

Density-dependent recruitment in grassland small mammals

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Summary

1. Density dependence has an important influence on the dynamics of many species of small mammals. To regulate population growth, density must affect negatively a vital rate (e.g. fecundity); however, little is known about which vital rates are most affected by density.
2. We used a long-term data set for five species of rodents from north-eastern Kansas, USA to test for relationships between density and the proportion of pregnant females, per capita fecundity and recruitment. We estimated proportion of pregnant females using data collected in the field and fecundity using data on survival, proportion of pregnant females and literature-based density-dependent litter size for each species. We used reverse capture histories to estimate per-capita recruitment.
3. The proportion of pregnant females was related positively to density in most species. Fecundity was related negatively to density in the cotton rat (*Sigmodon hispidus* Say & Ord, 1825) and not related to density in the four remaining species. Recruitment was related negatively to density in all five species, although not all relationships were statistically significant.
4. The signature of density-dependent recruitment was strongest in the prairie vole [*Microtus ochrogaster* (Wagner, 1842)] and cotton rat and less so in the remaining species.
5. Our analyses indicate that density affects recruitment negatively in grassland small mammals either through a reduction in immigration or reduced survival of nestlings. Models that seek to include empirical estimates of density dependence may need to include immigration in addition to survival and fecundity.

Key-words: immigration, *Peromyscus*, population regulation, *Reithrodontomys*.

Introduction

The abundance of a population can vary considerably over time, and the cause of change in the trajectory of population growth is a central focus of population ecology. Density dependence affects the population dynamics of many species (Sibly *et al.* 2005), whereas seasonal changes in vital rates (e.g. survival and fecundity) appear to exert great influence on other populations (Boonstra & Krebs 2006). The relative influence of density dependence in the dynamics of populations is a matter of considerable debate (Krebs 2002; Berryman 2004). Nevertheless, population growth rates are often related negatively to density, in that population abundance is likely to decline when high and increase when low (Turchin 1999). Further, in the absence of significant seasonality in vital rates, some factor, which often is related to density, will cause the population to decline from previous high levels.

Negative relationships between population density and population growth rate must be driven by negative feedback between population density and the vital rates that underlie the growth rate. A rich theory exists regarding which vital rates are most likely to affect population growth rate. Populations of short-lived organisms, such as rodents, appear more sensitive to changes in fecundity than adult survival (Oli & Dobson 2003; Gaillard *et al.* 2005); therefore, one might expect the signature of density dependence to be found in fecundity. However, vital rates with the highest sensitivity are also under the greatest selection pressure. The result of this selection is canalization, a reduction in the variance associated with a vital rate with high sensitivity (Gaillard & Yoccoz 2003). Reduced variability in vital rates with high sensitivity may mean that change in the population growth rate is due to variability in vital rates other than those with the highest sensitivities (Oli, Slade & Dobson 2001). Recruitment of young and adults into a population has also been cited as an important demographic process related to density (Hodges,

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Krebs & Sinclair 1999; Coulson, Gaillard & Festa-Bianchet 2005). Canalization of recruitment is less likely as populations are less sensitive to changes in this parameter, yet realized population change has been attributed to changes in recruitment in at least some species of mammal (Coulson *et al.* 2005)

Stochastic demographic models use variability in vital rates to model population dynamics (Caswell 2001), often assuming independence among vital rates. Vital rates that are influenced by density violate this assumption. Failing to include density dependence in a demographic model would allow simulated populations to grow to unrealistic densities and provide unrealistic estimates of population dynamics and viability. However, to include density dependence in demographic models one must either use some function from theoretical population models (e.g. carrying capacity) or have empirical measures of the negative feedback between density and vital rates (Henle, Sarre & Wiegand 2004). Although some estimates of density dependence in vital rates exist (e.g. Coulson, Milner-Gulland & Clutton-Brock 2000; Jones & Coulson 2006), these estimates are uncommon both because of the large data sets required for parameter estimation and the fact that density dependence may act on several vital rates, making description difficult (Fowler, Overath & Pease 2006).

