A general model of site-dependent population regulation: population-level regulation without individual-level interactions

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In this paper, we use a modeling approach to explore the population regulatory consequences of individual choices for where to breed in heterogeneous environments. In contrast to standard models, we focus on individuals that interact only indirectly through their choices of breeding sites (i.e., individuals preempt the occupation of a breeding site by others when they choose to breed there). We consider the consequences of individuals choosing breeding sites either randomly or sequentially from best to worst. Our analysis shows that average per-capita fecundity of the population is independent of the number of occupied breeding sites if individuals choose sites at random and that variation in average per-capita fecundity increases as population size declines. In contrast, if individuals choose breeding sites sequentially from highest to lowest quality, then as population size increases average per-capita fecundity declines and variation in average per-capita fecundity increases. Consequently, aggregate population-level demographic rates can change in ways that generate population regulation, even when change in population size does not change the demographic performance of any individual on any particular breeding site. However, such regulation occurs only when individuals make adaptive choices of where to breed. Because variation in average per-capita fecundity decreases when population size declines, populations regulated in a site-dependent manner should be much less susceptible to the vicissitudes of small population size than those which choose breeding sites at random.

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Individual behavior can affect the regulation of population size (Łomnicki 1988, Sutherland 1996), particularly when individuals interact. By regulation, we mean the negative feedback process that causes populations to grow when small or decline when large, relative to some equilibrium size (Murdoch 1994) or boundary (Chesson 1978). Such negative relationships between population size and demographic rates can occur in many ways, for example through exploitative competition among individuals of the same or different species (e.g., Tilman 1982, Arcese and Smith 1988), territoriality and other forms of interference competition (e.g., Reichert 1981,

Newton 1992; reviewed by Sutherland 1996 and Newton 1998), predation (e.g., Murdoch and Oaten 1975, Hassell 1978, Murdoch et al. 1996), disease (e.g., Anderson 1981, Begon et al. 1996b), etc. The usual notion of how intraspecific or interspecific interactions among individuals affect population regulation is by the interaction among individuals lowering either survival or fecundity rates. But to what extent might the behavior of non-interacting individuals generate negative feedback that affects population processes? By "non-interacting", we mean that the survival, growth, and fecundity rates realized by an individual from a particu-

lar breeding site are determined solely by the quality of the breeding site, and site quality (in terms of these demographic rates) is independent of population size. Individuals interact only via their preemption of sites from being used by others in the population.

Theoretical studies suggest that the behavior of non-interacting individuals may influence population processes. For example, the strategy of habitat selection or dispersal used by individuals can strongly alter the overall size and stability of a population (Holt 1993). Where source and sink habitats occur, active habitat choice by individuals can theoretically regulate population size to a single, stable equilibrium (Pulliam 1988), even when the ability to choose is imperfect (Pulliam and Danielson 1991). However, applications of this theory have until recently typically included interactions among individuals (e.g., Pulliam 1988, Rosenzweig 1991). For example, habitat selection and dispersal are usually considered consequences of dominance relationships (e.g., Fretwell and Lucas 1970, Łomnicki 1988), or reproductive performance is considered to vary directly with population density (e.g., Pulliam and Danielson 1991).

Recently, Rodenhouse et al. (1997, 1999) and Both (1998) have explored how non-interacting individuals might contribute to population regulation. These studies focused on how the use of breeding territories (Rodenhouse et al. 1997) or habitats (Both 1998) that differ in suitability might influence reproductive performance and population regulation, in the absence of density-related interactions among individuals. Rodenhouse et al. (1997, 1999) demonstrated that the size of a black-throated blue warbler (*Dendroica caerulescens*) population could potentially be regulated even in the absence of interactions among individuals. Both (1998) focused at the scale of the habitats occupied by great tits (*Parus major*) and found that clutch size was better predicted by population density than by habitat suitability. Neither of these studies, however, provided a general framework within which to examine how non-interacting *individuals* might contribute to population regulation.

