), winter 10.8% (CI: 8.9–13.4), grey-sided voles: summer: 51.6% (CI: 47.8–55.3), winter: 9.1% (CI: 7.3–13.2)).

For summer recruitment (Fig. 3), the temporal variation could be adequately modelled as a quadratic function of date (difference in AIC_c between different models for temporal variation: bank voles full temporal variation 0 (best model), quadratic function: 1.76, linear function: 161.3, constant: 238.1, grey-sided voles: full temporal variation: 10.55, quadratic function: 0 (best), linear function: 11.69, constant: 59.32).

There was a significant negative effect of bank vole density on bank vole recruitment rate in the summer (Fig. 4), and a significant positive effect of bank vole density on immigration during the winter (Table 3). There seemed to be negligible effects of intraspecific density on the recruitment parameters of grey-sided voles. No evidence was found for interspecific effects.

When testing for the effect of intraspecific density on maturation rate in bank voles, a negative effect was found (logistic regression, $b = -3.76$, S.E. = 0.78. $p < 0.0001$, $n = 223$, using females first captured as immature and captured at least twice). Further, I did not find any effect of grey-sided vole density on maturation probability of young grey-sided vole females ($b = -0.79$, S.E. = 1.0, $p = 0.42$, $n = 68$).

Discussion

The most salient feature of my results was the lack of evidence for effects of interspecific competition on demographic parameters of the two potentially competing species. The lack of a negative effect of bank vole density on grey-

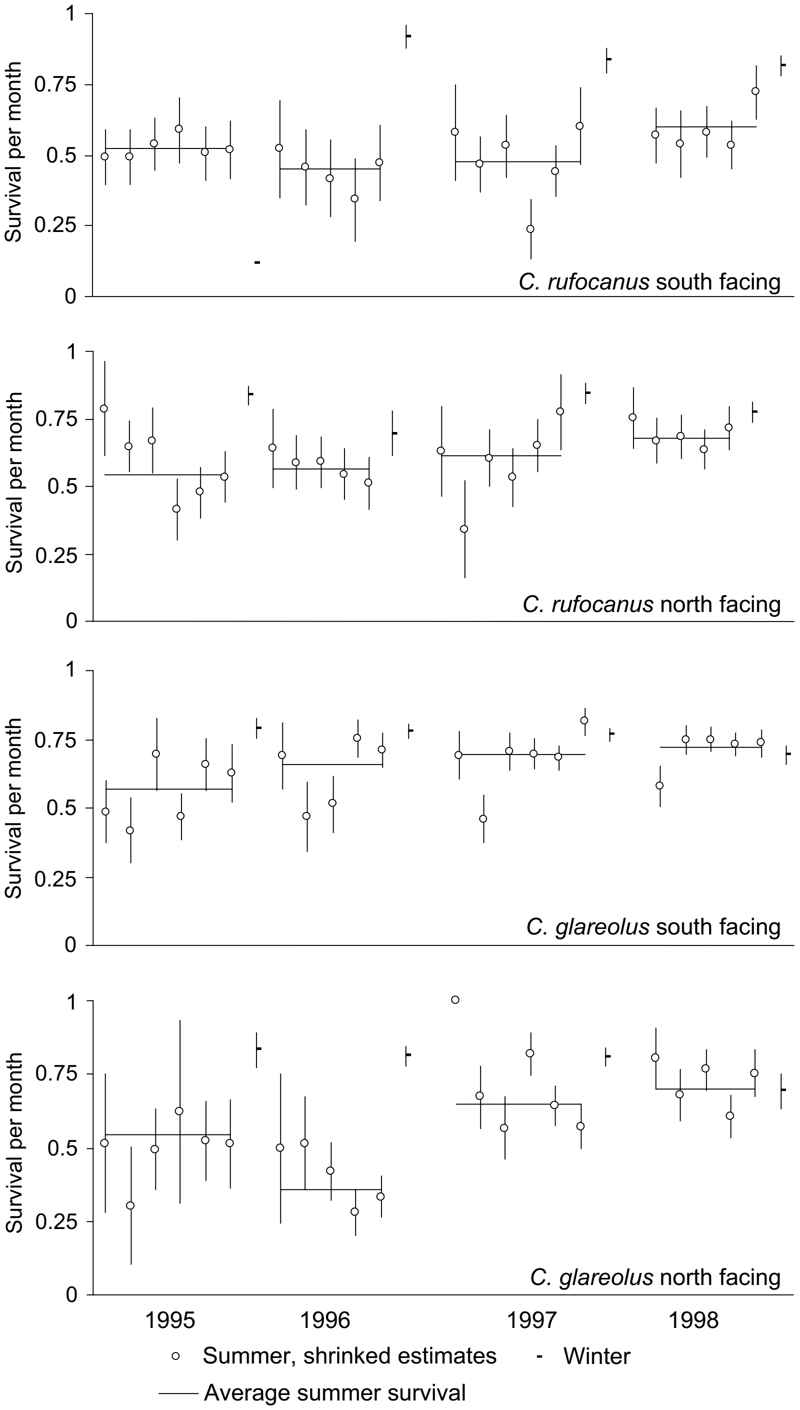

Fig. 2. Constant (solid line) and time varying survival estimates. Time varying summer survival probabilities (open squares) and standard errors (presented as bars) were derived using shrinkage, accounting for sampling variation (Burnham & Anderson 1998). There were no recaptures in 1996 of grey-sided voles marked in 1995 on the south-facing plot, hence the winter survival and its standard error could not be estimated for grey-sided voles the winter 1995–1996 on the south-facing plot.