Herein, we use a long-term mark–recapture data set for five species of grassland rodent – the prairie vole [*Microtus ochrogaster* (Wagner, 1842)], the hispid cotton rat (*Sigmodon hispidus* Say & Ord, 1825), the white-footed mouse [*Peromyscus leucopus* (Rafinesque, 1818)], the deer mouse [*P. maniculatus* (Wagner, 1845)] and the western harvest mouse [*Reithrodontomys megalotis* (Baird, 1857)] – to assess the presence and magnitude of negative feedback between population density and fecundity and recruitment. Previous analyses of this data set found no relationship between density and survival of trappable individuals and little evidence of seasonality in survival in any species (Reed & Slade 2006a,b, 2007). Therefore, density dependence, if present, must be found in either fecundity or recruitment (defined herein as both recruitment of young and immigration of adults into the population). We expect to find a significant delayed negative feedback between density and recruitment in both *M. ochrogaster* and *P. leucopus*, as numbers of both species exhibit some periodicity in north-eastern Kansas (Brady & Slade 2004). Populations of *P. maniculatus* and *R. megalotis* are not characterized by large fluctuations in abundance or by periodicity. This apparent stability seems to imply the presence of regulatory mechanisms (i.e. density dependence without a time delay). Conversely, we expect *S. hispidus* to be less affected by density-dependent regulation as the study area is near the northern border of the taxon's geographical range and populations are expected to be influenced more by environmental variation (Williams, Ives & Applegate 2003).

Materials and methods

We trapped small mammals from August 1975–July 2003 on a 2.25-ha grid at the Nelson Environmental Study Area (NESA), located

c. 14 km NE of Lawrence, Kansas (Swihart & Slade 1990). The grid consisted of 99 trap-stations with two Sherman live traps (H. B. Sherman Traps Inc., Tallahassee, FL, USA) at each station and trapping was conducted over 3 consecutive days approximately monthly. Small mammals were sexed, weighed and marked with either an ear tag or toe clip and released at the point of capture. Trapping and handling methods followed guidelines of the Animal Care and Use Committee of the American Society of Mammalogists (Choate *et al.* 1998) and were approved by the University of Kansas IACUC. For each trap period, individual *S. hispidus* and *M. ochrogaster* were separated by sex and then classified into one of three stages based on mass (*S. hispidus*: 1 = 60 g; 2 = 61 g–110 g; 3 > 110 g; *M. ochrogaster*: 1 = 20 g; 2 = 21 g–32 g; 3 > 32 g; Reed & Slade 2006a,b). *Peromyscus* spp. and *R. megalotis* were not marked individually until April 1989; therefore our data set for these species covers the period April 1989–July 2003. Captured *P. leucopus* and *P. maniculatus* were designated as juvenile or adult based on pelage and *R. megalotis* was not separated by stages due to low numbers of juveniles captured. We used interpolated jack-knife estimates from program CAPTURE to estimate the monthly abundance of each species of small mammal on the grid. We filled in missing or unreliable estimates using previously established regression equations that predict population estimates from the number of animals captured (Brady & Slade 2004).

FECUNDITY ESTIMATES

We estimated the probability of an individual being pregnant from data collected in the field. Captured females of all species were scored on three reproductive characteristics: vaginal condition (perforate or imperforate), nipple size (small, medium or large) and pubic symphyseal opening (closed, partly open or fully open). Females were considered reproductive (i.e. pregnant and/or lactating) only when at least two of these characters indicated reproductive activity. We then calculated the monthly proportion of females that were reproductive.

We estimated fecundity using a post-breeding census, which required estimates of maternal survival, probability of being reproductive and litter size. We used the multistrata model within program MARK (White & Burnham 1999) to estimate monthly survival for *S. hispidus*, *M. ochrogaster*, *P. leucopus* and *P. maniculatus* and a Cormack–Jolly–Seber (CJS) model to estimate survival of *R. megalotis* (Reed & Slade 2006a,b, 2007). Negative association between density and fecundity could be the result of density dependence in pregnancy rates or litter size. We did not have direct estimates of litter size, so we estimated the distribution of litter sizes and then forced litter size to be negatively density-dependent to assess the maximum impact of density dependence on fecundity. We used published estimates of mean and variance of litter size within a few km of our study area for *M. ochrogaster* (Rose & Gaines 1978) and from elsewhere for *R. megalotis* (Webster & Jones 1982), *P. leucopus* (Lackey, Huckaby & Ormiston 1985) and *P. maniculatus* (Meyers & Master 1983). We used a published regression equation based on female mass (Campbell & Slade 1995) to estimate mean and variance in litter size for *S. hispidus*. We generated a random series of litter sizes in MATLAB (version 7, MathWorks Inc., Natick, MA, USA), sorted the randomly generated litters in descending order and matched the smallest litter with the highest abundance, which resulted in negatively density-dependent litter sizes. We estimated fecundity by multiplying survival, probability of being pregnant and litter size to estimate monthly per-capita fecundity for all species.