Theoretical studies (e.g., Holt 1985, Morris 1988, 1994) and their applications (e.g., Morris 1991, Both 1998) both indicate that environmental heterogeneity creates the context in which individual behavior can affect population-level processes. In heterogeneous environments, the spatial and temporal distributions of resources create the options from which individuals choose, and those choices in turn can affect individual fitness and the demographic rates of populations. Population dynamics, therefore, result from a complex interaction between the environments experienced by individuals and the choices those individuals make in the environments they actually experience (Caswell and Werner 1978, Kalisz and McPeek 1992, 1993, Sutherland 1996). According to this view, it is possible for the choices of individuals to have consequences at the level of the population independent of interactions among individuals.

In this paper, we develop a general model to explore the population regulatory consequences of individual choices for where to breed in heterogeneous environments. This paper elaborates on the population regulatory consequences of the model of population dynamics described by Pulliam and Danielson (1991) and on the mechanism of population regulation called site-dependence by Rodenhouse et al. (1997, 1999). We show that even without any change in demographic performance at the individual level, population-level demographic rates can be changed in ways that act to regulate population size. Moreover, such regulation only occurs when individuals make adaptive choices of where to breed.

The model

Consider an environment that presents N possible breeding sites to individuals. For birds these would be nesting sites; for insects they would represent oviposition sites, etc. For simplicity assume that a semelparous organism inhabits this environment, and each site can be occupied by only one female. A female reproduces at a site and then dies. Individuals occupy sites such that once in place an individual cannot be displaced from the site. The number of offspring produced by a female is defined only by the ecological conditions of the site (i.e., the "suitability" of the site) she occupies and is independent of population size and the characteristics of other sites occupied. Site suitability may be determined by the resources available to the female for egg production and/or in ways that would affect the survival of young (e.g., fledgling success in birds or offspring survival based on provisioning in many insects). Define f_i as the number of offspring that a female will contribute to the next generation by occupying site i for reproduction, with N available sites. Throughout this paper, we order the sites such that

$$f_1 > f_2 > \cdots > f_i > \cdots > f_{N-1} > f_N \qquad (1)$$

Site quality is assumed to decline in a negative exponential fashion (all analyses presented in this paper were replicated with a number of other equations for the site suitability function; all give qualitatively identical results). Females are assumed to choose sites at random or sequentially from best to worst, and no cost is associated with either method of choice. We also assume throughout this paper that all offspring produced will survive to reproductive age. Thus, throughout this paper fecundity (f), which is determined by site quality, is considered to be the sole determinant of

population growth (λ). Obviously, this latter assumption will not hold in natural populations, but we make it here to highlight the features of site-dependence. Incorporating this mechanism of regulation into more sophisticated life cycles and more realistic demographic scenarios will generate similar effects.

The two scenarios developed below clarify how the choices of non-interacting individuals can theoretically affect regulation of population size. Conservation implications of the site-dependence mechanism are then developed from these scenarios.

Individuals fill sites at random

If individuals choose sites at random, the expected average number of offspring produced by individuals in the population is simply the average site suitability available to them:

$$\bar{f} = \left(\sum_{i=1}^{N} f_i \right) \Big/ N \tag{2}$$

The variance of (2) is

$$\mathrm{Var}(f) = \frac{\sigma^2}{n} \left(\frac{N-n}{N-1} \right) \tag{3}$$

Fig. 1. Population size may either grow or decline depending on the distribution of site suitability when individuals choose breeding sites at random from those available. Here we assume in two examples that site suitability declines with rank according to a negative exponential curve; the functional relationship is given as Site suitability = BestSite × exp(− b × rank). BestSite = 1.5 in both examples, but $b = 0.00075$ in example A and $b = 0.001$ in example B. The upper panels in both A and B give the quantitative relationships between site suitability and rank. The lower panels give the population trajectories assuming the site suitability distributions above each, and assuming that individuals choose breeding sites at random from among those available. In panel A average fecundity is 1.056, and in B, it is 0.949. The population simulations for this and all other figures assume a semelparous life cycle in which individuals die immediately after producing offspring, and all offspring survive to reproduce.

where σ^2 is the variance in suitability for all acceptable sites, n is the number of occupied sites, and N is the number of available sites.

