



# Metapopulation Collapse: The Consequences of Limited Gene-Flow in Spatially Structured Populations

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## Introduction

The importance of spatial structure has long been recognized in the ecological and evolutionary literature, beginning with early work on island biogeography, where there was a clear recognition of the relation between the degree of isolation, colonization rates, and species diversity.<sup>1</sup> However, only in recent decades have both empirical and theoretical studies explicitly focused on investigating the ecological and evolutionary dynamics of spatially distinct populations connected by dispersal, migration and gene-flow. A key development in promoting research in this area has been the widespread acceptance of “metapopulations” (systems of populations connected in space and time by processes of colonization and extinction<sup>2</sup>) as a meaningful phenomenon in nature. The metapopulation paradigm has become widely recognized as an important conceptual tool within which to address applied problems (e.g., maintenance of species and genetic diversity within increasingly fragmented landscapes), as well as more abstract issues (e.g., group selection, stability of predator-prey and host-pathogen dynamics, genetic structure and relatedness among populations). For example, it has become very clear that local populations are often ephemeral.<sup>3</sup> This has led many researchers to focus on metapopulation structure and dynamics as an ecological explanation for the maintenance of long-term regional stability in the face of significant rates of local population extinction. From a genetic perspective, investigations of spatial structure have focused on the relationship between colonization and extinction processes, and the distribution of genetic variation. However, in spite of the interconnected nature of genetic and ecological processes, and

perhaps due to the relatively recent emergence of metapopulation studies, there is still very little communication between ecologists and geneticists working on spatial problems.

### Inbreeding and Population Dynamics

One topic that has concerned conservation biologists in recent years is the role of genetics in population viability.<sup>4-10</sup> When a species is confined to small populations, its genetic characteristics will be influenced by the related processes of genetic drift and inbreeding.<sup>11,12</sup> This is usually manifested by an increase in homozygosity, and a generalized decrease in viability or vigor due to 'inbreeding depression'. Most obviously, one consequence of an increase in homozygosity is increased phenotypic expression of deleterious recessives, the effect thought to be the primary cause of inbreeding depression.<sup>13</sup> Moreover, decreased heterozygosity can have a negative impact on fitness when heterozygote genotypes are the most fit (heterozygote advantage). Additionally, decreased genetic diversity that accompanies small population size can have substantial fitness consequences when associated with ecological processes such as disease transmission.

All of these effects threaten the viability of small populations since the decrease in fitness is often manifested by such demographic effects as decreased birth rates or higher rates of mortality. These effects may become self-reinforcing if inbreeding depression begets even smaller populations which beget more severe inbreeding depression (i.e., the "extinction vortex" discussed by Gilpin and Soule<sup>14</sup> or a form of "mutational meltdown"<sup>15,16</sup>). This is potentially of great significance to conservation biologists because many species are becoming confronted with locally small population sizes owing to habitat destruction or fragmentation, over-exploitation, or the negative impacts of exotic introductions. Theoretical and empirical studies suggest that the species that should be most prone to inbreeding depression are those that have existed in large, outbred populations over much of their recent evolutionary history. These conditions are favorable for the maintenance of high levels of genetic diversity, but also the accumulation of large genetic loads as a consequence of the balance between mutation and selection. In population genetic terms, it is the expression of this genetic load following a radical change in population structure that is a major cause of inbreeding depression. Since many species that are currently threatened by small population size were much more common until recently, inbreeding depression may be of real concern.

While population extinction owing to the self-reinforcing effects of inbreeding depression is a theoretical possibility, how important a concern should this be to conservation biologists in a world in which numerous species are confronted by numerous problems? Theory suggests that, in some regards, inbreeding depression resulting from genetic drift might only come into play after a population has become so severely compromised by other factors as to be threatened with extinction by demographic or environmental uncertainty.<sup>9,15-17</sup> Consider, however, that in systems where colonization/extinction processes are important, most local populations will be founded by small numbers of individuals. If inbreeding can arise immediately following colonization, then it seems likely that any reductions in fitness would have consequences, not only for population growth, but also for the rate at which new populations are

### Genetics of Metapopulations

From a conservation perspective, high rates of population turnover are predicted to have two important consequences. First, the frequent turnover of local populations may reduce the global effective population size.<sup>18-21</sup> In a theoretical system with a constant number of populations ( $n$ ), each capable of growing to size  $N$ , the total or global number of individuals is  $nN$ . With extinction and recolonization the global effective population size would be considerably less than  $nN$  because the individuals occupying recently founded populations trace their ancestry to the populations from which the original colonists were derived. This effect is most important when  $n$  is small and the extinction rate high.

Second, it must often be the case that local populations are founded by a much smaller number of individuals (represented by the variable  $k$  in some models) than eventually come to occupy a habitat patch (that is,  $k < N$ ). Thus, with frequent extinction and recolonization, local populations might contain a limited amount of genetic variability (because  $k$  is small) even if  $N$  were fairly large; the individuals comprising even relatively large populations could be related to a much smaller number of founders. This may result in inbreeding depression in a seemingly abundant species. For example, if a population were founded by two unrelated individuals, members of the next generation would be the products of outbreeding, but the members of the generation following that would be equivalent to the products of sib mating. If the population had been founded by two siblings, the inbreeding effects would be manifested one generation earlier. These inbreeding effects can compound if populations undergo slow population growth,<sup>22</sup> especially if there is limited gene flow via migration into the newly established populations.

The events occurring in the first few generations following the initial establishment of a population are likely to be of crucial importance. In particular, it is critical whether populations receive additional input via immigration during those first few generations. The effect of immigration can be viewed from both demographic and genetic perspectives. From a purely demographic perspective, immigration can increase population persistence by simply contributing to population growth. This is the well known "rescue effect."<sup>23</sup> From a genetic perspective, numerical immigration leads to an increase in population size and will reduce genetic drift when the immigrants breed and reproduce. More critically, gene flow into a small population is likely to alleviate the negative impact of inbreeding depression. The greater reproductive success of this outbred group will increase the probability that the population at large will persist, as well as the probability of subsequent colonization of new sites. We will refer to this genetic effect of immigration as 'genetic rescue.' In plants, often the pathways of immigration of individuals will not be identical to the pathways for the immigration of genes. For example, in plants, immigration of genes can occur by pollen flow, and assuming pollen is not limiting seed set, this may have no direct effect on population growth through seed production, although it may have genetic consequences. However, immigrant seeds can have two effects; they may increase numerical abundance directly (= demographic rescue) or they may reduce the levels of inbreeding (= genetic rescue).

