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Are small-scale landscape features important factors for field studies of small mammal dispersal sinks?

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Abstract

Interest in the influence of landscape features on animal movement has been widespread; however, few field studies of the emigration of small mammals from patches of habitat directly consider the effects of the small-scale landscape features. The simulation models of Stamps *et al.* (1987a, b) and Buechner (1987a, b) suggest that the size of a dispersal sink relative to the size of the source patch, the average distance traveled by dispersers in the sink, the ease with which dispersers cross the edge between the sink and a source patch, and source patch perimeter:area ratio may all be important influences on emigration rates. **A** review of field studies of small mammal dispersal into sinks suggests that in a substantial fraction of such studies the values of these factors fall within the ranges that the simulation models indicate have the greatest potential effect on emigration rates. New field studies of dispersal sinks that include a consideration of these factors are necessary in order to evaluate the magnitude of the impact of these factors on natural populations.

Introduction

The role that landscape features play in the dispersal of animals has been recognized for many years (*e.g.*, Stickel 1946; Van Vleck 1968; Brown 1969) and both theoretical and empirical studies have suggested that small-scale landscape features can influence the movement of animals of many taxa into or out of habitat patches (*e.g.*, Kareiva 1983, 1985; Wiens 1985; Wilcove 1985; Forman and Godron 1986; Schonewald-Cox and Bayless 1986; Buechner 1987a, b; Hansson 1987; Stamps *et al.* 1987a, b). Ecologists studying small mammals have been especially interested in the functioning of 'dispersal sinks', areas which absorb more dispersers than they produce, effectively removing animals from the source population. **A** number of studies of small mammal populations have included a consideration of general landscape features such as the number or overall connectivity of habitat patches (*e.g.*, Wegner and Merriam 1979; Fahrig *et al.* 1983). However, relatively few empirical studies address the possible influences of more detailed landscape features such as the size, shape, or edge permeability of individual habitat patches. The goal of this paper is to assess the potential importance of certain small-scale landscape features for studies of small mammal emigration from habitat patches into dispersal sinks.

Stamps *et al.* (1987a, b) and Buechner (1987a, b) used a series of computer simulation models to examine the influence of several small-scale landscape features on the proportion of dispersing animals emigrating from source patches. These models simulated a rectangular habitat patch contiguous with a second type of habitat which func-

Table 1. Summary of the simulation models of Stamps *et al.* (1987a, b) and Buechner (1987a, b). Variables shown in italics are considered in this paper.

Parameter analyzed	Range of values examined in the simulations	Range where changes in this parameter had the greatest affect on emigration rate
Source patch	6–600 home ranges per patch	Little effect of patch size *per se* was found
Number of dispersers produced per home range	0–4 dispersers per home range in the source patch	No effect on the proportion of dispersers emigrating from the source patch
Source patch perimeter:area ratio	9–100% of patch home ranges contiguous with patch edge	Low P:A ratio (P:A = .09–0.35)
Permeability of edges of source patch	Probability of a disperser at the patch edge moving into sink = 0.0–1.0	Low edge permeability (probability of crossing edge = 0.0–0.30)
Relative size of sink and source patch	Sink size divided by patch size = 0.10–17.0	Small sink size (S/H = 0.10–1.0)
Average distance dispersers move through the sink, i.e., stopping rate in the sink	Probability that a disperser will stop moving with each unit of area crossed = 0.05–1.00	Low stopping rates (stopping rate = 0.05–0.30)
Sink location with respect to source patch	Embedded in or surrounding the source patch	Little effect of sink location was found

tioned as a dispersal sink. Dispersers were generated within the source patch and moved throughout the simulated areas; stopping rates for dispersers were defined for both the source patch and the sink. The models distinguished between ‘dispersal’ and ‘emigration’. Dispersers were defined as those individuals which left their natal home range and moved one or more home range diameters before stopping (dying or settling into a new home range). Short movements entirely within a habitat patch were still considered dispersal; thus, dispersers might stop moving either within the source patch or within the dispersal sink. Only those dispersers which left the source patch were defined as having emigrated. Thus, animals leaving their home ranges but stopping within the source patch were operationally defined as having dispersed but not having emigrated. The emigration rate from the source patch was defined as the proportion of those dispersers originating within the source patch which stopped moving outside of it (= number of emigrants divided by the total number of dispersers).

In all, the effects of seven factors on emigration rates were examined by Stamps *et al.* (1987a, b) and Buechner (1987a, b). The models were designed to be relevant to species from three vertebrate taxa (reptiles, birds and mammals) and the range of values of parameters examined reflect this broad approach. The range of parameters examined and the results of the models are summarized in Table 1.

