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SITE-DEPENDENT REGULATION OF POPULATION SIZE: A NEW SYNTHESIS

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Abstract. The nature and extent of population regulation remains a principal unanswered question for many types of organisms, despite extensive research. In this paper, we provide a new synthesis of theoretical and empirical evidence that elucidates and extends a mechanism of population regulation for species whose individuals preemptively use sites that differ in suitability. The sites may be territories, refuges from predation, oviposition sites, etc. The mechanism, which we call site dependence, is not an alternative to density dependence; rather, site dependence is one of several mechanisms that potentially generate the negative feedback required for regulation. Site dependence has two major features: (1) environmentally caused heterogeneity among sites in suitability for reproduction and/or survival; and (2) preemptive site occupancy, with the tendency for individuals to move to sites of higher quality as they become available. Simulation modeling shows that these two features, acting in concert, generate negative feedback when progressively less suitable sites are used as population size increases, reducing average demographic rates for the population as a whole. Further, when population size decreases, only sites of high suitability are occupied, resulting in higher average demographic rates and, thus, population growth. The modeling results demonstrate that this site-dependent mechanism can generate negative feedback at all population sizes in the absence of local crowding effects, and that this feedback is capable of regulating population size tightly. Operation of site dependence does not rely on the particular type of environmental factor(s) ultimately limiting population size, e.g., food, nest sites, predators, parasites, abiotic factors, or a combination of these. Furthermore, site dependence operates in saturated or unsaturated habitats and over a broad range of spatial scales for species that disperse widely relative to site diameter. A review of relevant field studies assessing the assumptions of the mechanism and its regulatory potential suggests that site dependence may provide a general explanation for population regulation in a wide variety of species.

Key words: density dependence; despotism; habitat quality; population regulation; preemption; simulation model; territoriality; territory suitability.

INTRODUCTION: THE PROBLEM OF POPULATION REGULATION

Populations of many species fluctuate as though regulated, but the underlying mechanisms have often eluded identification, even in well-studied organisms (Sinclair 1989, Murdoch 1994). Indeed, whether and how most animal populations are regulated remains one of the principal unanswered questions in ecology, despite the many important applications of this knowledge

(Murdoch 1994). For example, understanding population regulation is essential for explaining species abundances, predicting the success of biological controls, and designing management plans for species conservation.

Failure to understand regulation stems, in part, from the ambiguous usage of concepts such as regulation and density dependence. Although defining regulation is problematic (Murdoch and Walde 1989, Berryman 1991, Murray 1994), the present consensus is that a regulatory process involves some negative feedback mechanism that increases demographic rates when pop-

ulation size declines (and vice versa), relative to some equilibrium (Murdoch 1994, Turchin 1995) or boundary (Chesson 1978, Strong 1986). This definition thus assumes the operation of one or more negative feedback mechanisms. Similarly, density dependence is often used broadly to indicate an inverse relationship between some measure of population density and a demographic rate (Begon et al. 1996), but density dependence does not necessarily refer to any particular mechanism generating negative feedback.

Various mechanisms potentially regulate single populations (as opposed to metapopulations; see Gilpin and Hanski 1991). Most investigations have focused on crowding effects that operate locally via direct and indirect interactions among individuals (Sinclair 1989, Murdoch 1994). Other mechanisms proposed include the buffer effect and regulation via territoriality (Kluyver and Tinbergen 1953, Brown 1969), refuges from predation or parasitism (Hassell 1978, May 1978, Cappuccino et al. 1995), source–sink structure of subpopulations (Wiens and Rotenberry 1981, Pulliam 1988, 1996), and differences in the suitability of oviposition sites (Craig et al. 1989, Ohgushi 1995). Among these other mechanisms, the common theme is spatial heterogeneity. In this paper, we build on this theme by synthesizing theory and empirical evidence to elucidate a mechanism of regulation that we call site dependence.