Might inbreeding within newly established demes threaten the stability of entire metapopulations? In simple metapopulation models the proportion

extinction and colonization.<sup>24</sup> If colonization rates are not sufficient to offset extinction, the entire system will collapse. More realistically, colonization could be considered to consist of two stages. The first stage requires that colonists make their way to an empty patch of suitable habitat. This depends largely on the rate at which surrounding demes export dispersing individuals. Once a site is occupied, the second stage of colonization is that in which the newly founded population grows to be large enough to itself export colonists. Only until this second phase is completed (which we will refer to as 'effective colonization') does the colonization event increase the long-term stability of the metapopulation. It must be a common occurrence in nature that populations fail to undergo the transition from stage one to stage two of colonization, owing to demographic stochasticity or environmental uncertainty. The success of a colonizing propagule has been evaluated according to the probability that the population it founds will grow to some critical size or according to the expected time to extinction.<sup>25-28</sup> Theory suggests that the probability of successful establishment is largely a function of the number of original colonists and the potential population growth rate. In stochastic models, local populations founded with small numbers of individuals and low population growth rates are likely to undergo a random walk to extinction before reaching a critical size.<sup>26</sup> This problem is exacerbated when environmental catastrophes are included in the models.<sup>28</sup>

Inbreeding depression could reduce the probability of effective colonization by reducing the population growth rate in the early generations of population establishment. It is our contention that this could have a 'ripple effect' across an entire metapopulation. Goel and Richter-Dyn<sup>26</sup> develop a stochastic model in which the occupancy rate of a metapopulation is a function of the birth and death rates within local populations (which determine persistence times at the local level and thus both the extinction and colonization rates). We suggest that if inbreeding depression decreases the probability of effective colonization, this should result in lowered occupancy rates which will, in turn, limit the number of emigrants from the remaining established populations. Not only would this reduce the frequency of successful colonization events, but any reduction in  $k$  would further reduce the rate of successful transition from stage one to stage two of colonization, since the smaller the number of founders the greater the potential for inbreeding depression. In this chapter, we address the question of whether this process could become self-reinforcing and lead to the collapse of metapopulations in nature. We explore this issue in the context of theoretical and empirical studies of local and metapopulation dynamics of the common ruderal plant, *Silene alba*.

## The *Silene alba* Metapopulation System

### Background and Natural History

Over the past decade, our interests have focused on various aspects of the population biology of the plant *Silene alba*. *S. alba* is a short-lived dioecious perennial herb, originally introduced from Europe in the mid-1800s, that has since spread throughout eastern North America and Canada.<sup>29</sup> In Giles County in southwestern Virginia, where we have studied population dynamics and genetic structure of this system in nature, the plant is found primarily

Although much of our research has centered on the local and metapopulation dynamics of the host and its pathogen *Ustilago violacea*,<sup>330-36</sup> in recent years we have also begun to investigate other aspects of spatial structure in this system, including within and among population genetic structure,<sup>37,38</sup> the consequences of inbreeding (CM Richards unpublished data) and the evolution and maintenance of biased sex-ratios.<sup>39</sup> Here, we first briefly describe results from a long-term census of natural populations. We focus primarily on the plant host, as such data are central to many of our other studies, particularly those on genetic structure and inbreeding (where knowledge of population history is crucial). We show that there is a high rate of population turnover in the *S. alba* system, and that it conforms to genetic expectations for a metapopulation where local dispersal predominates.<sup>40</sup> We then discuss some empirical results from field studies documenting the magnitude of inbreeding in *S. alba*, and the importance of connectedness (= among population dispersal) for genetic rescue. Finally, we develop a spatially explicit simulation model to illustrate how demographic and genetic rescue might operate to sustain the metapopulation in the face of inbreeding effects accompanying colonization.

### The Roadside Census of Natural Populations

Central to our overall goal of understanding the regional dynamics of the *Silene-Ustilago* system has been a large-scale longitudinal survey of hundreds of natural populations of *Silene*. This survey has taken place annually since 1988 within a 25 x 25 km<sup>2</sup> area in Giles County, Virginia, where both the plant and pathogen are common along roadsides.<sup>34</sup> Within this area, we have defined populations as the number of healthy and infected individuals in a 40 m segment of roadside or "pilon" (sensu Thrall and Antonovics<sup>3</sup>). Our definition of what constitutes a population was based on reasons of practicality as well as biology. First, it is generally difficult to delineate population boundaries in nature except in some situations (e.g., aquatic species in systems of lakes). Second, 40 m segments can easily be relocated using a car odometer. Finally, seed and pollen dispersal are limited such that the scale of 40 m encompasses at least one, but not many ecological and genetic neighborhoods.<sup>34,41</sup>

During the first two weeks of June of each year, roadsides are censused for the number of healthy male and female plants (and the number of infected plants). A total of 7500 segments are included; between 400 and 500 are occupied at any one time, and most of these (80%) have no disease present.<sup>3</sup> The census results for the first nine years indicate a high rate of population turnover, with substantial colonization and extinction.<sup>33,4</sup> These colonization and extinction processes are dependent both on population size and proximity to other populations.<sup>33,4,42</sup>

### Empirical Studies of Genetic Structure and Inbreeding Effects

#### Genetic Structure in the *Silene* Metapopulation

An issue of considerable theoretical interest has been the relationship between spatial structure, colonization and extinction processes, and the de-

systems which display significant population turnover and local dispersal, should also have considerable potential for among population genetic variation. In contrast, others have concluded that high turnover rates will only be found in 'weedy' species, which are likely to be good dispersers, and this will tend to eliminate such variation.<sup>42</sup> Regardless, interpretation of results from studies of population genetic structure requires knowledge about population history. In the case of *S. alba*, crucial information about time since establishment (for newly founded populations) and changes in population size is readily available from the census data.