RECRUITMENT

We used the temporal symmetry method to estimate the proportion of individuals within each sex and stage that were recruited into the population during a time period (Nichols *et al.* 2000). This technique uses reversed capture histories that regress in time (time = $t + n \dots t + 2, t + 1, t$) to estimate seniority probabilities (γ) – the probability that an individual was in the population during the previous time period. We first constructed reverse capture histories for all individuals in the population. Due to the large size of our data sets we were unable to estimate γ in a single model. Therefore, we subdivided the data set into 2–3-year intervals with a six trap-period overlap between subsets of data (Reed & Slade 2006a), and used the multistrata or CJS models within program MARK to estimate seniority probabilities. We tested goodness-of-fit of the global model using program U-CARE (Pradel, Wintrebert & Gimenez 2003) and corrected for any overdispersion by adjusting the variance inflation factor (c) before model selection. We used Akaike's information criterion, corrected for small sample size (AICc), to select the most parsimonious model from each set of candidate models for each subset of data. We considered models to have good support if the difference in AICc values (Δ AICc) was > 2 . If no single model received good support we used model averaging within program MARK to estimate γ (Buckland, Burnham & Augustin 1997). After the most parsimonious models were selected, we combined the subsets of data by discarding the first and last 3-monthly estimates within each subset.

The output from a reverse capture history is the proportion of individuals in the population in time t that were not in the population at time $t - 1$ and provides no direct information on the number of recruits. To estimate per capita recruitment from seniority probabilities, we estimated the stage-specific proportion of individuals that were new recruits (B_t) by subtracting the seniority probability for each stage from 1. We calculated our estimate of the number of recruits by multiplying B_t for each stage by the number of individuals in each stage that were captured during that trap period. We then calculated an estimate of per capita recruitment by dividing the estimate of the number of recruits by the number of females in the largest or adult stage.

STATISTICAL ANALYSIS

We tested for density dependence in the proportion of females pregnant, fecundity and recruitment by calculating correlations of each with estimated numbers. We arcsine-transformed proportion of reproductive females and recruitment data before analysis and log-transformed density for all analyses. We paired our dependent variables in a given month with our estimated density for that month and the 3 previous months and analysed data by season (spring: March–May; summer: June–August; autumn: September–November; winter: December–February). We restricted our analyses to a lag of only 3 months, so no analyses spanned a period greater than the normal life-span of an individual. We used correlation analysis rather than including density as a covariate within MARK because we were interested in rates of recruitment per adult female rather than proportional recruitment.

Results

Several correlations between density and proportion of reproductive females in both *S. hispidus* and *M. ochrogaster* were significant during all seasons (Fig. 1). However, the

Table 1. Correlation coefficients relating density to proportion of pregnant females and per-capita fecundity in *Reithrodontomys megalotis*, *Peromyscus maniculatus* and *P. leucopus*. Coefficients in bold type indicate statistical significance ($P = 0.05$)

	Lag (months)			
	0	1	2	3
<i>R. megalotis</i>				
Winter				
Pregnancy	0.042	-0.248	-0.269	-0.347
Fecundity	-0.082	-0.391	-0.301	-0.365
Spring				
Pregnancy	0.194	0.23	0.169	0.246
Fecundity	-0.023	-0.19	-0.256	0.072
Summer				
Pregnancy	0.73	0.192	0.126	0.192
Fecundity	0.294	0.006	-0.218	-0.144
Autumn				
Pregnancy	0.26	0.263	0.241	0.298
Fecundity	0.366	0.442	0.282	0.357
<i>P. maniculatus</i>				
Winter				
Pregnancy	0.099	-0.22	-0.301	-0.252
Fecundity	0.077	-0.236	-0.253	-0.248
Spring				
Pregnancy	-0.032	-0.152	0.013	0.04
Fecundity	-0.357	-0.07	-0.046	-0.229
Summer				
Pregnancy	0.352	0.466	0.336	0.311
Fecundity	0.286	0.531	0.47	0.491
Autumn				
Pregnancy	0.042	-0.06	-0.083	-0.181
Fecundity	-0.277	-0.244	-0.248	-0.448
<i>P. leucopus</i>				
Winter				
Pregnancy	0.204	0.129	-0.018	0.257
Fecundity	0.271	0.153	0.016	0.271
Spring				
Pregnancy	-0.166	-0.217	-0.308	-0.269
Fecundity	-0.021	-0.14	0.035	-0.135
Summer				
Pregnancy	-0.028	0.134	-0.193	-0.275
Fecundity	0.122	-0.01	-0.108	0.004
Autumn				
Pregnancy	0.201	-0.019	0.054	0.263
Fecundity	-0.118	-0.285	-0.177	0.053

majority of these correlations were positive. No correlations between density and proportion of reproductive females in *P. maniculatus* and *P. leucopus* were significant and only two correlations in *R. megalotis* were significant – probability of being reproductive was related positively to density at lag 0 in *R. megalotis* in summer ($r = 0.78$; d.f. = 82; $P < 0.001$; Table 1) and related negatively to density at a lag of 3 months ($r = -0.35$; d.f. = 76; $P = 0.3$).

