Individual behavior can affect the regulation of population size (Lomnicki 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, Rzenzweig 1991). For example, habitat selection and dispersal are usually considered consequences of dominance relationships (e.g., Fretwell and Lucas 1970, Lomnicki 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

\[
f_1 > f_2 > \cdots > f_i > \cdots > f_{N-1} > f_N
\]  

(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 ($\lambda$). 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:

$$f = \left( \frac{\sum f_i}{N} \right)$$

(2)

The variance of (2) is

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

(3)

where $\sigma^2$ 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., $f = 1$). Growing populations will fill all sites if $f > 1$, or will decline exponentially to extinction if $f < 1$ (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 $f > 1$.

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,
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 ($\sigma^2$) declines as the number of occupied sites ($n$) becomes smaller. Conse-
quenty, \( \text{Var}(f) \) may increase, remain the same or even decrease as population size declines, depending on the size of the concurrent changes in \( \sigma^2 \) and \( n \). If \( \text{Var}(f) \) 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., \( \sigma^2 \) was fixed and independent of population size).

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
designed to identify regulatory mechanisms usually
search for such relationships (e.g., Turchin 1995, Fox
and Ridskill-Smith 1996, Newton 1998). In the mecha-
nism of site-dependence presented in this paper, indi-
vidual-level demographic performance does not change
with population size, because the demographic rewards
of each site are invariant (see also Pulliam and Daniel-
son 1991). However, in spite of this individual-level
demographic constancy, populations can be regulated
because population-level growth rate declines as popu-
lation 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 [Roden-
house 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 mech-
anism 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 breed-
ning sites probably exists to some degree in most if not
all natural populations and can be substantial. Evi-
dence 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 heteroge-
neous 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 de-
pendence 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, popula-
tion-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), popu-
lation-level growth rates would be expected to in-
crease. Parallel studies of individual behavior and
demography must therefore accompany studies of pop-
ulation 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 con-
tributes 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 popu-
lation 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 as-
sume 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 includ-
ing 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 in-
crease as population size declines, even when demo-
graphic stochasticity increases, because the site-de-
dependence may compensate for the effect of demo-
graphic stochasticity. The operation of site-dependence,
therefore, has important implications for the conserva-
tion 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 suitable areas 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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