Genetic structure was first estimated from allele frequencies calculated from 12 persistent populations located within the metapopulation census area (all within 10 km of Mountain Lake). Two classes of genetic markers were used. First, seven polymorphic allozyme loci were used to estimate the local geographic partitioning of nuclear genetic variance. From these data  $F_{st}$  was estimated as 0.12, suggesting moderate genetic structure at the local level. In addition, the  $F_{st}$  estimated from the distribution of four cpDNA haplotypes was 0.67, clearly much greater than that seen with the allozymes.<sup>37</sup> These differences in the  $F_{st}$  estimates were in part due to the higher level of gene flow expected for nuclear genes relative to chloroplast genes, since the former can also move between populations in pollen.<sup>37-44</sup> Most importantly, the results showed that  $F_{st}$  for newly founded populations was much greater than for older, established populations. This pattern supports the idea that most colonization events occur as a result of a small number of founders.<sup>38</sup>

### Levels of Inbreeding and Among Population Gene-Flow

In 1994 and 1995, Richards and McCauley (unpublished data) used arrays of experimental populations to examine the effects of population size and distance between populations on rates of gene flow. These populations were composed of genotypes homozygous at diagnostic allozyme loci, making it possible to explicitly identify pollen movement into a focal patch. The experiment was conducted in a long clearing in the Jefferson National Forest where no naturally occurring populations of *S. alba* exist, which ensured that the experimental system was closed off from any outside pollen. Each experimental array consisted of 8 deer-exclusion cages separated from one another by either 80 or 20 m. Population sizes/cage ranged from 4-24 potted individuals at a 1:1 sex ratio. A regular census of the cages was taken to record the numbers of open male and female flowers and any seed capsules that had formed. The phenology data were crucial in understanding how the abundance of flowers in neighboring cages affected the influx of foreign pollen into the focal cage. These experiments were repeated three times over two field seasons.

The motivation for the study was to understand what factors might be influencing genetic connectedness among newly established sites. Along the census route, *Silene* populations are frequently small and isolated. Our results demonstrated that both size and isolation affect pollen movement among populations. Specifically, genotype data from over 2400 progeny produced in these arrays showed a clear effect of distance on the rate of gene flow receipt. In the cages spaced 20 m apart, over 47% of the pollen came from outside, whereas in the 80 m cages there was less than 6% gene flow. Both the number of flowers in the focal population (target) and the size of the neighboring populations

pollination success was higher in the widely separated arrays than in the arrays separated by only 20 m. This difference may be caused by an increase in the per capita pollination activity among more widely separated cages. These results suggest that in small natural populations, well isolated from their neighbors, there would be a great preponderance of within site pollinations, and therefore potentially substantial levels of inbreeding.

To investigate inbreeding depression directly, a second study examined the reduction of fitness from bi-parental inbreeding. A collection of outcrossed lines was made, from which lines were created with inbreeding coefficients ( $F$ ) of 0.125 (half sib mated), 0.25 (first generation full sib mated) and 0.375 (second generation full sib mated). These inbreeding coefficients represent values of inbreeding that might reasonably be expected to develop within a few years of colonization (recall that  $F_{st}$  values among recently founded populations in nature were approximately 0.20). Seed germination data from these crosses revealed a substantial amount of inbreeding depression in *S. alba* (Fig. 5.1). Germination rates of seeds produced by half and full sib mating were 67% and 37%, respectively, of the outcrossed controls; similar high levels of inbreeding have been shown for other outcrossing plant species.<sup>45</sup>

To sample the standing level of inbreeding depression in natural populations, a series of crosses within and among natural populations was conducted from 1994-1996. Germination rates from crosses within and among 10 recently colonized sites that were isolated by at least 160 m from any neighboring population were contrasted with germination rates of seeds derived from crosses within and among 2 recently colonized sites that were within 80 m of a large established population. Crosses were conducted at three levels: within families within sites ( $F > 0.125$ ), among families within sites ( $F$  was unknown) and lastly, among site crosses ( $F = 0$ ). In the more isolated populations, within family and among family-within site crosses reduced the seed germination to 43% and 52%, respectively, of the outcrossed controls. These same crosses conducted within and among the less isolated populations resulted in reductions to only 64% and 91% of the controls. These data support our conclusion that colonies founded beyond the influence of substantial gene flow may suffer inbreeding depression.

If moderate inbreeding can reduce the fitness of relatively small and isolated colonies, how might these effects be counteracted? To investigate how the relatedness of a founding cohort of colonists influences subsequent gene flow receipt, pairs of sibs, each homozygous at a locus for a diagnostic allele, were placed in cages 20 m away from another cage containing a sib pair from another lineage homozygous for an alternate allele. Replicate pairs of cages were separated by over 300 meters, ensuring that pollen exchange was solely among adjacent cages. Using this design, each cage could both send and receive pollen. As a group, females could be pollinated by a combination of local related pollen and foreign unrelated pollen. Genotyping of progeny revealed that unrelated pollen sired a disproportional number of seeds compared to what would be expected under random mating within and among paired cages. Even when the expected gene flow rate was corrected for inbreeding depression expected with pollen from full sibs, the observed gene flow rate was significantly higher than the expectation. These data suggest that gene flow into inbred populations is greatly enhanced by some type of discrimination, and this mechanism may facilitate genetic rescue of newly established populations

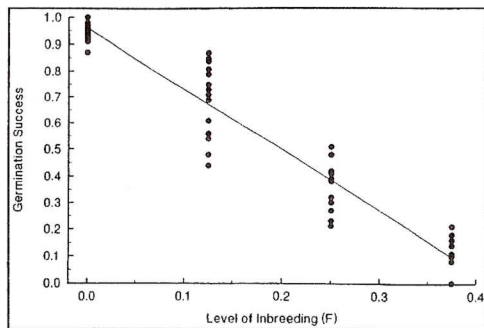


Fig. 5.1. Negative relationship between the fraction of seeds germinating for *Silene alba* and the level of inbreeding in a greenhouse experiment (see text for discussion). The slope of the regression line is  $-2.3$  ( $P < 0.0001$ ); this value was used to translate calculations of within-population values of  $F$  into germination success in the spatial simulation.

### Computer Simulation Studies

The empirical studies discussed above indicate that in *Silene alba*, a) there is a substantial amount of genetic structure at the among-population level, b) levels of inbreeding can potentially be quite high in small and/or isolated populations, and c) there is potential for gene-flow among populations to 'rescue' inbred populations to a significant extent from such effects. These results further suggest the possibility that changes in dispersal (e.g., through loss of a pollinator) could result in decreased potential for genetic rescue and cascading effects leading to collapse of the metapopulation. To investigate these issues further, we did a series of experiments using computer simulations of single populations and the metapopulation as a whole.

