

Source–sink dynamics: how sinks affect demography of sources

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Abstract

Models of source–sink population dynamics have to make assumptions about whether, and eventually how, demographic parameters in source habitats are dependent on the demography in sink habitats. However, the empirical basis for making such assumptions has been weak. Here we report a study on experimental root vole populations, where estimates of demographic parameters were contrasted between source patches in source–sink (treatment) and source–source systems (control). In the presence of a sink patch (simulated by a pulsed removal of immigrants), source-patch populations failed to increase over the breeding season, mainly due to a high spatially density-dependent dispersal rate from source to sink patches. The *per capita* recruitment rate was almost two times higher in source–sink than in the source–source systems, but this did not compensate for the loss rate due to dispersal from source to sink patches. Sex ratio in the source–sink systems became less female biased, probably as a result of an enhanced frequency of dispersal movements in females. Good knowledge of the degree of density- and habitat-dependent dispersal is critical for predicting the dynamics of source–sink populations.

Keywords

Demography, dispersal, experimental model system, metapopulation, *Microtus*, source–sink population.

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INTRODUCTION

Source–sink theory is currently one of the main frameworks for predicting population dynamics in spatially heterogeneous landscapes (Erikson 1996; Dias 1996; Diffendorfer 1998; Thomas & Kunin 1999). Source–sink models (e.g. Pulliam 1988; Pulliam & Danielson 1991; Howe *et al.* 1991) link demography and space by defining habitats according to whether they sustain positive (sources) or incur negative (sinks) net population growth. A key parameter in source–sink systems is dispersal. Obviously, the very existence of sink habitats depend on immigration from source habitats (at least in the long term). Moreover, the rate of dispersal affects the growth rate in source habitats (i.e. through emigration) and thus the dynamics and the likelihood of persistence of the entire (meta)population.

Despite the source–sink framework's prominent position in basic population theory (Holt 1996; Lemel *et al.* 1997; Rousset 1999) and applied modelling of vulnerable populations (e.g. Wootton & Bell 1992; Fahrig & Merriam 1994), several recent papers have noticed the scarcity of

convincing empirical demonstrations of source–sink dynamics (Watkinson & Sutherland 1995; Erikson 1996; Diffendorfer 1998; Kadmon & Tielbörger 1999). In his extensive review, Diffendorfer (1998) concluded that there was a “myriad of source–sink models”, but no proper experiments. Recently, the two first experimental studies on source–sink dynamics in plants were published (Kunin 1998, Kadmon & Tielbörger 1999), but as yet we are not aware of such experiments for any animal population.

Here we present the results from an experimental study on root vole populations where we aimed to explore some critical assumptions regularly made in source–sink models. Specifically, source–sink models must make explicit assumptions about the rate of dispersal from source to sinks and *vice versa*. Dispersal from the source, both dependent and independent of the actual demographic rates in the sink, has been assumed (Pulliam 1988; Howe *et al.* 1991; McPeck & Holt 1992; Watkinson & Sutherland 1995). Different assumptions regarding ‘sink-dependent’ dispersal rates may be expected to produce different outcomes in terms of population dynamics and genetics (Aars & Ims 2000), but have not yet been tested

experimentally. Here we provide such a test. Based on findings of earlier studies (i.e. showing that dispersal in root voles are spatially density-dependent, e.g. Aars & Ims 2000), we expected the rate of dispersal from source patches to increase in the presence of sinks, thereby reducing population growth. Moreover, most source–sink models do not explicitly consider whether *in situ* demographic parameters (e.g. survival, fecundity, sex and age structure) in sources may be affected by the presence of sinks. In the present experiment we also explored this possibility.

Similar to several theoretical models of spatial population dynamics and genetics, we used simple two-patch systems (see Hanski 1999 for a review) as our experimental model (Ims & Stenseth 1989; Ims 1999). We employed systems with two source patches as a control for our experimental source–sink systems. Sink demography may either be ruled by low fecundity or high mortality (or a combination thereof). Here we chose to simulate high mortality sinks. Such mortality sinks, sometimes also termed traps (Pulliam 1996), may represent an actual conservation problem when animals are harvested or persecuted in habitats surrounding reserves (Woodroffe & Ginsberg 1998; Haight *et al.* 1998).