sided vole demography was expected as grey-sided voles are considered to be dominant over bank voles (Henttonen & Hansson 1984). The lack of negative effect of grey-sided vole density on bank vole demography is surprising because Johannesen and Mauritzen (1998) found evidence of competition when studying the habitat selection of the two species in this research site. However, there was a non-significant effect of interspecific competition for summer survival of

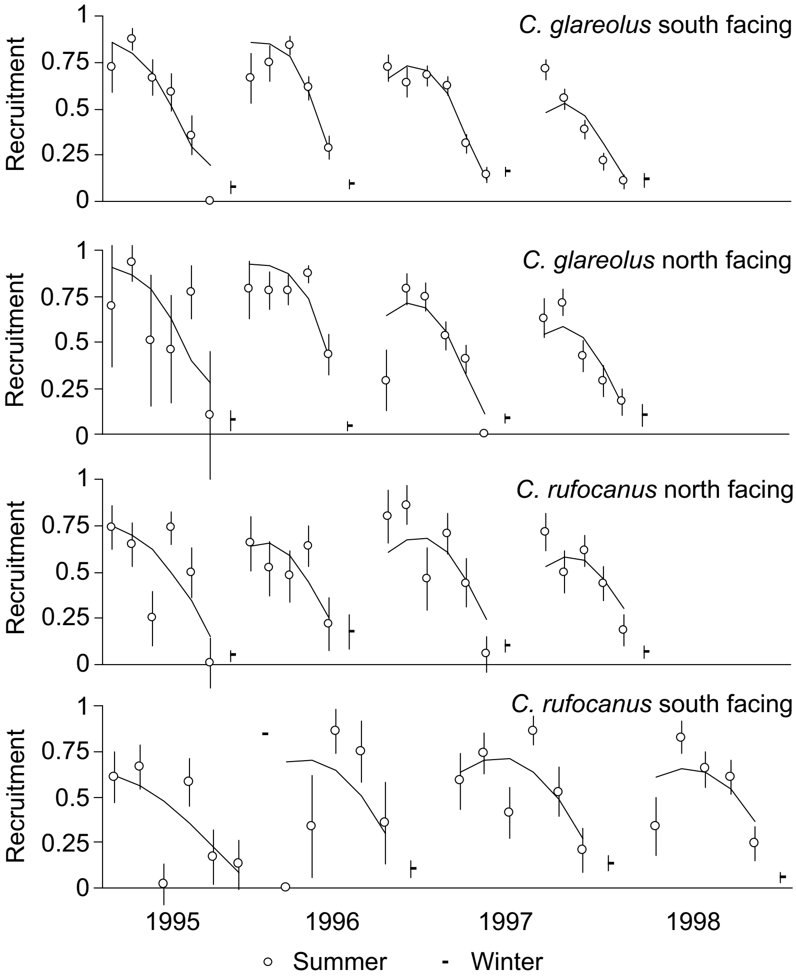

Fig. 3. Recruitment rate estimates presented as a quadratic function of date for summer (solid line) and full time varying recruitment estimates. Time varying survival estimates are presented with standard errors (bars). Winter recruitment and its standard error could not be estimated for grey-sided voles the winter 1995–1996 on the south-facing plot (no recaptures of old animals).

bank voles. The lack of significance here might partly be due to low bank vole densities when grey-sided vole densities were high in both plots in spring 1995 making the variance of bank vole demographic parameters large, and hence, any effects less likely to be detected.

No clear evidence of intraspecific density dependence was found in grey-sided vole demography. The precision of the parameters for grey-sided voles was low due to low popula-

Table 2. Model averaged estimates (with 95% confidence limits) of density dependence on survival for the null hypothesis of no relationship between demographic parameters and density.