We found density dependence, both direct and delayed, in fecundity in *S. hispidus* and *M. ochrogaster*. Fecundity was related negatively to density in *S. hispidus* during summer and autumn but was related positively to density in *M. ochrogaster* in spring and summer (Fig. 2). Fecundity and density were

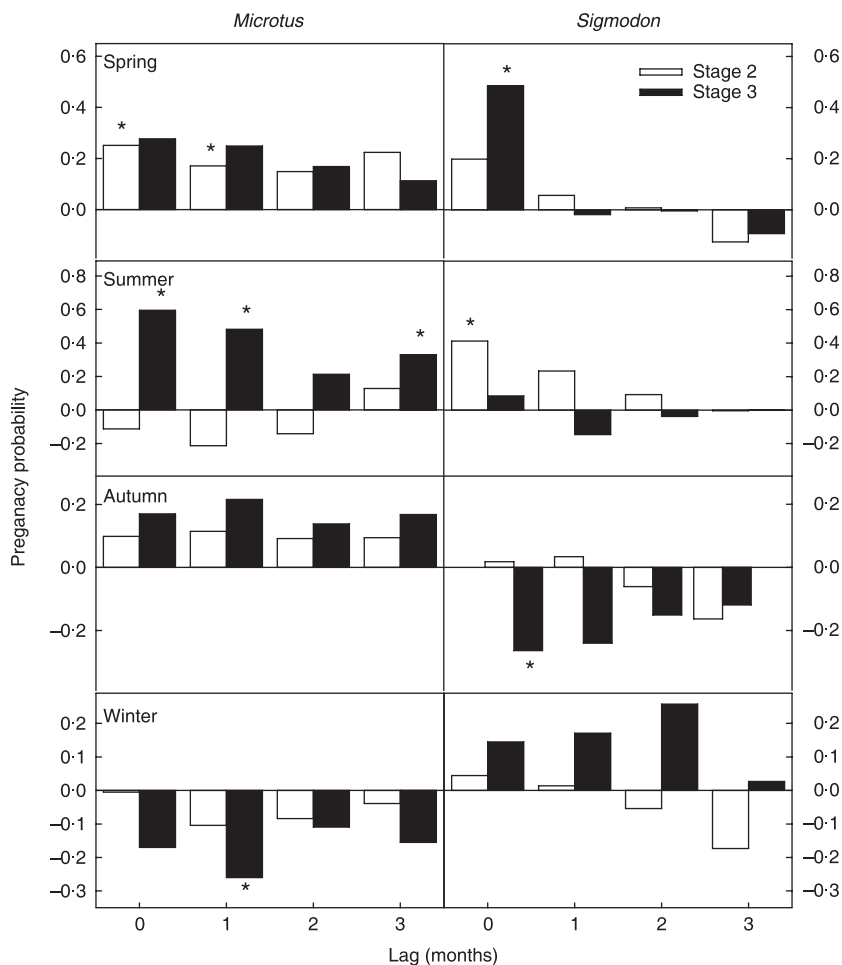


Fig. 1. Correlations between density and proportion of pregnant females in *Microtus ochrogaster* and *Sigmodon hispidus*. Bars indicated by an asterisk represent statistically significant correlations ($P < 0.05$).

not related significantly in either *P. maniculatus* or *P. leucopus*, and related negatively in *R. megalotis* in winter at lags of 1 and 3 months (lag 1: $r = -0.39$; d.f. = 68; $P = 0.02$, lag 3: $r = -0.37$; d.f. = 68; $P = 0.03$).

Time was included as a factor in all selected models of recruitment for all size stages for *M. ochrogaster*, *S. hispidus*, *P. leucopus* and *P. maniculatus* (Table S1, see Supplementary material). In contrast, recruitment in *R. megalotis* appeared to be time-invariant in each subset of data, although models that included either time or sex received support in some subsets of our data. We found few differences in recruitment between sexes, so we restricted the remaining analyses to recruitment of females only. Per-capita recruitment and fecundity were not correlated significantly in any season for *S. hispidus*, *P. leucopus*, *P. maniculatus* or *R. megalotis*. Recruitment in stages 1 and 3 was not related significantly to fecundity in any season. Fecundity in stage 3 and recruitment in stage 2 were related positively in spring ($r = 0.29$; d.f. = 76; $P = 0.01$) and negatively in autumn ($r = -0.26$; d.f. = 78; $P = 0.03$).