These equations show that the average per-capita fecundity of the population is independent of the number of sites occupied if individuals choose sites at random, but the variation in average per-capita fecundity increases as population size declines. This means that if population growth rate is more sensitive to variation in fecundity than to N (e.g., high potential fecundity or a large difference among individuals in the survival of their offspring), then populations of individuals that choose breeding sites at random will grow or decline exponentially, depending on whether average site suitability exceeds the demographic replacement level (i.e., $\bar{f} = 1$). Growing populations will fill all sites if $\bar{f} > 1$, or will decline exponentially to extinction if $\bar{f} < 1$ (Fig. 1). Moreover, when population size is small, the greater demographic variation in fecundity due to sampling in a small population may result in population extinction even though $\bar{f} > 1$.

The average growth rate of the population can be altered under these conditions simply by changing the range in suitability of the sites available. For example, Fig. 2 illustrates the outcomes of simulations in which site suitability is assumed to decline in a negative exponential fashion (Fig. 2A). In the first simulation,

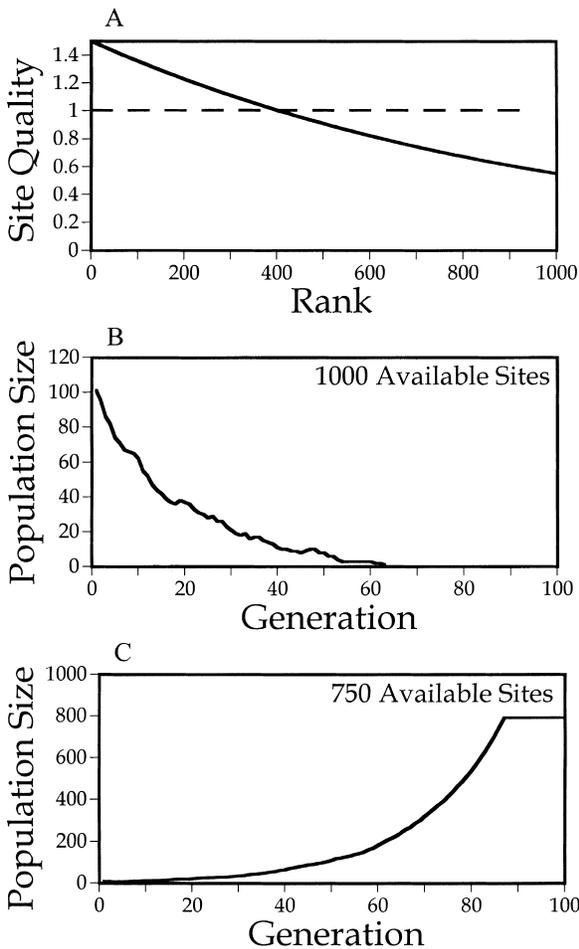A. Best Site = 1.5, b=0.00075

B. Best Site = 1.5, b=0.001
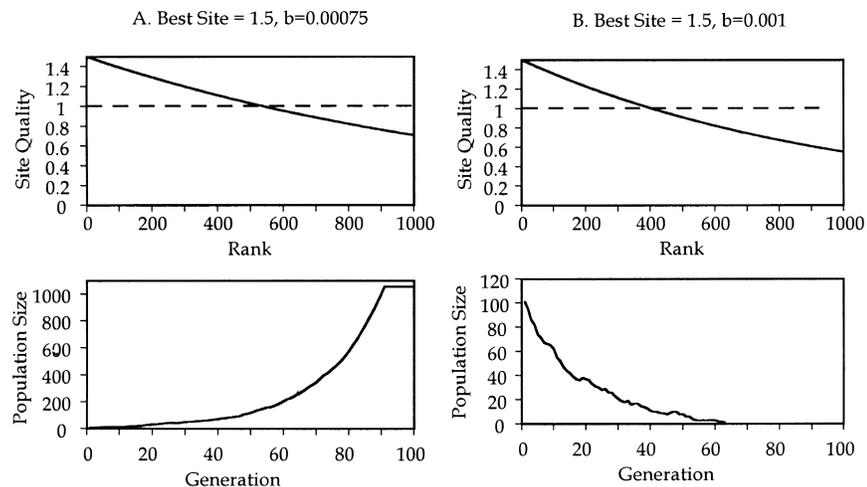
Fig. 2. The change in exponential population growth rate caused by a change in the number of available sites. In this figure, we assume that individuals choose sites at random and that site suitability declines in a negative exponential manner with a decay parameter of $b = 0.001$ (see Fig. 1 for equation), as shown in panel A. In panel B, 1000 sites are available, making the average site suitability 0.949. Populations in this environment decline exponentially until extinct. In panel C, only 750 sites are available, making the average site suitability 1.056. Populations in this environment grow exponentially until all available sites are filled each generation. Some overshoot in population size is achieved each generation because the population is censused following offspring births.

1000 sites are available, and the population declines to extinction because the average site suitability is < 1.0 (Fig. 2B). In the second simulation using the same quantitative distribution of site qualities but limiting it to the best 750 instead of 1000 sites, the population grows exponentially until all sites are occupied, because average site suitability is now > 1.0 (Fig. 2C). Dramatically different results are obtained, however, if sites are not filled randomly but sequentially.