MATERIALS AND METHODS

Experimental area and populations

This study took place between 18 June and 23 October 1998, at Evenstad Research Station, South-east Norway. The experimental area consisted of six 50 m × 100 m plots surrounded by vole-proof steel sheet fences extending 0.60 m above and 0.40 m below the ground. The entire area was surrounded by a 1.5-m high chicken mesh fence supplied with an electric wire to prevent mammalian predators from entering the area. Each enclosed plot had two meadow patches (20 m × 37.5 m) separated from each other by 50 m (Fig. 1), or approximately twice the length of the most distant locations within an adult male root vole home range, but well within dispersal range of both males and females (Aars & Ims 1999). These meadow patches were sown with a mixture of grass and clover in 1989 and were maintained to fulfil the habitat requirements of root voles (Ims *et al.* 1993), whereas the surrounding matrix was maintained barren and vole hostile by mowing and use of herbicides. The patches had previously been found to sustain independent root vole populations with positive growth over the summer (Aars *et al.* 1999), i.e. unmanipulated patches represent source habitats.

In each plot, a founder population consisting of 14 adult females and five adult males (74% females) was

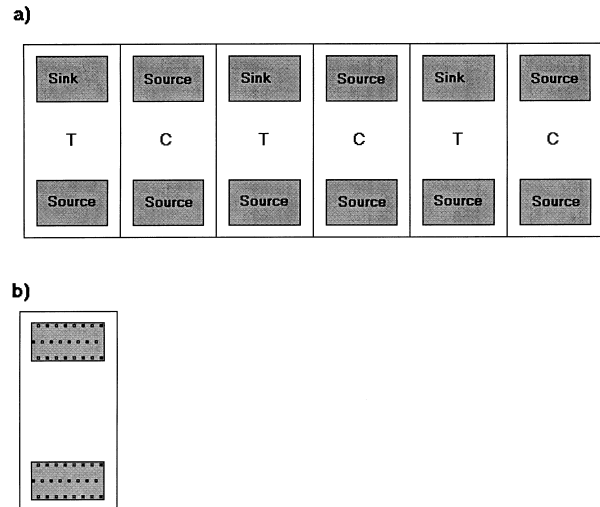


Figure 1 (a) Habitat configuration and treatment distribution in the six plots. Meadow habitats are shaded. T, treatment; C, control. (b) Location of trap stations. Filled squares: Ugglan trap, open squares: Ugglan trap and pitfall.

released in one of the two patches (i.e. the source patch, Fig. 1). The decision to use a female-biased sex-ratio was based on earlier studies showing that sex ratio of breeding adults often stabilizes at 60–80% females in root vole populations (Ims & Andreassen 1999). The root voles used in the present experiment originated from a southern Norwegian root vole race (Ims 1997). Both recently caught wild animals (only females) and third-generation animals (both males and females) raised from individuals captured the previous autumn (bred at the Animal Division, University of Oslo) were used in this study. Hence, the female population of released animals consisted of both field-born (mean number = 9.0 [SE = 0.26]) and laboratory raised animals (mean number = 5.0 [SE = 0.26]). Before release, animals destined to form a founder population were placed within olfactory and visual proximity so as to become familiar. We detected no difference between laboratory and field-born founder animals with respect to survival, dispersal or reproduction in the field.

Experimental treatment

The experiment was commenced by releasing the founder populations in one of the two patches per plot (hereafter termed source patch), while the other patch was initially empty (hereafter termed colonization patch). Four weeks later, three of the plots were experimentally manipulated to become source–sink systems by the removal of all animals that dispersed to the colonization patches. The removal of animals from the sink patches was continued

in each trapping period until the experiment was terminated on 23 October by removing animals during normal trapping events (see below). The remaining three plots served as controls, i.e. there was no removal of animals in the colonization patches. Every second plot was assigned as a treatment or control plot, respectively (Fig. 1).

Trapping procedure

The six populations were monitored by live-trapping throughout the season. Three trapping lines (10 m spacing), consisting of eight trap stations (5 m spacing) were established in each of the habitat patches (Fig. 1b). An Ugglan multiple capture live trap was situated at each station and a pitfall supplemented at every second station. Each trap was baited with carrots and whole grain oats.

Every trap session lasted for 3 days and consisted of six trapping events inside habitat patches (traps activated from 2400 h to 1200 h and checked at 0600 h and 1200 h). In previous studies at Evenstad, we have shown that this trapping protocol ensures an extremely high capture rate (97–100%; Aars & Ims 1999, 2000). In total, seven trapping sessions were completed through the 4 month duration of the experiment. The time schedule of the trapping and other activities during the course of the experiment are summarized in Table 1.