Density and per-capita recruitment were correlated negatively in both *M. ochrogaster* and *S. hispidus* (Fig. 3). *M. ochrogaster* recruitment in stage 2 and stage 3 was related negatively to density in all seasons, but negative relationships

were weakest in summer. We found no statistically significant relationship between recruitment and density for stage 1 *M. ochrogaster*. We found statistically significant relationships between density and recruitment in all stages of *S. hispidus*. While relationships were present in all seasons, density-dependent recruitment was least prevalent in winter. We observed one positive relationship between density and recruitment in *R. megalotis* ($r = 0.46$; d.f. = 26; $P = 0.01$). Per-capita recruitment decreased with increasing density in both species of *Peromyscus* and in *R. megalotis* for all seasons and time-lags; however, we found few statistically significant correlations between density and recruitment in these species (Table 2).

Discussion

Negative feedback between population density and growth rates is present in some form in many populations (Berryman 2004; Sibly *et al.* 2005; but see Krebs 2002) and delayed density dependence is a necessary condition for multi-annual cycles in abundance (Korpimaki *et al.* 2004), such as those observed in *M. ochrogaster* and *P. leucopus* in eastern Kansas (Brady & Slade 2004). Density dependence, if present, may be reflected as a negative relationship between density and a

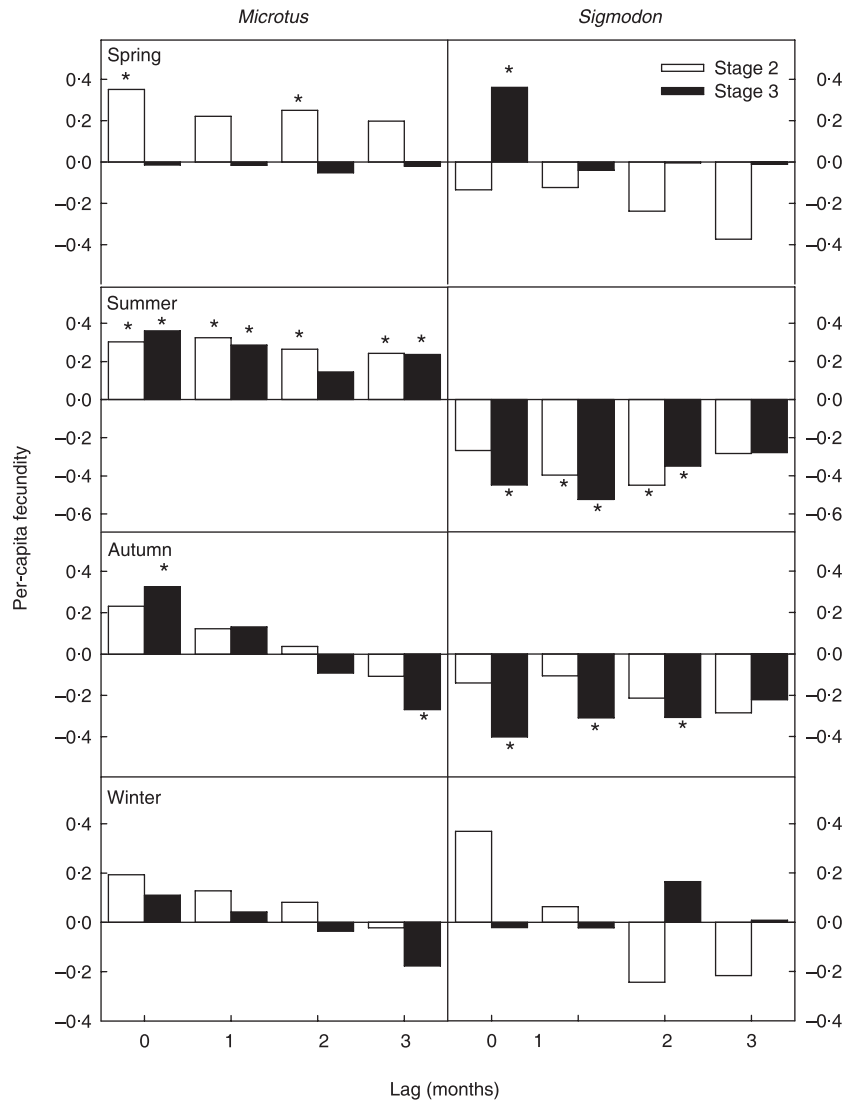


Fig. 2. Correlations between density and per-capita fecundity in *Microtus ochrogaster* and *Sigmodon hispidus*. Bars indicated by an asterisk represent statistically significant correlations ($P < 0.05$).