Individuals fill sites sequentially

The adaptive individual behavior, which females should display in choosing sites, is to occupy the best available site. This means that individuals should fill sites sequentially from the best (i.e., f_1) to the worst (i.e., f_N). Pulliam and Danielson (1991) termed this the "ideal preemptive distribution". Population dynamics are greatly affected by a shift from random to sequential use of sites. First, if some individuals can expect to leave more than one offspring by breeding on at least some of the sites (i.e., "break-even" replacement), these females will always contribute to population growth even when population sizes are small (obviously, demographic parameters in other parts of the life cycle may offset this contribution, but for illustrative purposes we assume that all offspring survive to reproduce). Because fecundity determines population growth rate, small populations will achieve the maximum growth rate possible in a given environment, which will tend to buffer small populations against extinction.

Second, average per-capita fecundity of the population declines as population size increases (e.g., Fig. 3). In this mechanism, the fecundity of an individual depends only on the suitability of the site chosen; the suitability of any particular site does not change as other sites are occupied. Therefore, the decline in average fecundity results from the sequential use of successively poorer sites and not from a decline of the returns from a site as other sites are occupied or individual performance as population size increases (Andrewartha and Birch 1954, Holt 1985). The result of this negative feedback mechanism is that population size will continue to increase in a sigmoidal fashion until all sites are filled or until the population stabilizes at an equilibrium value. Assuming that all offspring survive to reproduce, the equilibrium population size is reached when the average fecundity of the population reaches 1.0 (i.e., break-even replacement) (e.g., Fig. 3; Pulliam and Danielson 1991). If the average suitability of all available sites is > 1.0, the population will grow in a sigmoidal fashion until all available sites are filled. Floaters (nonbreeding individuals not occupying a site) may be produced when the number of sites available is limited and average site suitability is high. If the average suitability of all available sites is < 1.0, the population will stabilize at a level where some number of the lowest quality sites are never used (Fig. 3). This result implies that the range of breeding sites used by a population may be influenced as much by population size as by the behavioral choices of individuals.