Before release and at every trapping occasion, we recorded sex, weight and reproductive status (open/closed vagina, pregnancy and lactation for females and sexual maturity, i.e. visible testis for males) for each individual. At any given capture we also recorded trap station, trap type and time of capture. Field-born voles were marked by toe clipping upon their first capture.

Statistical analyses

Because we wanted to explore the effect the presence of sink patches had on the demography in source patches,

the focal statistical units in this experiment was the six source-patch populations. Due to the very high capture rate ($P \approx 1$), population size was set equal to the number of animals caught in a patch in a given trapping session. Survival rate was estimated from the patch-specific proportion of animals that survived from one trapping session to the next, while dispersal rate was estimated from the (patch-specific) proportion of animals dispersed from one patch to another between two trapping sessions. Population size (at the patch level) and the various demographic parameters were analysed with repeated measures linear and generalized linear models implemented by PROC Mixed in SAS version 6.12 (SAS Institute 1996). In these models, population identity was specified as a subject-level random effect nested in the treatment effects. Estimates from these models are given with replication-based error. Trapping session (time) and time*treatment interaction were modelled as the (repeated) within-subject effects. The most appropriate variance-covariance structure for the temporally auto-correlated repeated measures was selected according to the Akaike Information Criterion (AIC) (Littell *et al.* 1996). Sex and cohort (founder and field born animals) were included as fixed effects (in addition to treatment and time) whenever appropriate. Non-normal error terms (binomial) and non-identity link functions (logit or logarithmic) were implemented by the SAS-macro GLIMMIX (Littell *et al.* 1996). For the analysis of patch-specific population growth rate (r) over the experimental period we applied the model

$$N_{\text{session}7,i} = \text{Quasi} - \text{Poisson} (N_{\text{session}1,i} * \exp [r_o + r_j])$$

where $N_{\text{session}t,i}$ is the population size for a source patch i in the first ($t = 1$) or the last ($t = 7$) trapping session and where r_j is the treatment effect. This model was fit to the data with a logarithmic link and with $N_{\text{session}1}$ as an offset term (see Lebreton 1991).

The demographic structure (i.e. cohort and sex ratio) of the source-patch populations was analysed with a log-

Table 1 Time schedule of the experiment showing dates of the starts of the various activities. All trapping and removal sessions lasted 3 days

Date	Activity	Description
18.06	Release	Fourteen females and 5 males released in the source patches.
02.07	1. Trap session	Trapping in source and colonization patches.
15.07	Removal session	Removal of animals in the sink patches.
05.08	2. Trap/removal session	Trapping in source and colonization patches, removal in sink patches.
25.08	3. Trap/removal session	Trapping in source and colonization patches, removal in sink patches.
08.09	4. Trap/removal session	Trapping in source and colonization patches, removal in sink patches.
22.09	5. Trap/removal session	Trapping in source and colonization patches, removal in sink patches.
06.10	6. Trap/removal session	Trapping in source and colonization patches, removal in sink patches.
21.10	7. Trap/removal session	Trapping in source and colonization patches, removal in sink patches.

linear model. Numerical problems in this case, when implementing repeated measures poisson error models by means of the GLIMMIX-macro, prompted the use of a more conventional analytical procedure which did not include modelling of the variance-covariance structure of the period specific measurements. However, deviance from pure poisson residual error from the model (i.e. overdispersion) was accounted for by quasi-likelihood estimation of the error variance (McCullagh & Nelder 1989).

RESULTS

Population size and growth rate

As could be expected, the size of the source-patch populations did not differ between treatment and control plots before the onset of the experimental treatment (i.e. trapping session 1; Fig. 2a). However, after the treatment plots were turned into source-sink systems, that is: removal of animals from the colonization patches (i.e. sink patches), the source-patch populations in the source-sink systems were generally smaller ($F_{1,4} = 15.28$, $P = 0.0174$)