The models indicate that four factors may have major influences on the movement of animals from habitat patches into dispersal sinks: (1) the perimeter:area ratio of the source patch; (2) the size of the dispersal sink relative to the size of the source patch; (3) the average distance which dispersers can travel through the dispersal sink, and (4) the ease with which individuals move across the edges of the source patch (Table 1). The simulations also suggest in which part of their range changes these parameters are expected to have the greatest effect on emigration (Table 1). In this paper, I compare the ranges of these parameters that occur in field studies of small mammals that involve emigration into dispersal sinks with the ranges that the simulations suggest are most likely to influence emigration rates.

Methods

Many field studies of small mammal populations involve the capture of individuals leaving source populations and moving into dispersal sinks. I reviewed available issues of the journals Acta Zoologica Fennica, American Midland Naturalist, Canadian Journal of Ecology, Ecology, Journal of Animal Ecology, Journal of Mammalogy and Oecologia for field studies of rodents in which the movement of animals into dispersal sinks was measured and from which the relevant parameters could be estimated. In each case, the dispersal sink was an area which more animals moved into than moved out of (as measured by the authors of the reports). In studies of naturally occurring sinks movement was habitat-related. In most, but not all, cases of artificially produced sinks this occurred because animals entering the sink were snapped trapped by the researchers; in one case (Table 2 #9) animals were attracted to the sink by the addition of food.

Studies selected for analysis employed some combination of snap and live trapping to measure the demographic characteristics of the populations involved, the number (and in some cases the direction and length) of dispersal movements, and the population densities and/or population growth rates in source areas and in the dispersal sink. In some cases, I analyzed a portion of an extensive study without discussing the rest of the larger work (*e.g.*, Pokki 1981). The most common questions asked by the reviewed studies concerned the demographic characteristics of dispersing animals such as their sex, age, weight or breeding condition, or the relationships between the magnitude of dispersal and the density or growth rate of the source population. The majority of the studies reported dispersal rates, however, because experimental designs varied widely, direct comparisons of the magnitude of dispersal are not possible in this analysis.

In each of the 17 empirical studies reviewed, I noted the following information:

1. Sink type: This refers to whether the sink was naturally occurring or artificially produced by the investigators. Many investigators produce sinks artificially by removing resident animals from an area of good habitat (Table 2; see also brief reviews in Dobson 1981 and Wolton and Flowerdew 1987) or by adding attractive resources (*e.g.*, food; Dobson 1981) to an otherwise suboptimal area. Sink type was assessed straightforwardly from the methods reported by the author(s) of each report.

2. Sink and patch habitat: This category provides additional information about the experimental design employed in the reviewed studies. I noted the general habitat types that occurred within the source patch and within the sink. Although no direct estimates of the ease with which individuals could move across patch edges were obtainable, the difference in habitat types may provide some information about the permeability of the edge between the source patch and the dispersal sink (as defined by Stamps *et al.* 1987a, b).

3. Relative sink size: This was estimated from illustrations or written information in each report and was calculated as the area of the dispersal sink divided by the area of the source patch.

4. Patch perimeter:area ratio: This ratio, as the term is used in the simulations, refers to the part of the patch that is in contact with the sink (Buechner 1987a, b). Stamps *et al.* (1987a, b) and Buechner (1987a, b) calculated patch perimeter: area ratio as the proportion of home ranges within the patch that are contiguous with the dispersal sink. Although numerical estimates of this measure of perimeter: area ratio could not be calculated for any of the studies reviewed, I was able to estimate roughly whether the proportion of home ranges within the source patch that adjoined the sink was most likely high (0.65–1.0), moderate (0.35–0.65), or low (0.0–0.35). This was done based on information about the size and shape of the patch, arrangement of sink and patch habitats and the home range size of the animals living in the patch.

5. Fate of dispersers: I noted whether dispersing animals captured in the sink were removed from the population or were released to continue their movement. This dichotomy is related to disperser stopping rate as defined in the simulations – the probability that a disperser will stop moving with each unit of distance crossed (Stamps *et al.* (1987a, b). For example, if all dispersers stop moving as soon as they enter the sink, the stopping rate in the sink

would be 1.0. In field studies, where dispersers may stop moving because they are captured and removed by the researchers conducting the study, stopping rate in the sink may approach 1.0 if dispersers entering the sink are immediately captured and removed from the population.