The narrower range of breeding sites occupied as population size declines implies that the variance of average demographic rates, e.g., fecundity (f) may also decline. If sites are occupied sequentially, variance in suitability for all acceptable sites (σ^2) declines as the number of occupied sites (n) becomes smaller. Conse-

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quently, Var(f) may increase, remain the same or even decrease as population size declines, depending on the size of the concurrent changes in σ^2 and n. If Var(f) decreases as n declines, small populations would be more tightly regulated than large ones and no more likely to become extinct due to sampling variance than large ones. This result is opposite of that found when sites were occupied randomly. In that scenario, the variance of demographic rates increased as population size declined because the sites used were a random selection from the full range of potential sites whether population size was small or large (i.e., σ^2 was fixed and independent of population size).

Fig. 4. Differences in population growth result if individuals choose breeding sites randomly or sequentially. The populations depicted in the figure both had the first 750 sites from the distribution of sites used in Figs 2 and 3 available to them. The thick line tracks out the size of a population in which individuals filled sites sequentially from best to worst. The thin line tracks the size of a population in the same environment, but individuals in this population choose sites randomly.

When population size and variance in demographic rates are small, filling sites from best to worst can result in rapid population growth. For example, Fig. 4 compares the growth of two populations in the same habitat; one population fills sites randomly and the other fills sites sequentially. The population choosing sites randomly grows exponentially at the average per-capita fecundity for the habitat. In contrast, the population choosing sites sequentially from best to worst initially grows at a rate near that afforded by the best available site and slowly declines from that rate as successively poorer suitability sites are used. Consequently, the population that fills sites sequentially reaches its maximum size many generations before the population that chooses randomly. This population-level phenomenon arises from the adaptive site use by non-interacting individuals, i.e., from individuals preemptively filling sites in a heterogeneous environment.

Discussion

The mechanisms of individual site use and the consequent population regulation first discussed in Pulliam and Danielson (1991) and further highlighted in this paper illustrate how population regulation can be accomplished without the need for altering individual demographic rates as population size changes. Generally, mechanisms generating population regulation are assumed to operate at the level of the individual via decreased survival or fecundity as population density increases (e.g., Begon et al. 1996a). Empirical studies
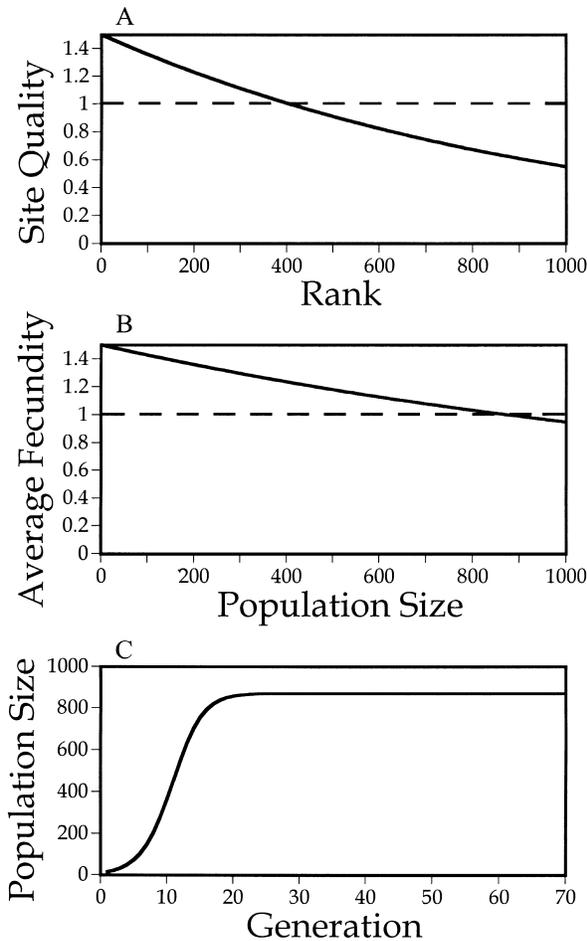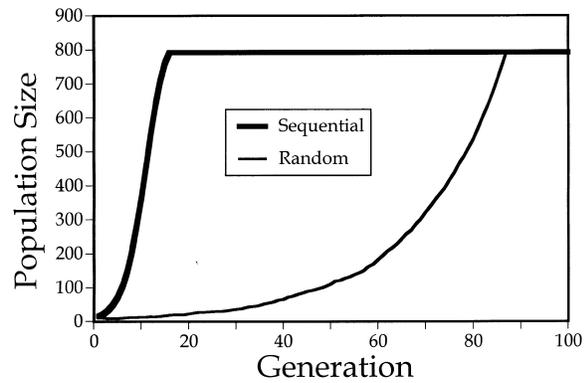
Fig. 3. Site-dependent population regulation generated by adaptive individual site choice. Here we assume the same site suitability/rank relationship as in Fig. 2 (i.e., BestSite = 1.5, $b = 0.001$), but individuals fill in sites for breeding sequentially from best to worst (panel A). Panel B shows that the average fecundity of individuals in the population smoothly declines as population size increases. The average fecundity line reaches 1.0 at a population size of 870 under these conditions. This is the eventual equilibrium population size as the population grows from small size (panel C) or declines from very large size (not depicted).