Sites are defined as the areas occupied exclusively by individuals or mated pairs, and site-dependent species are defined as those in which individual fitness depends on exclusive use of a site (e.g., territory). Sites may differ in what they provide, e.g., food resources, a refuge from predation, an oviposition site, etc. Species that are not site-dependent, by contrast, are those in which individuals do not preempt resources, i.e., scramble competitors. Some site-dependent species, namely territorial ones, seem to be among the most tightly regulated (Hanski and Tiainen 1989), but even for site-dependent species, evidence of regulation, and particularly the mechanism of regulation, is equivocal at best (Sinclair 1989, Murdoch 1994). Explaining this tight regulation of site-dependent species is the primary objective of this paper.

The concept of site-dependent regulation derives from a variety of sources: theoretical arguments concerning individual responses to habitat heterogeneity (Andrewartha and Birch 1954, Brown 1969, Łomnicki 1988, Fahrig 1992, Morris 1992, Bjornstad and Hansen 1994, Bowers 1994, Goss-Custard et al. 1994, Sherry and Holmes 1995), ideal-despotic and preemptive territoriality (Fretwell and Lucas 1970, Pulliam 1987, Łomnicki 1988, Bernstein et al. 1991, Pulliam and Danielson 1991), source–sink dynamics (e.g., Wiens and Rotenberry 1981, Pulliam 1988, 1996), queuing of individuals where territories differ in suitability (Bernstein et al. 1991, Zack and Stutchbury 1992, Ens et al.

1995), and from empirical responses of organisms to environmental heterogeneity (e.g., Andrén 1990, Dhondt et al. 1992, Ferrer and Donazar 1996). We couple these ideas with data generated from our own field studies of migratory birds in breeding and wintering areas (Holmes et al. 1992, 1996, Rodenhouse and Holmes 1992, Sherry and Holmes 1995, 1996).

Site dependence operates when individuals or breeding pairs living in spatially heterogeneous environments preemptively use sites that differ in suitability for reproduction and/or survival. Preemptive use of sites means that the most suitable (i.e., best) sites are filled before those of lesser suitability (see Pulliam and Danielson 1991). This mechanism complements, and indeed for certain kinds of species may preclude or encompass, both local crowding mechanisms and regional source–sink processes. As we will argue, site dependence potentially generates negative feedback at all population sizes, sometimes independently of local population density (i.e., numbers per unit area), and it functions over both local and regional spatial scales. In the following sections, we describe the mechanism of site-dependent regulation, demonstrate its regulatory effect in a simulation model, examine its assumptions, consider selected implications of the mechanism, and compare and contrast it with other mechanisms that potentially regulate single populations. We conclude by discussing ways to test site-dependent regulation.

SITE-DEPENDENT REGULATION

The mechanism

The negative feedback mechanism generating site-dependent regulation results because the preemptive use of sites by a growing population relegates subordinate individuals to sites of progressively lower suitability. Use of progressively less suitable sites reduces average demographic rates for the population as a whole (Fig. 1), as proposed by Brown (1969) and Holt (1985, 1987), which slows population growth. Conversely, when population size declines (e.g., due to catastrophic mortality or a period with low breeding productivity), only the best sites are used, which results in higher average demographic rates and, thus, population growth. Population size will not continue to grow indefinitely, even with continued use of sites of highest suitability, because breeding productivity on these sites will be balanced at some population size by low breeding productivity or survival on sites of lower suitability.