### Inbreeding and Genetic Rescue Within Single Populations

To simulate how within-population persistence might be affected by growth rate, carrying capacity, and genetic rescue, we assume that the population is genetically variable in two alleles at a single locus, and that the three genotypes  $A_1A_1$ ,  $A_1A_2$ , and  $A_2A_2$  differ in both their intrinsic growth rates,  $r_{ij}$ , and in their carrying capacities,  $K_{ij}$  (where  $ij$  refers to the  $ij^{\text{th}}$  genotype;  $i, j = 1$  or  $2$ ). If  $X_{ij}$  and  $N_t$  are, respectively, the number of plants and total population size (the sum of the  $X_{ij}$ ) at time  $t$ , the basic model for within population dynamics can be written as:

$$X_{ij,t+1} = X_{ij,t} \left[ 1 + \frac{b_{ij}}{1 + \gamma_{ij} N_t} - d_{ij} \right] \quad (1)$$

where  $d$  is the intrinsic death rate,  $b$  is the maximum reproductive rate (i.e., the limit of  $N_t$  as it approaches zero) and  $\gamma$  is a constant that determines the strength of density dependence. The per capita reproductive rate declines hyperbolically as population density ( $N_t$ ) increases (46,47).

Demographic and genetic stochasticity were introduced as follows. The fecundity of each genotype was assumed to be given by  $\gamma_{ij} = 1 + r_{ij}$  (where  $r_{ij}$  = the hyperbolic birth function -  $d_{ij}$ ). A fecundity was assigned to each individual by randomly drawing a number from a Poisson distribution with a mean and variance of  $\gamma_{ij}$  for that individual.<sup>48</sup> This was done for every individual of every genotype. Expected genotype frequencies in the progeny were then calculated by assuming that each individual had mated randomly, and that therefore the progeny genotypes of the  $ij^{\text{th}}$  seed parent were produced in proportion to the frequency of  $A_1$  and  $A_2$  in the pollen pool. This gave a set of expected genotype frequencies following stochastic variation in individual fecundity, but assuming fertilization and segregation events were deterministic. Genetic stochasticity was then introduced by assigning individuals to genotype in proportion to these expected genotype frequencies. This was done by generating a uniform random variable between 0 and 1 for each individual, and using this to assign each individual to a specific genotype according to the overall frequency expected in the progeny.

Genetic rescue was instantiated as follows. For each run, it was assumed that the population initially consisted of individuals homozygous for, say  $A_2A_2$ . To allow the possibility of genetic rescue, a single individual was introduced as a heterozygote ( $A_1A_2$ ). Because we assumed that  $A_2$  was a deleterious recessive allele that had become fixed, we assumed that  $A_1A_2$  and  $A_1A_1$  were equal in fitness, and that this fitness (calculated as lifetime expected reproductive success,  $b/d$ ) was greater than that of the 'resident inbreds'  $A_2A_2$  (Fig. 5.2).

The results showed that whether genetic rescue can impact on population persistence depends on both carrying capacity and the severity of the inbreeding effect. For small population sizes, genetic rescue greatly increased average population persistence, especially when the relative fitness of the  $A_1A_2$  genotype was low (Fig. 5.2); however, if inbreeding caused only small reductions in fitness, then genetic rescue was of less importance. For larger population sizes, persistence almost always occurred, regardless of whether or not genetic rescue was included, although for severe fitness differences, there was some increase in persistence.

### Genetic Rescue or Metapopulation Collapse?

#### Basic Model Structure

The computer simulation models discussed below were originally developed to better understand the dynamics of the *Silene-Ustilago* host-pathogen system. Our strategy was to begin with simple and general heuristic models of pollinator transmitted diseases, and to successively add degrees of complexity so as to capture the essential features of the real world metapopulation. Towards this end, we developed a spatially explicit simulation model of sets of local populations incorporating both within population dynamics and among-population dispersal, migration and extinction processes. In the context of the current chapter, we assume the disease is absent, and additionally incorporate the possibility of inbreeding and genetic rescue, as discussed below. Although the model incorporates diploid genetics, for simplicity we assume here that all genotypes are equivalent (with the same birth and death rates) and focus on population level processes. As stated earlier, our

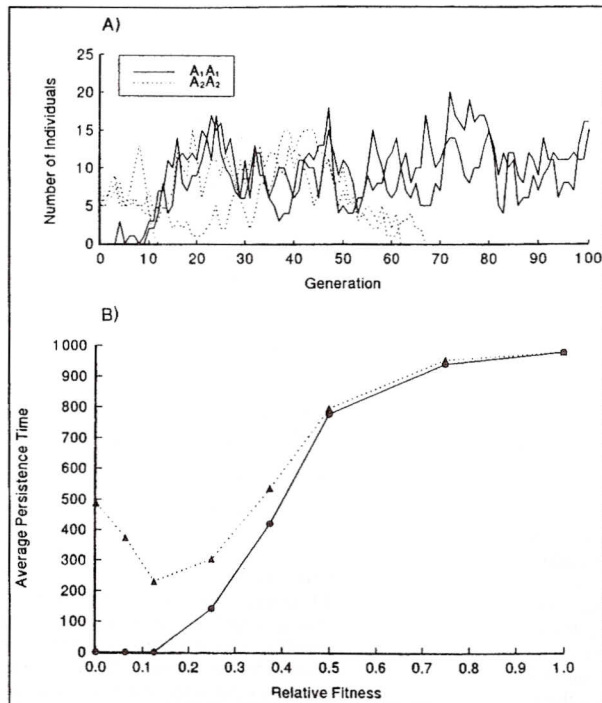


Fig. 5.2. Genetic rescue and population persistence in a single population, where fitness was calculated as expected lifetime fitness ( $b/d$ ). A) Typical output from the stochastic simulation of dynamics in a single population. For runs in which rescue did not occur and extinction was the outcome, we show dynamics for the less fit resident (dashed lines); for runs in which the population persisted (due to successful rescue), we show dynamics for the invader (solid lines). B) Average persistence time as a function of the fitness of the less fit resident vs an invader with greater fitness; solid and dashed lines represent situations with and without the possibility of genetic rescue, respectively. For all runs, the carrying capacity was fixed at 12. Data shown are the mean of 1000 runs.

level effects of inbreeding using a phenomenological approach, rather than to make precise predictions about the dynamics of *Silene alba*. Nevertheless, where possible, we parameterize the model using data from prior field experiments,<sup>32,33</sup> the roadside censuses,<sup>33,4</sup> and experimental studies of inbreeding depression and genetic rescue (Richards and McCauley unpublished data). In this way, we demonstrate that metapopulation 'collapse' is possible under realistic conditions.