single vital rate that underlies the population growth rate, or it may be reflected in several vital rates, making the signal difficult to detect (Fowler *et al.* 2006). In previous analyses we found no relationship between density and survival in any of the five species assessed (Reed & Slade 2006a, 2b, 2007); therefore, any influence of density must be expressed in either recruitment or fecundity. Our current analyses suggest that the negative feedback between density and the population growth rate is found in recruitment (births and immigration) in all our species, but that the strength of signal varies among taxa.

DENSITY DEPENDENCE AND FECUNDITY

Fecundity is an influential vital rate in the population dynamics of short-lived species, such as small mammals (Oli & Dobson 2003). Changes in fecundity related to density have been identified as influential in the dynamics both in free-living populations (Norrdahl & Korpimäki 2002) and through simulation analyses (Oli & Dobson 2001). Therefore, one might expect density dependence to act through a negative feedback

between density and fecundity. However, we found little evidence of negative density dependence in the proportion of reproductive females and negative density dependence only in *S. hispidus* after including (perhaps artificially high) density dependence in litter size. Although fecundity has the greatest potential effect on future population growth in small mammals, variability in fecundity may be less than variability in other vital rates (Gaillard & Yoccoz 2003). Variability tends to be correlated negatively with sensitivity of vital rates (Pfister 1998; but see Doak *et al.* 2005). That is, the greater effect a vital rate has on population growth rate, the greater the canalization of that vital rate due to heavy selection pressure that reduces the variability associated with that vital rate.

One response to high density might be delayed reproduction that may negatively affect fitness in species with short-generation times (Charnov 1990). If the likelihood of surviving until environmental conditions are more favourable for breeding is relatively low, it is advantageous for an individual to breed and then assess the cost of completing reproduction. In many mammal species gestation is less energetically expensive