designed to identify regulatory mechanisms usually search for such relationships (e.g., Turchin 1995, Fox and Ridskill-Smith 1996, Newton 1998). In the mechanism of site-dependence presented in this paper, individual-level demographic performance does not change with population size, because the demographic rewards of each site are invariant (see also Pulliam and Danielson 1991). However, in spite of this individual-level demographic constancy, populations can be regulated because population-level growth rate declines as population size increases, if individuals choose sites adaptively.

The key features of site-dependence are (1) variation in the demographic suitability of sites, (2) exclusive use of a site (i.e., site holders cannot be displaced [Rodenhouse et al. 1997]), and (3) adaptive site choice (i.e., sites are occupied sequentially from best to worst; called preemption by Pulliam and Danielson [1991]). Variation in site suitability provides the "environmental template" (sensu Southwood 1977) on which this mechanism of population regulation operates. Individuals are confronted with sites of differing suitability and must choose where to establish breeding territories or oviposit. Variation in the suitability of potential breeding sites probably exists to some degree in most if not all natural populations and can be substantial. Evidence for exclusive use of sites and adaptive site choices can be found in many groups of animals (reviewed by Rodenhouse et al. 1997).

With adaptive choice and exclusive use of heterogeneous sites, population-level fecundity must necessarily decrease with increasing population size, since smaller numbers are continually being added for averaging as population size increases. At equilibrium, some fraction of individuals will produce more than enough offspring for replacement, while the rest will not. Recognizing the potential operation of site-dependence has important implications for field tests of population regulation.

First and foremost, the lack of negative density dependence at the individual level does not necessarily imply the lack of population regulation. For example, in a natural population regulated by site-dependence, an experimental manipulation of population size would not alter the demographic performance of individuals already in the population if they did not change the sites they occupy. Also, the results of experimental manipulations of population size would depend on the identity and behavior of the particular individuals manipulated. Individuals added to an already existing population would fill poorer suitability sites, which would decrease the population-level growth rate *without* altering individual-level rates. Experimentally removing individuals may however have complicated effects. If individuals are removed from the best sites, and others do not shift sites to fill those newly vacated, population-level growth rate may decrease because of the manipulation. If individuals are removed from the poorer sites, or individuals shift to fill experimentally vacated sites (e.g., birds shifting to higher suitability territories; reviewed by Marra and Holmes 1997), population-level growth rates would be expected to increase. Parallel studies of individual behavior and demography must therefore accompany studies of population regulation if the goal is to test or distinguish among specific regulatory mechanisms (Turchin 1999).