### Within-Patch Dynamics

Within each patch we assume that the dynamics are deterministic (as determined by Eq. 1, but when numbers become less than one (i.e., fractional individuals), population sizes are set to zero or one according to a uniform random number. For all simulation runs, the per-capita birth parameter ( $b$ ) was assumed to be 2.0 and the death rate ( $d$ ) was set at 0.5 (based on pooled data from several field experiments).<sup>32,33,49</sup>

Data from the census of natural populations indicated that sizes of populations that have always been present and healthy during the years of the study (1988–1996) are distributed according to a log-normal distribution. The average size of these populations roughly represented the distribution of carrying capacities [where  $K = (b-d)/\gamma d$ ]. In the simulation, we therefore distribute carrying capacities in the same proportions as observed in the natural metapopulation by varying the value of the parameter.

### Among-Patch Dynamics

After each time interval a small fraction,  $m$ , of the seeds and pollen produced in a given patch at time  $t$  are dispersed according to a Weibull probability distribution, where the probability of landing in a site that is  $i$  units from the source site is given by:

$$P(i) = e^{-\left(\frac{i}{\alpha}\right)^\theta} - e^{-\left(\frac{i+1}{\alpha}\right)^\theta} \quad (2)$$

and the parameters  $\alpha$  and  $\theta$  control the scale and shape of the dispersal curve respectively.<sup>50</sup> In the simulation we fix  $\theta$  at 1, and assume three ranges of values for  $\alpha$ : low ( $\alpha = 0.5$  for both seeds and pollen), medium ( $\alpha = 2.0$ ), and high ( $\alpha = 8.0$ ). We vary the maximum dispersal distance (in population units) for each of these situations (5, 15, and 45 units, respectively) such that the total probability of migrating seeds falling within the specified distance = 0.999; the remaining fraction (= 0.001) are dispersed randomly to simulate rare long-distance colonization events. We discount the number of resident seeds by the fraction of seeds that are dispersed out of each patch. Whether or not seeds that disperse out of patches actually colonize successfully is determined by a fixed probability of establishment. We consider initial colonists and subsequent migrants as part of the within-population dynamics. At the end of each time interval, subsequent to the migration phase, a size-dependent probability of extinction is calculated for each occupied patch, using empirically determined estimates from the census data.<sup>2</sup>

In the results reported here, each simulation was allowed to run for 300 generations, by which time spatial and temporal patterns (% occupancy and average population size) had generally become stable; data on % occupancy, average population size, colonization and extinction rates, and persistence were then collected and averaged over a subsequent 300 generations.

### Inbreeding Effects and Genetic Rescue

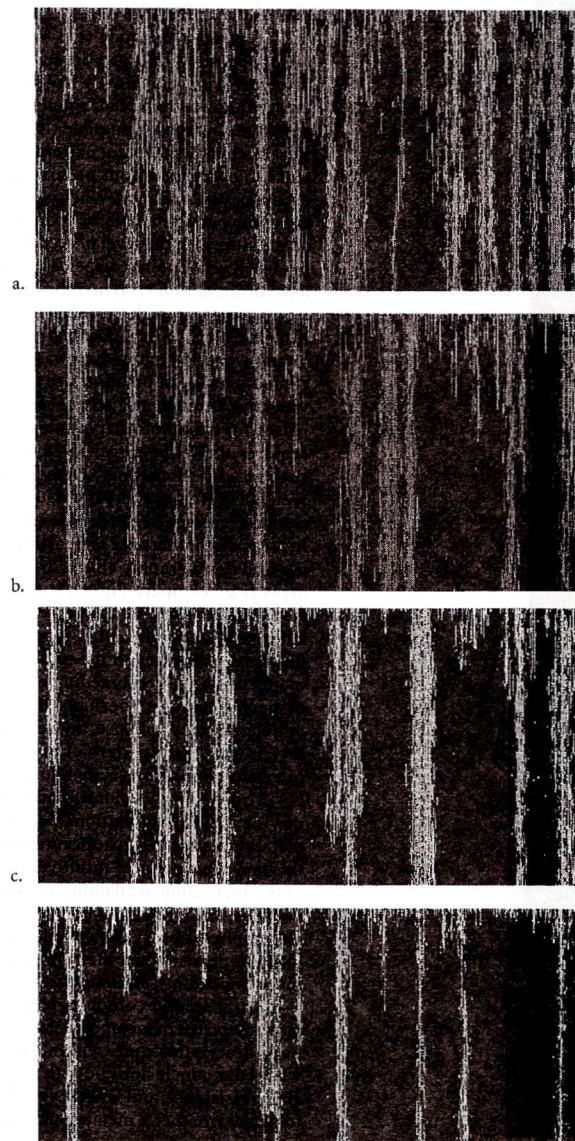
To investigate the issue of inbreeding and genetic rescue we assumed that the level of inbreeding within any population at a given time was determined by:

$$F_t = \frac{1}{2N_t} + \left(1 - \frac{1}{2N_t}\right)F_{t-1} \quad 3)$$

Because in the simulation we keep track of population size and time since the last gene-flow event,  $F$  can be calculated for each population in every time interval. In general,  $F$  will always increase unless there is a gene-flow event, in which case it will either increase more slowly or it will decrease. While the function describing the impact of gene-flow on  $F$  in the neutral case is well known theoretically,<sup>91</sup> the consequences of gene-flow when there is selection and spatial structure is not known and is undoubtedly extremely complex. We have therefore incorporated genetic rescue at the population level by assuming that any genes migrating into a population will result in complete removal of inbreeding effects. While this approach is likely to overestimate the strength of genetic rescue, it is conservative in that it results in a reduction in inbreeding effects, and therefore the possibility of metapopulation collapse. Single population simulations (see above) show that when a beneficial allele is introduced into a population fixed for a deleterious recessive allele, the spread of the beneficial allele (if it occurs) occurs very quickly. Whether this would be the case for other more complicated causes of inbreeding depression is not known (and deserves further study). In *Silene*, the effects of inbreeding can be quite severe. This suggests that in small populations, the fitness of any heterozygotes entering the population will vastly outweigh that of inbred individuals and the 'outbred' forms will contribute disproportionately to the subsequent generation (thus gene-flow may effectively set  $F = 0$ ). In large populations,  $F \sim 0$ , and resetting  $F$  to 0 following a gene-flow event is likely to result in only trivial change.