Note that some of these estimates were obtained from figures and descriptions in the papers, rather than from direct, quantified, reports by the authors, and although useful for relative comparisons, should not be treated as precise values.

Results

Patch perimeter:area ratio

In the simulations the perimeter:area ratio of a patch was strongly positively related to the magnitude of emigration, and changes in patch perimeter: area ratio most strongly influenced emigration when patch perimeter:area ratio was low. (*i.e.*, less than 0.35; Table 1). Among the 13 reviewed studies in which source patches were contiguous with artificially created sinks, three were estimated to have low perimeter:area ratios and ten to have moderate perimeter:area ratios. The four studies of naturally occurring sinks encompass a greater range of perimeter:area ratio values, with two patches having low perimeter:area ratios and two having high perimeter:area ratios (Table 2). Thus, five of 17 reviewed studies appear to have perimeter:area ratios falling in the range where the models suggest that differences in patch perimeter:area ratios are most likely to influence emigration rates.

Sink size

In the models, the relationship between relative sink size and emigration from the source patch followed a decelerating, asymptotic curve (Buechner 1987a) such that when sinks were smaller than the source patch ($S/H \leq 1.0$) relatively small changes in sink size produced substantial changes in emigration rate. The effect of changes in sink size gradually decreased, so that when sinks were more than two and a half times larger than the source patch ($S/H > 2.5$) changes in sink size had relatively little effect on emigration (Table 1; Buechner 1987a, b).

Although only four studies of naturally occurring dispersal sinks were found, even this small number of examples indicates that a wide range of relative sink size may be found in natural situations. Three naturally occurring dispersal sinks were equal in size to or smaller than the area occupied by the source population (Table 2). The simulations suggest that in situations like this, even small changes in sink size could produce substantial differences in emigration rate. In one of the four studies of naturally occurring sinks an area of poor habitat much larger than the source patch acted as a sink (Table 2); in such situations differences in sink size between studies or between patches were unlikely to confound measures of emigration rate.

Sinks created artificially by researchers vary widely in size with respect to the source patches (Table 2), however, most artificial sinks in the reviewed studies were smaller than the source patches. S/H for the reviewed studies of artificial sinks ranged from .002– 1.63. Eleven of the studies of artificial sinks had estimated S/H values less than or equal to 1.0 (Table 2), the range over which changes in sink size are expected to have the substantial influence on the magnitude of emigration (Table 1).

Distance traveled by dispersers through the sink

Stamps *et al.* (1987a) defined the ‘stopping rate’ of dispersers in the sink as the probability per move (each unit of sink habitat crossed) that a disperser will stop (see also Buechner 1987c). The inverse of this stopping rate thus represents the average distance moved by dispersers through the sink before stopping. In the models, as stopping rates increased, emigration increased (this occurred because when stopping rates were high in the sink very few dispersers returned to the patch after having entered the sink; see Stamps *et al.* 1987a). Emigration rate declined substantially with changes in sink stopping distance only when stopping rates were low (< 0.30) (Buechner 1987a, b).

Table **2.** Characteristics of the small mammal dispersal sinks in the 17 studies reviewed here.

Species	Sink type[1]	Sink habitat	Patch habitat	Sink S/H[2]	Patch P:A[3]	Rel./rem.[4]
Microtus agrestis, Pokki 1981	nat.	woods	old field	1.0	high	rel.
Microtus pennsylvanicus, Tamarin 1977	nat.	woods	old field	1.0+	low	rem.
Peromyscus leucopus Krohne and Baccus 1985	nat.	old field	forest	0.2	low	rel.
Microtus ochrogaster and *M. pennsylvanicus,* Verner and Getz 1985	nat.	agricul. field	bluegrass	20+	high	rel.
Peromyscus leucopus Stickel 1946	art.	mature forest	mature forest	0.1	low	rem.
Microtus pennsylvanicus, Van Vleck 1968	art.	old field	old field	0.01 - 0.07	low	rem.
Sigmodon hispidus and *Reithrodontomys fulvescens* Joule and Cameron 1975	art.	coastal prairie	coastal prairie	1.0	mod	rem.
Peromyscus maniculatus Fairbairn 1978	art.	coastal	coastal	0.002	mod	rem.
Spermophilus beecheyi, Dobson 1979	art.	oak savanna	oak savanna (food added)	0.05	mod	rel.
Microtus ochrogaster, Gaines *et al.* 1979 (a)	art.	old field	old field	1.0	mod	rem.
(b)	art.	burned field	old field	?	mod	rem.
Microtus townsendii, Beacham 1980	art.	grassy field	grassy field	0.9	mod	rem.
Sperrnophilus beechyi, Dobson 1981	art.	savanna	savanna	1.0	mod	rem.
Microtus pennsylvanicus, Baird and Birney 1982	art.	meadow	meadow	0.33 - 0.49	mod	rem.
Peromyscus leucopus, Krohne *et al.* 1984	art.	mature forest	mature forest	1.63	mod	rel.
Microtus pennsylvanicus, Tamarin *et al.* 1984	art.	woods	field	0.20	low	rem.
Peromyscus leucopus, Krohne and Miner 1985	art.	mature forest	mature forest	1.63	mod	rem.
Microtus californicus, Heske 1987	art.	coastal prairie	coastal prairie	0.08	mod	rel.