Site-dependence also differs from the typical notions of how territoriality associated with breeding sites contributes to population regulation. Breeding sites are not necessarily saturated until all available sites are filled (e.g., Fig. 3). Moreover, regulation by site-dependence does not require territory size to expand or contract as population size changes to alter individual survival or fecundity rates (cf. Fretwell and Lucas 1970, Reichert 1981, Newton 1992). Note also that regulation can be achieved in the complete absence of changes in territory size or suitability with population size (Rodenhouse et al. 1997).

Last, site-dependence predicts that variance in population growth rate tends to be positively related to population size – smaller populations having *lower* variance in population growth rate. This is clearly different from standard population models, which assume that variance in growth rate is either independent of population size (e.g., most deterministic models or those including only environmental stochasticity) or is inversely related to population size (e.g., models including demographic stochasticity; Goodman 1987, Lande 1998). The implications for population dynamics of these different predictions are profound. For example, the variance in population growth rate may not increase as population size declines, even when demographic stochasticity increases, because the site-dependence may compensate for the effect of demographic stochasticity. The operation of site-dependence, therefore, has important implications for the conservation of species.

Conservation implications

Widely accepted models predict that the likelihood of extinction for a population increases as the size of the population decreases (Goodman 1987). Therefore, the dynamics of populations when small strongly influences their susceptibility to extinction. The results of the general model presented in this paper suggest that species that display site-dependence should be much less susceptible to the vicissitudes of small population size than species that choose breeding sites at random. When breeding site selection is random (or substantially less than ideal, cf. Pulliam and Danielson 1991), the population will grow exponentially at a rate defined by the average suitability of the habitat. Even with a positive population growth rate, recovery can be ini-

tially very slow under exponential growth (e.g., Figs 1 and 4). The population may therefore remain small for quite some time, and hence, be susceptible to extinction via the forces of demographic or environmental stochasticity. Also with random site selection, the variance in population growth rate is inversely related to population size (eq. 2). This variation is induced by individuals randomly sampling the demographic environments available to the population and would add to the growth rate variation generated by demographic stochasticity. Thus, variation in the population growth rate resulting from these two sources might greatly enhance the chances of population extinction even for populations that should, on average, recover from small size.

In contrast, species that choose breeding sites adaptively have much greater potential to recover from small population size (Fig. 4). By choosing the best sites first, population growth rates can be substantially increased over the average of those available when the population size is small (Fig. 4). The actual size of this effect depends on the shape of the suitability function. However, even where average site suitability would result in negative population growth if sites were chosen at random, populations displaying adaptive site choice would increase because they would fill in the best sites first. Furthermore, reduced variation of the high demographic rates found at small population sizes would further speed the recovery of small populations.

Thus adaptive use of sites provides a strong buffer against population extinction because (1) the population would spend substantially less time at small sizes where demographic and environmental stochasticity create the greatest potential for extinction, and (2) viable populations could be maintained even in habitats where the average suitability is relatively poor. These considerations imply that the breeding biology of species, in particular site-dependent relationships, should be an important consideration in deciding where to focus conservation efforts. Efforts should be focused primarily on species that minimally exercise adaptive site choice (e.g., due to behavioral stereotypy or an inability to shift among sites) because their breeding biology makes them much more susceptible to environmental vicissitudes at small population sizes.

Species demonstrating site-dependence would be of conservation concern when the most suitable sites are lost or the average suitability of all sites is lowered, such as might occur due to habitat fragmentation or climate change. However, little is known about the distribution and dynamics of site suitabilities because the environmental causes of site heterogeneity are seldom measured (Pulliam 2000). Rather demographic performance is typically used to infer differences in site suitability. When only performance is measured, it is impossible distinguish the contributions of individuals and their interactions from those of the sites they occupy. We have demonstrated in this paper that regulation can occur among non-interacting individuals whose individual performance does not change with population size. Documenting the ubiquity of this site-dependent mechanism, however, will require experimental tests, because only with such tests will it be possible to distinguish the effects of interactions among individuals on population regulation (i.e., conventional crowding mechanisms) from those associated with site characteristics.

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