Often the pathways of immigration of individuals will not be identical to the pathways for the immigration of genes. For example, in plants, immigration of genes can occur by pollen flow, and assuming pollen is not limiting seed set, this may have no direct effect on population growth through seed production. However, immigrant seeds can have two effects; they may increase numerical abundance directly (demographic rescue) or they may reduce the levels of inbreeding (genetic rescue). We therefore explore several cases: where the scale of pollen dispersal can be less than, equal to or greater than the scale of seed dispersal, and for low, intermediate and high levels of seed dispersal. In all cases, for comparison we also discuss results from the analogous situation with no inbreeding effects.

Fig. 5.3. (Opposite page) Example of graphical output from the metapopulation simulation with intermediate dispersal for seeds (see text). The horizontal axis represents a linear array of 600 "roadside" segments, and the vertical axis represents a time period of 300 generations starting at the top. Each screen pixel is therefore one roadside segment at one time interval. Dark blue (background) represents unoccupied sites. Light blue represents populations in which there is no inbreeding depression ( $F = 0$ ), red represents populations with low to intermediate levels of inbreeding depression ( $0 < F < 0.2$ ), and yellow represents high levels of inbreeding ( $F > 0.2$ ). Note from Fig. 5.1 that the fraction of seeds germinating will be 0 for  $F > 0.43$ . A) no inbreeding depression, B) inbreeding depression, with pollen dispersal  $<$  seed dispersal, C) inbreeding depression, with pollen



## Simulation Results

Overall occupancy (the % of possible sites actually occupied) in the metapopulation changed dramatically for different levels of pollen and seed dispersal (Figs. 5.3, 5.4A-C). Not surprisingly, occupancy was highest when no inbreeding was assumed; when inbreeding was incorporated, but with only demographic rescue possible (through seeds), metapopulation extinction always occurred, except for extremely high levels of seed dispersal where persistence to 600 generations occurred in 3 out of 100 runs, but with less than 1% occupancy (not shown). When genetic rescue was included, the metapopulation generally persisted, with % occupancy increasing with the scale of pollen dispersal, and with the level of seed dispersal. Regardless of seed dispersal, at the highest level of pollen dispersal, % occupancy was nearly that seen in the ecological simulation with no inbreeding effects.

Average population size also varied with the scale of pollen and seed dispersal (Fig. 5.4D-F). Contrary to expectations, average population size was lowest when no inbreeding was assumed. Overall, when inbreeding was included, average population size was largest for the case where pollen dispersal was most limited, and where seed dispersal was low as well (Fig. 5.4D). The reason for this somewhat counter-intuitive result is that population persistence requires that  $N$  be large; when fewer new (small) populations are founded, such as with inbreeding, average population size increases. This can also be seen in Figure 5.3, where the visual maps show that as the possibility of genetic rescue decreases due to decreased pollen movement, persistence is most likely in areas where there are several large populations close together, while inbreeding and demographic effects are most important along the margins of these areas (e.g., compare Fig. 5.3A with 5.3C or 5.3D). Therefore, the simulations also demonstrate that the perceived metapopulation structure (e.g., core-satellite vs a 'classical' Levins-type scenario) is likely to depend on changes in dispersal, even though the underlying environmental heterogeneity may remain constant. As inbreeding effects become more severe, or as the scale of dispersal changes (perhaps through loss of a key pollinator), the metapopulation may collapse, thus giving the appearance of a core-satellite structure. Inferring the pattern of suitable habitats from the pattern of distribution of extant populations is therefore likely to be misleading.

Interestingly, colonization and extinction rates (calculated as number of new or extinct populations per existing population) appear to increase as metapopulation collapse occurs (i.e., with decreasing dispersal; Fig. 5.5). While this may seem counter-intuitive (at least for colonization), this pattern reflects: a) the increasing availability of empty sites for colonization as % occupancy declines, and b) the fact that fewer populations are contributing proportionately more to observable colonization events; because new populations are less likely to persist when they are more isolated (and inbreeding effects become more important), extinction rates also increase (Fig. 5.5D-F).

In a second computer "experiment," we imagined that we were ecologists interested in metapopulation structure and persistence. If we were to carry out a descriptive study within an interacting set of natural populations, what would our conclusions be with respect to the relationship between population size, persistence, and whether genetic rescue was occurring? Would we be able to detect whether a metapopulation was in 'poor health' by surveying a subset

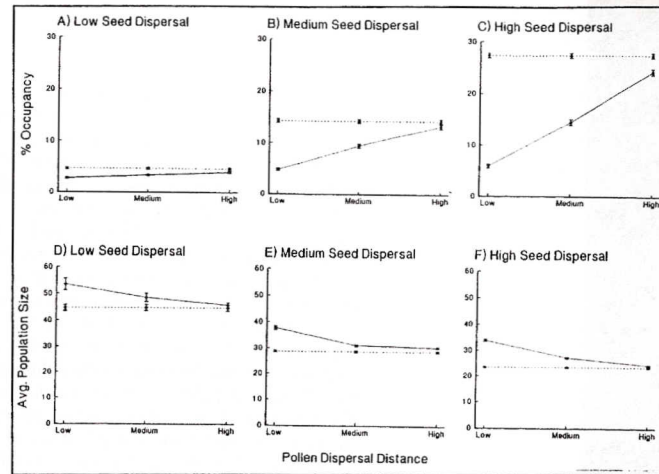


Fig. 5.4. Relationship between % occupancy, average population size and the scale of seed and pollen dispersal. Within each level of seed dispersal (low, medium, high), pollen dispersal was simulated at one of three levels (low to high). Graphs A-C show how % occupancy changes with increasing seed and pollen dispersal; graphs D-F show changes in average population size. For each graph, the dashed lines indicate values without inbreeding depression for comparative purposes. Data shown are the mean and standard errors of 100 random runs.

set of conditions) where we did an initial 'census' at 150 generations, and then followed the fate of those populations until they went extinct; this was done without 'knowledge' of prior population history, level of inbreeding or site carrying capacity (as would be true in general for any ecological study). Our a priori expectations were that within any single size class (and for any fixed scale of seed dispersal), population persistence would be lowest when pollen dispersal was most localized, intermediate for somewhat higher levels of dispersal, and highest when there were no inbreeding effects; this would mirror the results seen for % occupancy and persistence in the metapopulation as a whole. Not surprisingly, the results showed a strong positive effect of population size on persistence (intermediate seed dispersal case shown; Fig. 5.6). However, within individual size categories, there were no clear trends (this was also the case for the low and high seed dispersal scenarios).