	Summer		Winter	
	Estimate	*p*	Estimate	*p*
Bank voles				
Intra	0.500 (0.184 to 0.817)	0.002	–0.311 (–0.709 to 0.086)	0.12
Inter	–0.346 (–0.824 to 0.132)	0.16	–0.093 (–0.318 to 0.132)	0.42
Grey-sided voles				
Intra	0.249 (–0.186 to 0.684)	0.26	–0.315 (–0.664 to 0.033)	0.08
Inter	0.137 (–0.158 to 0.431)	0.36	–0.088 (–0.431 to 0.256)	0.62

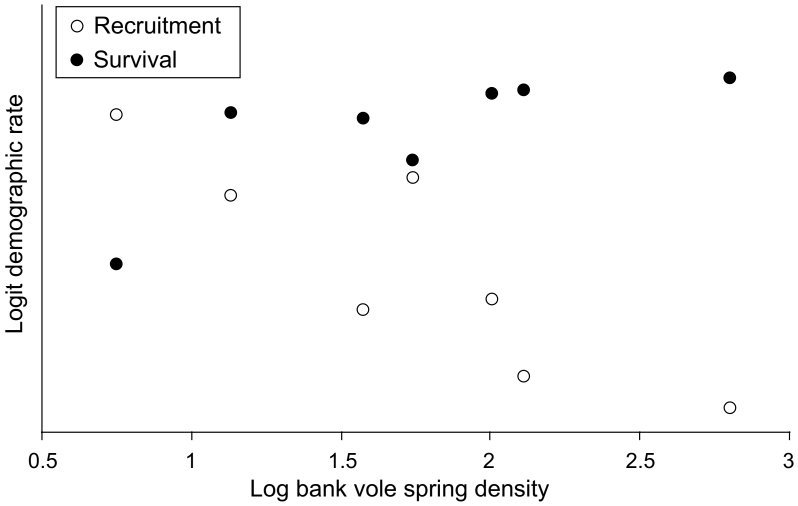

Fig. 4. Intra-specific density in summer demography of bank voles. Open circles represent recruitment, filled circles represent survival.

tion densities, especially in the south facing plot (Figs. 1–3). Nevertheless, albeit not significant, there was an indication of a negative effect of intraspecific density on winter survival, suggesting that competition for overwintering sites might be an important determinant of winter survival (*see also* Hambäck *et al.* 1998). This indication of negative density dependence in winter survival, but not for any of the summer parameters for grey-sided voles agrees with the results of Hansen *et al.* (1999b), who found stronger density dependence in population growth rate in winter than during summer for the grey-sided voles.

Intraspecific density and summer survival probabilities were positively correlated in bank voles. This could be an effect of intraspecific density on survival, e.g. by some positive factor leading to high spring density that continued into summer. Nonetheless, there was no indication of this and winter survival was negatively correlated with survival during the following summer ($r_s = -0.83$, $n = 7$, $p = 0.02$). Rather, it is more likely that this effect comes about due to reduced dispersal at high densities — a phenomenon known as 'social fence' (Hestbeck 1982, Aars *et al.* 1999) — and higher philopatry due to lower maturation of yearborns at high density. This was supported as mean squared distance moved between first and second primary trapping sessions was negatively affected by spring density (linear regression of log-transformed distance moved on log-transformed spring densities, $p = 0.035$).

The significant positive effect of autumn density on immigration of bank voles during winter is likely to be due to, possibly together with positive effects of thermoregualtion at high density, that more bank voles were present in springs after autumns with high densities and an interchange of

Table 3. Model averaged estimates (with 95% confidence limits) of density dependence of recruitment for the null hypothesis of no relationship between demographic parameters and density.

	Summer		Winter	
	Estimate	*p*	Estimate	*p*
Bank voles				
Intra	–1.105 (–1.551 to –0.659)	0.0001	0.804 (0.255 to 1.353)	0.04
Inter	0.196 (–0.499 to 0.891)	0.58	–0.046 (–0.465 to 0.372)	0.83
Grey-sided voles				
Intra	0.188 (–0.433 to 0.81)	0.55	0.217 (–0.145 to 0.58)	0.24
Inter	0.111 (–0.264 to 0.487)	0.56	0.306 (–0.257 to 0.869)	0.29

animals at the onset of reproduction (*see* Aars *et al*. 1999 for an example on root voles). This phenomenon might also explain the non-significant negative density dependence on winter survival of bank voles, i.e. a higher disappearance rate due to interchange of animals in springs.

Recruitment in summer was negatively affected by intraspecific density in bank voles. Intraspecific density dependence in maturation probability is well-established for *Clethrionomys* (Bondrup-Nilsen & Ims 1988, Prévot-Julliard *et al*. 1999). The negative density dependence in the maturation rate of bank voles (and the lack of density dependence in maturation rate of grey-sided voles, *see* results) are consistent with the results on recruitment rate and suggests that maturation rate determines recruitment rates in summer. The stronger negative intraspecific density dependence found for summer recruitment than for winter survival is consistent with the finding of Yoccoz *et al*. (2001). They found stronger density dependence during summer than during winter for population growth rate of bank voles.

In conclusion, no interspecific effects on vole demography could be detected in this study, although previous findings on habitat selection indicated competition. I found differences in density dependence in summer recruitment between the two species, with strong negative density dependence in summer recruitment for bank voles, but not for grey-sided voles. In winter, the two species had similar negative, albeit non-significant effect of density on survival. Further work is needed to shed light on the interplay between season, habitat use and demography.

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