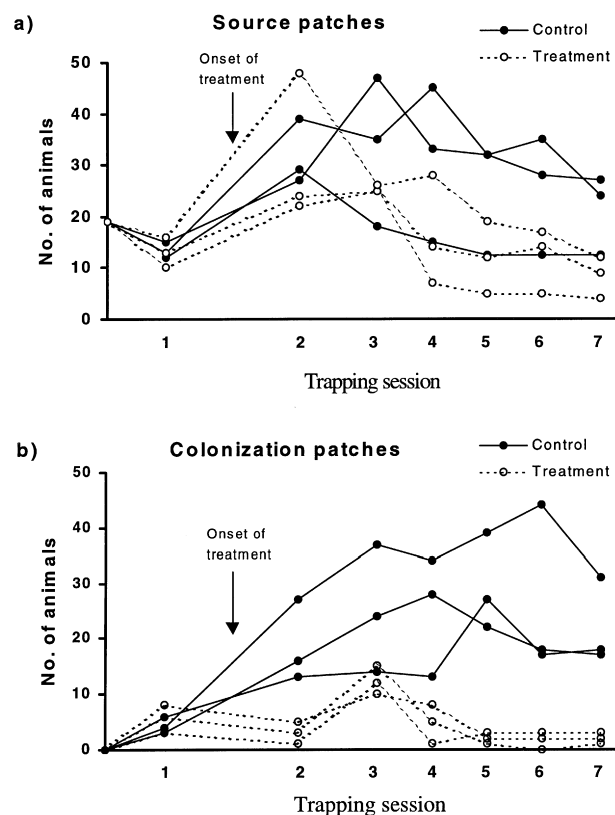


Figure 2 Population size trajectories in the two types of source and colonization patches over the 4-month experimental period. Colonization patches in the treatment populations are sink patches. “Onset of treatment” means removal trapping in the sink patches from this time and all following trapping sessions.

than those in the control plots (mean size of source-patch population for trapping sessions 2–7 in treatment: 17.09 [SE = 2.16] individuals; in control: 28.35 [SE = 2.16] individuals). In the control plots, the colonization patches had attained the population size of the source patches in session 5 (Fig. 2b), i.e. approximately 3 months after the release of animals.

The log-linear estimates of population growth rate (r) over the three 1/2-month period between sessions 1 and 7 showed that, while source-patch populations in the control plots increased (estimate of intrinsic growth rate: $r = 0.45$ [SE:0.15]), the source-patch populations in the source-sink systems decreased ($r = -0.45$ [SE:0.23]) (treatment effect: $\chi^2 = 10.58$, d.f. = 1, 4, $P = 0.001$). The colonization patches in the control populations had a much higher, positive growth rate ($r = 1.55$ [SE:0.16]) than the source patches in the same systems ($\chi^2 = 10.58$, d.f. = 1, 4, $P < 0.0001$). Thus, based on patch-specific growth rates, the control plots can be termed source-source systems.

Demographic processes

Dispersal

On the first trapping session (i.e. 2 weeks after release and 1 week before the experimental treatment commenced), on average 4.2 (SE = 0.57) females and 0.8 (SE = 0.57) males had settled in colonization patches, while 9.3 (SE = 0.55) females and 3.8 (SE = 0.55) males remained in the source patches. Dispersal of animals from source to colonization patches before the removal of animals commenced, did not differ significantly with respect to treatment or between the sexes ($P > 0.363$). In later periods (i.e. after the treatment commenced) dispersal events were extremely rare in the source-source systems; only five animals (proportion = 0.009, 95% CI: [0.004, 0.020]) dispersed. The estimated odds of dispersal over the total treatment period was 30.71 (95% CI = [13.7, 68.9]) times higher in source-sink than in source-source systems ($F_{1,4} = 68.93$, $P = 0.0011$). We recorded no dispersal from the colonization patch to the source patch in the source-source systems.

Due to the extremely low dispersal rate in the source-source systems, period-specific analysis split on sex and cohort could only be done for the source-sink systems. For the founder animals, dispersal probability modelled by a logistic-binomial model did not depend on period or sex (all $F_{1,14} < 0.69$, $P > 0.4187$). For field-born animals the dispersal probability was sex and period specific (sex*period interaction: $F_{1,24} = 5.34$, $P = 0.0297$). The dispersal probability was higher for females than males early in the season, but decreased more strongly for females than for males with time.

Survival and recruitment

Survival probability was generally high for all animals (0.803, 95% CI: [0.768–0.834] per 14 days) and was affected by neither treatment, sex and cohort, nor interaction terms (all $P < 0.20$). Survival probability increased somewhat with time (logit slope = 0.239, SE = 0.077, $P = 0.0026$).