Overall, our results suggest that it will generally be very difficult to predict the fate of individual populations or to distinguish how dynamics might differ for different dispersal or inbreeding scenarios. Persistence in individual populations may be much more affected by history (whether or not gene-flow occurred, how long the population has been inbred, where the colonists came from) and site quality (= carrying capacity). Therefore, the study of one or only a few populations (e.g., if we were to experimentally compare populations where pollinators had been excluded with ones where they were not) may not show any consequences of reduction in gene-flow, even though at the



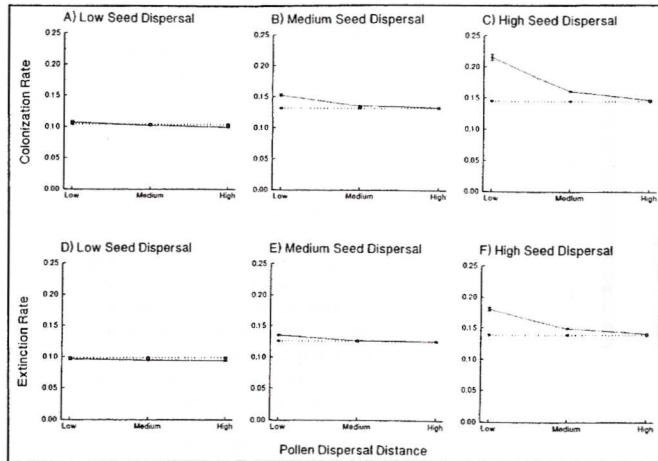


Fig. 5.5. Relationship between colonization and extinction rates (calculated as number of newly established or extinct colonies per existing population) and the scale of seed and pollen dispersal. Within each level of seed dispersal (low, medium, high), pollen dispersal was simulated at one of three levels (low to high). Graphs A-C show how colonization rate changes with increasing seed and pollen dispersal; graphs D-F show changes in extinction rate. For each graph, the dashed lines indicate values without inbreeding depression for comparative purposes. Data shown are the mean and standard errors of 100 random runs.

changes in colonization and extinction rates, increases in extinction rates, and possible metapopulation collapse.

The simulations indicate that the interplay between demographic and genetic processes causes a feedback effect which produces highly counter-intuitive results. If dispersal among populations (and gene-flow) is great enough, then the result is increasing persistence, leading to increasing birth rates but ultimately to decreased rates of colonization once regional stability has been reached (reflected in Figs. 5.3-5.5). On the other hand, decreasing persistence (when dispersal is lower) leads to decreasing numbers of colonization events which leads to further decreases in persistence; however, the 'apparent' rate of colonization actually increases. This effect is most obvious when inbreeding effects are most severe (pollen dispersal < seed dispersal: Figs. 5.3D, 5.5A-C). The decrease in % occupied sites results in increasing isolation (greater average distance between populations) and increased within-population levels of inbreeding (these, in turn, cause further decreases in effective colonization, and so on). Therefore, collapsing metapopulations might on average, actually display larger population sizes and greater observable colonization rates than stable systems. Without historical knowledge of the system (e.g., former species range, distribution of suitable habitat) one might well be tempted to conclude that the collapsing system was more likely to persist!

## General Discussion

### Gene Flow and Genetic Rescue in Plant Metapopulations

From a metapopulation perspective, the significance of a given level of gene flow into newly established populations depends, in large part, on the relative rates at which genes move into either empty habitat patches (colonization) or occupied habitat patches (migration). McCauley<sup>52,53</sup> has discussed ecological conditions under which those two types of movement might differ. Consider the following four possible cases:

- 1) Colonization and migration both frequent: low likelihood of inbreeding depression because  $k$  is large and subsequent gene flow extensive.
- 2) Colonization frequent, migration rare: low likelihood of inbreeding depression because  $k$  is large, even though subsequent gene flow is limited.
- 3) Colonization rare, migration common: opportunity for inbreeding depression (i.e., small  $k$ ) offset by gene flow and genetic rescue.
- 4) Colonization rare, migration rare: opportunity for inbreeding depression because  $k$  is small and subsequent gene flow limited.

What life history attributes might distinguish species whose demographies place them close to case 3 or to case 4? McCauley<sup>52</sup> has suggested that many outcrossing seed plant species might fit into category 3. This is because in outcrossing seed plants, colonization requires the movement of seeds, but once populations become established, gene flow can occur by the movement of pollen. In many species of plants, pollen may move much more freely than seeds.<sup>54</sup>

### Metapopulation Stability with a Shrinking Pool of Pollinators

The simulation results show that colonization of vacant habitat patches by small numbers of individuals can result in conditions under which inbreeding depression may occur locally in an otherwise abundant species. The reality of this scenario is confirmed by empirical studies showing that the degree of isolation in newly colonized populations is positively correlated with inbreeding depression; as a consequence, there is a much greater potential for genetic rescue in more isolated populations (Richards and McCauley, unpublished data). Because the rate at which new populations become established is a major determinant of regional stability, inbreeding depression within some populations could have repercussions for the entire metapopulation. The effect would be greatly ameliorated by gene flow subsequent to population founding, a condition likely to obtain in wind and animal pollinated plants. This argument becomes important from a conservation perspective when human activity pushes a plant species from category 3 to category 4.