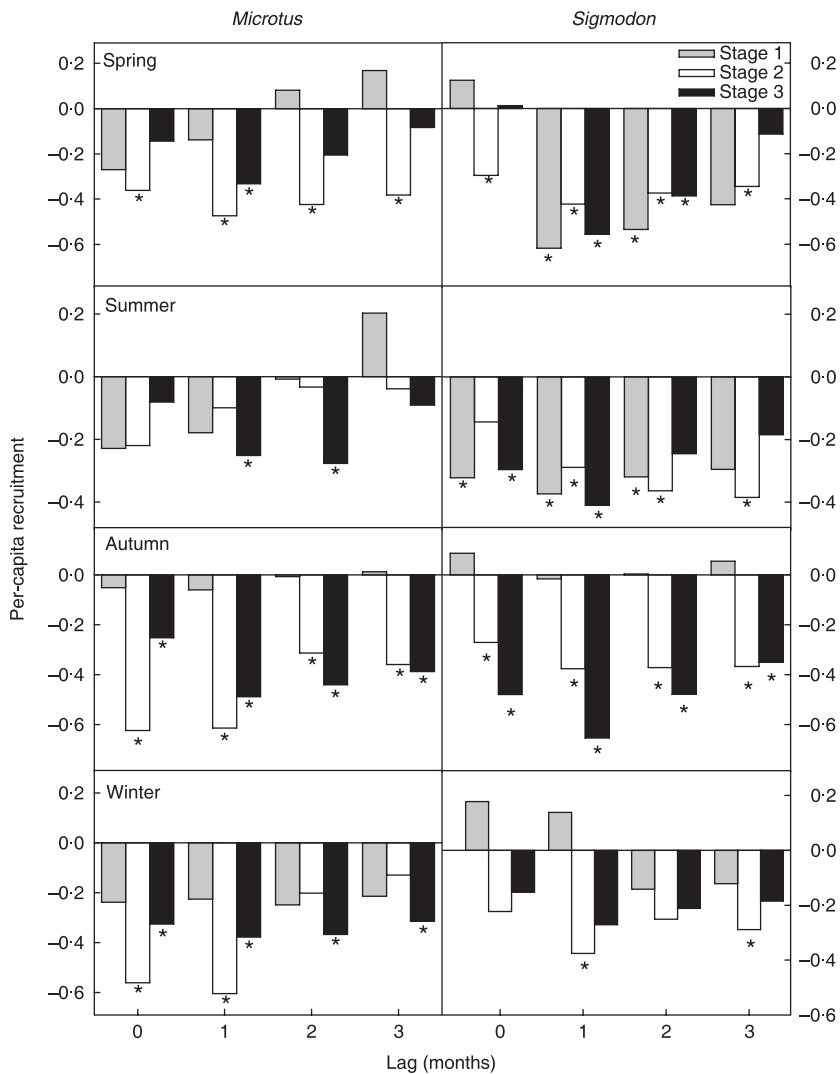


Fig. 3. Correlations between density and per-capita recruitment in *Microtus ochrogaster* and *Sigmodon hispidus*. Bars indicated by an asterisk represent statistically significant correlations ($P < 0.05$).

than lactation (Clutton-Brock, Albon & Guinness 1989), so the greatest costs associated with reproduction are incurred after parturition. Therefore, the strategy that might impart the most benefit would be to mate and become pregnant and then assess the environmental conditions. If conditions are favourable the young can be raised, whereas if conditions are not favourable and the cost associated with raising the litter is too high, the litter could be resorbed or abandoned. Hence, assessing reproduction by external appearance may not have detected perinatal fecundity adjustments in the species we studied.

Negative density dependence could also be expressed in litter size; females may become pregnant at the same rate regardless of density, but reduce litter size with increasing density. We have no data on litter size of these five species of small mammal on our area, so instead we generated random litter sizes from published sources. We then made this maximally negatively density dependent by matching the smallest litter size with the greatest estimated density. Even when we forced litter size to be density dependent we found few nega-

tive relationships between density and fecundity; indeed, many of the statistically significant relationships were positive. The single exception is *S. hispidus*; fecundity and density were related negatively in summer and autumn.

Estimates of the relationship between litter size and density are uncommon in small mammals; the data available suggest both density dependence and density independence in litter size. Litter size in Australian house mice (*M. musculus* Linnaeus, 1758) was negatively density dependent (Singleton *et al.* 2001). Conversely, vole populations in Finland showed either no change in litter size or a positive relationship between density and litter size (Norrdahl & Korpimäki 2002) and embryo counts of voles near our study area showed no relationship to density (Rose & Gaines 1978). Similarly, litter size in *P. leucopus* was related positively to density in Oklahoma (McMurry *et al.* 1996). Litter size in *S. hispidus* is related positively to body mass (Campbell & Slade 1995; Slade, McMurry & Lochmiller 1996) and it is possible that mean body mass is related negatively to density, which would result in negative density dependence in litter size. Nevertheless, our

Table 2. Correlation coefficients relating density to per-capita recruitment in *Reithrodontomys megalotis*, *Peromyscus maniculatus* and *P. leucopus*. Coefficients in bold type indicate statistical significance ($P = 0.05$)

	Lag (months)			
	0	1	2	3
<i>R. megalotis</i>				
Winter	-0.164	-0.625	-0.589	-0.538
Spring	0.464	0.066	-0.056	-0.083
Summer	-0.089	-0.263	-0.361	-0.286
Autumn	0.178	0.181	0.162	-0.184
<i>P. maniculatus</i>				
Winter	-0.08	-0.086	-0.198	-0.056
Spring	0.18	-0.203	-0.116	0.296
Summer	-	-	-	-
Autumn	-0.069	-0.306	-0.045	0.192
<i>P. leucopus</i> stage 1				
Winter	0.206	-0.325	-0.508	-0.305
Spring	-0.105	-0.574	-0.234	0.122
Summer	-0.196	-0.342	-0.446	-0.171
Autumn	0.043	-0.296	-0.062	-0.329
<i>P. leucopus</i> stage 2				
Winter	-0.203	-0.241	-0.26	0.097
Spring	-0.132	-0.303	-0.344	-0.225
Summer	0.116	-0.129	-0.399	-0.144
Autumn	-0.269	-0.314	-0.168	-0.41

results suggest that reproduction is not negatively density dependent and is, in this data set, positively density dependent. This indicates that vital rates other than fecundity must be responsible for population regulation.