Only founder females contributed to offspring production, i.e. none of the field-born females became evidently lactating. Reproductive intensity was measured as the proportion of lactating founder females out of all founder females present in a given source patch during a trapping session. Reproductive intensity in the source–sink systems (estimated proportion lactating females from logistic-binomial model: 0.79, 95% CI: [0.47, 0.94]) was generally higher than the equivalent estimate from the source–source systems (0.43, 95% CI: [0.27, 0.61]) (treatment effect: $F_{1,4} = 7.50$, $P = 0.052$). The number of new recruits per lactating female (an index of litter size) also tended to be higher in the source–sink systems (estimate from linear model: 3.95 recruits, 95% CI: [2.57, 5.33]) than in the source–source systems (2.90 recruits, 95% CI: [2.15, 3.64]) although this was not statistically significant ($F_{1,4} = 3.50$, $P = 0.135$). The product of reproductive intensity and litter size, which is an index of the *per capita* recruitment rate in the source patches, was almost two times higher in the source–sink systems (3.80, 95% CI: [2.45, 5.14]) than in the source–source systems (2.01, 95% CI: [1.11, 2.90]) (test of treatment effect: $F_{1,4} = 9.48$, $P = 0.037$).

Demographic structure

Sex ratio was less female biased (Fig. 3) in the source–sink than in the source–source populations (sex*treatment effect: $\chi^2 = 6.07$, d.f. = 1, 123, $P = 0.013$). Cohort structure was unaffected by the experimental treatment (cohort*treatment effect: $\chi^2 = 2.55$, d.f. = 1, 123, $P = 0.11$).

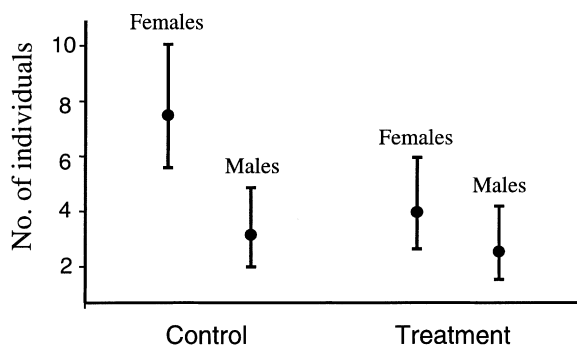


Figure 3 Source-patch population structure presented as sex-specific population densities in treatment (source–sink) and control (source–source) systems. Estimates with 95% confidence intervals are from the log-linear models presented in the main text.

DISCUSSION

Mechanisms underlying the observed effects

Although the two habitat patches per experimental system were separated by a stretch of barren non-habitat that exceeded the length of two male home-range diameters, the demography of source patches was tightly linked to the demography of the adjoining colonization patch. In the neighbourhood of a simulated mortality sink, the source patch failed to grow over a period which corresponds to the length of a normal breeding season of northern root vole populations (Steen 1995). Hence, the source-patch populations of the source–sink systems themselves became sinks. In contrast, in the presence of another patch with positive growth rate, the source-patch populations in the control systems exhibited positive growth rate over the breeding season.

Dispersal from source to sink patches was clearly the decisive demographic process underlying the experimentally induced difference in source-patch dynamics in our study, i.e. a high emigration rate from the source patch in the source–sink systems drove the source-patch population into negative growth. No *in situ* demographic processes contributed to this effect. On the contrary, a higher recruitment rate in the source–sink systems somewhat counteracted the negative effect dispersal had on population growth. However, the enhanced recruitment rate, here probably conditional on a lower patch-specific population density, was not fully compensatory. The less female-biased sex ratio in the source–sink systems is also explicable in terms of dispersal. The dispersal rate of females in the source–sink systems was higher than that of males early in the season when most of the recruits were produced. This indirect effect of dispersal also acted to lower the growth potential of the source–sink populations due to relatively fewer females.

The observed dispersal response in our experiment represents a demonstration of spatially density-dependent dispersal by which individuals immigrate to habitat patches with lower population density than the patch they originate from. This phenomenon, which is particularly pronounced in young females, has been elucidated thoroughly in earlier studies of root voles (e.g. Aars & Ims 2000; Andreassen & Ims 2000), albeit not in a source–sink dynamics context. Recent reviews have revealed that spatially density-dependent dispersal is a widely occurring phenomenon, particularly in bird and mammals (Wolff 1997; Lambin *et al.* 2001; Ims & Hjermann 2001). It seems to be enhanced by the formation of social fences (Hestbeck 1982) by which individuals prone to disperse either avoid patches inhabited by groups of unfamiliar conspecifics or are actively expelled when attempting to establish in such groups.