One emerging concern for both conservation and agricultural biologists is the depletion of insect pollinators. Most obvious in the United States is the decline in honey bee (*Apis mellifera*) populations owing to mite infestation. More generally, there is increasing concern that many native insect pollinators are in decline as well, for various reasons.<sup>55</sup> If so, many plant species whose demography approximates the metapopulation paradigm may be undergoing shifts in the scale at which gene-flow occurs (i.e., from category 3 to category 4). A reduction in the rate of gene flow could increase the likelihood of local

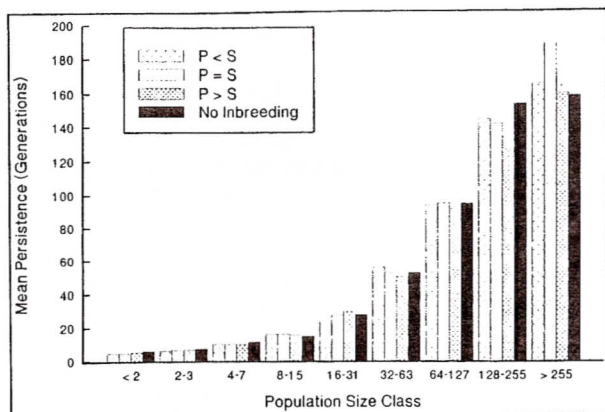


Fig. 5.6. Population persistence as a function of size, and the relative scale of seed vs pollen dispersal, where seed dispersal is fixed at the medium level (see text). Data are from 100 random simulation runs for each of the four cases (pollen < seed dispersal, pollen = seed dispersal, pollen > seed dispersal, no inbreeding). Populations were initially censused at 150 generations, placed into logarithmically increasing size categories, and then tracked until extinction.

remain abundant, simple habitat fragmentation that increases the distance among local demes could reduce the rate of gene flow via pollen to the point where genetic rescue becomes limited. These genetic processes could be set in motion long before the plant species becomes truly rare.

### Implications for Conservation Biology

In the present study, we have used a phenomenological approach to sketch out the combined effects of demographic and genetic parameters in a metapopulation setting, where inbreeding is determined simply as a function of population size, and by the degree of isolation. Clearly, incorporating the genetic consequences of inbreeding in a more explicitly biological fashion would entail a much more complicated model. For example, explicit models of the genetic effects of inbreeding could be done either assuming heterozygote advantage (and therefore a one locus model might be sufficient, where the frequency of homozygotes is a measure of the level of inbreeding). Alternatively, one could assume some interplay between a mutation/selection balance (which is likely to require a multilocus model). Ultimately, a realistic assessment of the potential for inbreeding/recovery would require knowledge of the genetic structure of nearby populations (i.e., not only where colonists come from but who they are). Furthermore, we currently have no data on processes that occur after the initial gene-flow event. For example, how quickly are the effects of a gene-flow event diluted (and what does this rate depend on)? It is difficult to know to what extent, the additional work required to quantify such factors is likely to change the general scenario presented here.

Perhaps the most critical issue from a conservation perspective, is "Given the need to assess the status of a species or community, how does one identify systems that may superficially appear to be stable but may be in trouble in the future, given current trends?" There is often no difficulty in identifying species that have already become so rare that they are in imminent danger of extinction. However, conservation measures may be of little value at this point, therefore our goal should be preventative rather than prescriptive. What are the early warning signs of collapse? The simulation results show that conservation biologists studying one or a few populations would be hard pressed to see the effects of metapopulation collapse (despite dramatic differences between the different scenarios depicted in Fig. 5.3). This implies the need for metapopulation level assessments of 'health' (currently undefined) because there are too many variables affecting dynamics within single populations (e.g., habitat quality, demographic and genetic stochasticity, and disease). The simulations indicate that without longitudinal studies of many populations, even metapopulation measures of health may be difficult to interpret, particularly in cases where there is no clear way of assessing how much of the available habitat could be occupied that is currently vacant (this may only be possible in situations where suitable habitat is unambiguous, such as physical islands).

Overall, the simulations show that the effects of inbreeding depression can have consequences, not only at the level of single populations, but may cascade to produce effects across an entire metapopulation. Two other important points emerge from these studies. First, detection of such effects is likely to be difficult if based on short-term cross-sectional studies, regardless of whether these studies encompass few or many populations. Second, these studies suggest the need for a whole body of empirical and theoretical studies to understand the nature of inbreeding and the impact of immigrants in natural systems.

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## CHAPTER 6

## On Wolf Territoriality and Deer Survival

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### Introduction

Territoriality is commonly observed among mammal and bird species and, by its very nature, gives rise both to spatial and temporal heterogeneity in land use and in the interactions between and within species. Interest in territorial behavior is apparent within the ecological literature where it has inspired many definitions. These range from the general "any defended area"<sup>1</sup> to the more specific "a fixed exclusive area with the presence of defence that keeps rivals out."<sup>2</sup> These examples are just two of many,<sup>3</sup> all of which incorporate the idea that the area is actively defended and that the holder has exclusive use of the land. The exclusivity of land use may, however, vary between individuals over time, particularly around the territory boundaries.<sup>4</sup>

Territory formation also incorporates elements of temporally varying land use as the holder develops and establishes the area which it will defend. In addition, and as we further discuss below, territory defense often makes use of temporally varying signals (usually vocal<sup>6</sup> or olfactory<sup>7</sup>) which may allow variations in the defended area over time. In both of these respects, it appears that territoriality is a spatiotemporal phenomenon and hence an obvious candidate for spatiotemporal modelling. Despite this, few mathematical models of territoriality have explicitly incorporated both space and time effects (but see Taylor and Pekins<sup>8</sup>).

In addition to the extensive theoretical discussions of territoriality, field studies on a variety of species have investigated such issues. These include studies of pack territoriality for predatory mammals such as wolves,<sup>9-11</sup> African wild dogs,<sup>12</sup> lions<sup>13-16</sup> and badgers.<sup>17</sup> Motivation for the work which gave rise to this chapter came from the study of wolf (*Canis lupus*) and white-tailed deer (*Odocoileus virginianus*) interactions in northeastern Minnesota. Over the past three decades, there have been almost continuous studies of these interactions<sup>9,10,18-20</sup> from which some clear patterns have emerged.

This chapter reviews recent theoretical advances in modelling territorial interactions between wolf packs<sup>21-24</sup> and the predator-prey interaction be-