[1] Naturally occurring or artificially produced.
[2] Sink size divided by source patch size.
[3] Source patch perimeter:area ratio, *i.e.*, the proportion of home ranges in the patch which are contiguous with the edge between the patch and the sink.
[4] Whether dispersers captured in the sink were released to continue their movement or removed from the population.

In the reviewed studies one of the four studies of naturally occurring sinks and 10 of 13 studies of artificial sinks employed experimental designs in which all emigrants are captured and removed from the sink upon capture, a technique likely to produce relatively high stopping rates. Thus, 11 of the **17** reviewed studies employ designs which the simulations suggest make it unlikely that differences in stopping rate influenced emigration rates directly.

Barriers to emigration

The simulations measured the edge permeability of a patch as the probability that a disperser approaching the edge of the patch would cross it and move into the sink (Stamps *et al.* (1987b). In the simulations the edge permeability of a patch was strongly positively related to the magnitude of emigration (Table *2;* details in Stamps 1987b). In field studies the similarity of habitat types in the sink and source areas may affect the permeability of the edge to movement; presumably fewer animals will readily cross into unfamiliar or suboptimal habitat than would enter familiar or optimal habitat. In three of the four reviewed studies of naturally occurring sinks and two of the 14 studies of artificial sinks the sink is an area of poor habitat which dispersers may be reluctant to enter (Table 2).

The permeability of the edge between two areas may also be affected by the presence of resident animals. When the sink is an area of good habitat from which all residents have been removed dispersers are expected to enter the cleared area at a rate greater than if residents were present in the sink. This has been shown to be the case for some species and has been labelled the 'vacuum effect' (*e.g.*, Tamarin *et al.* 1984 or Krohne and Baccus 1985). Emigration rates in studies in which the sink and source patch contain similar habitat and in which all animals captured in the sink are removed, as was done in 9 of the 14 studies of artificial sinks reviewed here, may be influenced by this effect.

In the simulations the effect of small differences in edge permeability on emigration are expected to be greatest when patch edges are relatively impassable (Stamps *et al.* 1987b). This implies that variations in the permeability of edges may be most important for studies in which the sink and source habitats are very different or where artificial barriers substantially impede movement. Some studies use semi-permeable barriers such as drift fences (*e.g.*, Beacham 1980; Johnson and Gaines 1987) or mowed strips (*e.g.*, Verner and Getz 1985) surrounding source habitat patches. Unfortunately, no information is available about the extent to which movement across the edge is reduced by these barriers.

Interaction effects

In order to assess the potential importance of the above parameters for field studies of dispersal, it is necessary to relax the 'all-else-being-equal' assumption implicit in analyzing one variable at a time and to consider the ways in which the parameters interact to influence emigration. The simulation models showed that the value of stopping rate occurring in a given situation can affect the magnitude of the influence of both patch perimeter:area ratio (Stamps *et al.* 1987a and b) and sink size (Buechner 1987a and b) on emigration. The influence of patch perimeter:area ratio on emigration is expected to be strongest when dispersers stop as soon as they enter the sink (Stamps 1987b; Buechner 1987a, b). In 11 of the 17 reviewed studies dispersers captured in the sink were removed from the population (Table *2):* four of these studies also had low patch perimeter: area ratios. Such designs are especially likely to have measurements of emigration rate confounded by small differences in patch perimeter:area ratio.