RECRUITMENT

We found negative correlations between density and per-capita recruitment rates in all five species of grassland rodent, although statistically significant correlations were most common for *M. ochrogaster* and *S. hispidus*. The negative feedback between density and recruitment in our data probably indicates both reduced immigration onto our grid and reduced survival of pups with increasing density. Dispersal is reduced in some small mammal populations during periods of high density (Smith & Batzli 2006); individuals are more likely to stay in their natal range if few new territories are available (Lin & Batzli 2001). Immigrants are also less successful at colonizing a patch with high densities than those with low densities (Gundersen, Andreassen & Ims 2002). The inverse relationship between density and immigration has been codified in the social fence hypothesis (Hestbeck 1982) and the fence hypothesis (Krebs 1985). A reduction in the successful dispersal of immigrants onto our grid would account for the density-dependent relationship observed at short time-lags (e.g. 0–1 month); especially for young individuals.

The density-dependent recruitment we observed, particularly at longer time lags, could also be a reflection of reduced survival of nestlings. We found little evidence of a

negative feedback between density and survival of independent individuals (Reed & Slade 2006a,b, 2007) or between density and fecundity; however, we had no measure of survival of nestlings. High population densities probably lead to increased intraspecific competition (Lima, Berryman & Stenseth 2006) and food limitation over short time-scales (Turchin & Batzli 2001). Environmental stress then can lead to a reduction in the success of females in raising young to weaning (Lambin & Yoccoz 1998; Koskela, Mappes & Ylonen 1999) or to lower weights (Webb *et al.* 2005), and presumably lower quality, of offspring (i.e. maternal effects; Rossiter 1994). Reduced survival and quality of nestlings would lead to reduced recruitment of individuals into the population in the subsequent months, as few individuals are dispersing, regardless of their size. Reduced abundance of dispersing individuals would appear as density-dependent recruitment at time-lags of more than 1 month.

We had expected the signal of density dependence to be strongest in *M. ochrogaster*, which was confirmed by our data, as all the correlations were significant when we used all data in a single analysis and the taxon had the most significant correlations when we grouped the data by month. We did not expect to observe density dependence in *S. hispidus*, as the study area lies near to the northern extent of the geographical range of the species. However, our data did indicate negative feedback between density and recruitment in *S. hispidus*. We found equivocal evidence of negative relationships between density and recruitment in both species of *Peromyscus* and *R. megalotis*. The majority of correlation coefficients were negative, but few of the relationships were statistically significant. Some of the lack of statistical significance in our correlations can be attributed to small sample sizes and reduced statistical power due to low abundance of some stages on the study area. Density dependence is also difficult to detect in populations with relatively stable dynamics, such as *P. maniculatus* and *R. megalotis*, using only observational data (Fowler *et al.* 2006). Alternatively, density dependence may be less influential in these populations than in *M. ochrogaster* and *S. hispidus* and environmental factors or seasonal changes in vital rates may be the proximate cause of population variability in these taxa.

MODELLING DENSITY DEPENDENCE

Models that do not include some form of density dependence could provide unrealistic estimates of population viability (Hanski, Foley & Hassell 1996; Krüger 2007). Stochastic models without density dependence may result in populations that experience unchecked growth, resulting in unrealistically high abundance and estimates of population viability. Conversely, when density is low, the vital rate(s) influenced by density may be higher than the long-term mean, aiding recovery of the population from near extinction. Not including some function of density would keep these rates at the long-term mean, and projections from such a model would provide an inaccurate estimate of the viability of the population. Delayed density dependence is also a necessary condition for cyclic population dynamics (Korpimäki *et al.* 2004); models

of species that exhibit cyclic dynamics that do not include density dependence explicitly may not reproduce these cycles. Recruitment (i.e. immigration and perinatal survival) is often ignored in demographic models; populations are modelled using survival and fecundity of different age or stage classes (Caswell 2001). Demographic data are often collected over fine scales, areas as small as a few hectares, and from populations that are open to emigration and recruitment. Failing to include movement in a demographic model may provide unrealistically low estimates of survivorship in a population. Individuals that emigrate permanently from the study area would be included as mortality, whereas individuals immigrating into the study area would not be included in the estimate of survival.

The relative influence of density dependence is a persistent issue in population ecology (Turchin 1999; Krebs 2002; Berryman 2004). Although our analyses indicate that density-dependent recruitment is present in small mammals, it does not indicate the relative influence of density dependence in the dynamics of these taxa. Observational data, such as the current study, do not provide information on the sensitivity of a population to variability in a vital rate and therefore provide little evidence of the relative influence of changes in that vital rate. Experimental studies, or alternatively demographic models parameterized with and without density-dependent recruitment, would provide the data necessary to draw inference about the relative influence of density dependence in the demographics of small mammals.

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Supplementary material

The following supplementary material is available for this article.

Table S1. Model selection from program MARK.

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