Density-dependent dispersal and source–sink dynamics

Some general aspects

The population dynamic consequences of spatially density-dependent dispersal have rarely been explored either theoretically or experimentally (see Aars & Ims 2000 for a discussion). We identify and discuss briefly below some little-explored aspects of this type of dispersal which are likely to be crucial for the dynamics of source–sink populations. While our experiment shed new light on some of these aspects, all of them need further experimental and theoretical analyses.

Time-lags

In the present experiment, there was basically no time lag between the treatment and the dispersal response. Different time-lags in the coupling between population declines in the sink and dispersal from the sources may produce different dynamics at the population level (Ims & Hjernmann 2001). Such time-lags may be imposed by factors such as seasonality, ontogenetic delays and stage-dependent dispersal (see Ims & Hjernmann 2001 for a discussion).

Density-dependent compensation by in situ demographic responses

To what degree are spatially density-dependent losses in terms of emigration from source patches compensated for by density-dependent responses in *in situ* demographic parameters? In the present experiment, both the *per capita* recruitment rate in the source patches and the growth rate of colonization patches of the source–source systems appeared to be density-dependent. An even stronger compensatory recruitment rate could have been induced in the source–sink systems, given sexual maturation of the field-born cohort in our experiment. It is likely that the high initial density of old females in the source patches was responsible for the suppression of successful reproduction of young females. Density-dependent sexual maturation is a well-known phenomenon in microtine rodents (Krebs 1979, 1985).

Watkinson & Sutherland (1995) showed by means of theoretical modelling that negative density-dependence in recruitment as a result of immigration in theory may lead to misidentification of sources when using recruitment rates as a criterion. Herein, we have provided another demonstration, although this time empirical, that use of *per capita* demographic rates (i.e. recruitment) may give misleading indicators of what are source and sink habitats. Although the source–sink systems had the highest *per capita* recruitment rates, they nevertheless became sinks in terms of growth rates by the end of the breeding season.

Dispersal induced changes in demographic structure

Differential spatial density-dependence in the propensity for dispersal among different categories of individuals may alter the demographic composition of source-populations. In the root vole, density-dependent dispersal is much more pronounced in females than in males (Aars & Ims 2000, Andreassen & Ims 2000). Thus, in the neighbourhood of sink habitats, we could predict that female emigration would act as to decrease the proportion of females in source populations. Indeed, this prediction was confirmed in the present experiment. This result has two implications. First, in species with sex-specific, spatially density-dependent dispersal, spatially variable sex ratios can be indicative of spatially imbalanced dispersal (Doncaster *et al.* 1997), possibly due to source–sink dynamics. Second, a spatially variable demographic structure not only reflects spatial population dynamics, but it may also determine the dynamics. In the present experiment the decreased female-biased sex ratio also decreased the overall productivity of source patches in the presence of a sink.

Spatial scale

Spatial scale is a crucial aspect concerning the effect spatially density-dependent dispersal may have on the dynamics of source–sink populations. The kind of tight coupling between source and sink demography seen in our experiment may be only expected when sink patches are within the exploration range of putative dispersers in sources (Ims & Hjernmann 2001). A distance of 50 m, even over barren ground, is probably quite short for a dispersal-motivated root vole exploring its surroundings. However, as the distance between source and sink patches increases, it must be expected that vacant, suitable habitat patches will be less accessible and that the coupling between the dynamics will be weaker. Only further experimentation will be able to identify scale of correlated dynamics between sources and sinks (Bjørnstad *et al.* 1999).

Dependence of sink processes

In this experiment, we simulated sink habitats that was ruled by high periodic mortality rates. This situation may be the case when sink dynamics in productive habitats are induced by human exploitation/persecution or by periodic intrusion by patch-searching predators. Then, sink habitats may not be recognized as such by dispersing animals, which will be the case when sink demography is due to poor habitat quality (i.e. scarce resources). Animals may be expected to be more reluctant to disperse from source habitats so that spatial density-dependent dispersal may be less important if source-habitats are surrounded by recognizable sink habitats. New experiments are needed to address the effects of different types

of sinks, i.e. those ruled by high mortality vs. low recruitment rates.

CONCLUSION

In this study, we have shown experimentally that the demography of source-patch populations may be affected greatly by the presence of "mortality sinks" when such sink habitats are within the dispersal scale of the source populations, and particularly so when this population exhibits spatially density-dependent dispersal. Furthermore, we have provided the first empirical demonstration that sink-induced dispersal also may mould source-patch demography indirectly through changes in *in situ* demographic rates and population structure. Our results thus highlight new avenues for further experimental and theoretical analyses.

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