Stopping rates also influence the relationship between sink size and emigration rate. Changes' in sink size are not expected to have any effect on emigration rate if all dispersers stop as soon as they leave the sink (stopping rate = 1.0; Buechner 1987b). In those studies in which dispersers are captured and removed from the population as soon as they enter the sink, stopping rates in the sink may approach 1.0. The relative size of the sink is, thus, most likely to be an important factor in those studies in which dispersers are captured after having moved some distance through the sink or are released after capture. Six of the studies reviewed (including three natural and three artificial sinks) had designs in which dispersers were released after capture (Table *2);* of these, four had $S/H \leq 1.0$, a situation in which small differences in sink size are likely to have substantial effects on emigration rate.

Discussion

The results indicate that the parameters identified by the simulation models of Stamps *et al.* (1987a, b) and Buechner (1987a, b) are of potential importance for a substantial fraction of field studies of the movement of small mammals into dispersal sinks. All but one (# 16, Table **2)** of the reviewed studies had one or more parameters in the sensitive range indicated by the simulation models. Even when interaction effects were considered, over half (8 of 17) of these studies had combined parameter values in the sensitive range.

The designs of many of the studies reviewed here are such that uncontrolled or unmeasured small-scale landscape features may have influenced emigration rates, however, a number of problems complicate interpretation of these results. The studies reviewed here do not represent a direct test of the models. In some cases, parameter values had to be estimated by indirect means as they were not directly measured by the researchers. In the reviewed studies variables other than those analyzed here were of primary interest and the role of these variables, which is unknown, complicates any conclusions. None of the reviewed studies is concerned solely with the magnitude of emigration; for the most part they address questions related to population regulation or stability. Small-scale landscape features are likely to be confounding the results of these studies only to the extent that the magnitude of emigration is relevant to the questions they address.

Although the degree to which the results of the reviewed studies were confounded by small-scale landscape features is not clear, it is clear that studies of emigration rates, *per se*, will have to be designed to carefully consider such factors. If future studies which focus directly on the magnitude of emigration from small mammal populations utilize designs similar to those employed in the reviewed studies, variation in uncontrolled landscape features will make the comparison of results between studies difficult. In particular, comparisons of the magnitude of emigration into two or more sinks, or from two or more patches, could easily have their results confounded by uncontrolled landscape features.

Since methods are not always comparable, and emigration rates are not usually reported, the reviewed studies do not allow a detailed assessment of exactly how landscape features are influencing emigration rates in the populations being studied. New field studies of dispersal sinks which include a consideration of small-scale landscape factors are necessary in order to evaluate the magnitude of the impact of these factors on natural populations. The current review suggests some types of field experiments that could be used to test for confounding factors or to validate the implications of the models. Field studies in which all dispersers are captured and removed as soon as they enter the sink could be especially valuable for studying the effects of patch edge permeability and perimeter:area ratio. In this case, the effects of patch perimeter:area ratios could be studied without the additional complicating effects of variable sink sizes. Patches of varying sizes and shapes, embedded within the same sink habitat, could be used to estimate the effects of patch perimeter:area ratio on the proportion of potentially dispersing animals within the patch population that actually emigrate. The use of drift fences or other man-made barriers could serve to control for patch edge permeability. While difficult methodologically, it may also be possible to obtain field estimates of patch edge permeability from removal studies (see Stamps ***et** al.* 1987b), by estimating what percentage of the dispersers approaching the edge actually cross into the sink.

Studies in which captured dispersers are released may be yield information about the effects of sink size. Emigration rates could be compared for patches of the same size and shape, containing the same type of habitat and with the same type of edges (*e.g.*, a given type of drift fence) but adjacent to sinks of different sizes. In addition, designs which release dispersers could provide estimates of naturally occurring disperser stopping rates (due to settlement and/or mortality) by monitoring how far dispersers move before stopping (Buechner 1987c).

Although the models of Stamps ***et** al.* (1987a, b) and Buechner (1987a, b) strongly indicate that small-scale landscape features may be influencing emigration rates in some field studies of the movement of small mammals into dispersal sinks, they do not specify how such factors may influence population regulation processes. The simulations do not address the role of dispersal in population regulation, nor do they incorporate any density-dependence of dispersal rates (Stamps 1987a, b). This is because the simulations represent simplified 'snapshot' views of emigration into dispersal sinks, rather than modeling continuous dispersal from a growing or declining population. The simplifying assumptions of the simulations do not belie the potential importance of the implications of the models; instead they indicate the need for field studies designed to systematically examine the importance of landscape features in real populations. The details of the relationships between emigration rates and population dynamics or stability remain unknown (Lidicker 1985). Until an understanding of such relationships is elucidated, sink size and location, patch perimeter:area ratio and edge permeability, and the stopping rate of dispersers remain variables of potentially great importance for field studies of small mammal populations.

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