This site-dependent mechanism differs from previous syntheses in several ways. First, site dependence focuses at the level of the individual, rather than the subpopulation, within a habitat type (throughout this paper, habitat refers to a group of sites, e.g., territories within a vegetation type). Second, site dependence generates a locally operating negative feedback without necessarily involving any crowding mechanism, i.e., there is no reduction in the suitability of sites or in the
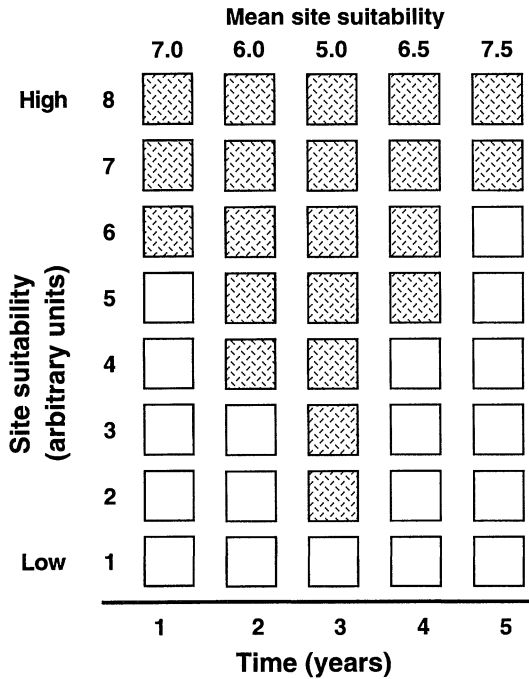
Mean site suitability

FIG. 1. Mean site suitability changes as the number of occupied sites, i.e., population size, increases or decreases. Hatched squares represent territories occupied in particular years as population size grows (years 1–3) or declines (years 3–5). Mean site suitability in each year is indicated above each column. Site-dependent, negative feedback that potentially regulates population size is created because mean site suitability declines as the number of sites occupied increases. Population growth is slowed by this negative feedback, because reduced site suitability is assumed to correspond with less favorable demographic rates.

fitness of individuals on already occupied sites as population size increases. Hence, saturation of habitats is not required for regulation by this mechanism, and local density of individuals may even decline at the same time as the population is growing and negative feedback is being generated by site dependence. Third, the regulatory potential of site dependence arises from an assumed continuous distribution of site suitabilities. Last, environmental characteristics determine potential reproductive success or survival on a site, avoiding the tautology of defining suitability by the same demographic measures used to assess suitability. Each of these features is illustrated and discussed in the ensuing sections.

The regulatory potential of site dependence: a simulation model

To assess the regulatory potential of site dependence, we performed simulations based on field data for the Black-throated Blue Warbler (*Dendroica caerulescens*), a territorial, forest-nesting passerine bird (Holmes 1994). We chose to construct a simulation model, parameterized with field data, because we felt

that this provided the most realistic test of regulation by site dependence possible at this time (model equations and parameter values are given in the Appendix). Each of the major features of site dependence was simulated by the models constructed. Heterogeneity of territory suitability was achieved by constructing four models that differed only in the number of levels of territory suitability (2, 4, 8, or 16 levels). Two levels of suitability represented a special case similar to source–sink population dynamics (see Pulliam 1988), whereas 16 levels were chosen to approximate the more continuous variability in territory suitability that is probably more typical in nature.

Preemptive use of sites was simulated in each model by filling available territories of highest suitability before those with lower suitability. Because better sites were always occupied before those of lesser suitability, the tendency for individuals to shift to more suitable sites between breeding seasons was implicitly included. The model did not include any intrinsic differences among individuals, such as age or experience. Neither did it include any other negative feedback mechanism that might be regulatory, e.g., a crowding mechanism that is modeled typically by a structural relationship, i.e., direct feedback, between the number of pairs per-hectare and demographic rates (e.g., clutch size).

Because territory-specific information was not available for Black-throated Blue Warblers or any comparable species, suitability levels for simulations were created by partitioning the field-measured ranges of fecundity (number of eggs laid per female per season) and the probability of nesting success into the desired number of levels (data from Holmes et al. 1992, 1996, Holmes and Sherry 1992). Thus, the parameter values of each model spanned the same range (e.g., annual fecundity ranged from 5 to 7 eggs), and this range was divided uniformly for each model (e.g., two levels of fecundity were 5.0 and 7.0 eggs; four levels were 5.00, 5.67, 6.33, 7.00; etc.). Each model included 144 territorial sites, and each simulation began with 20 breeding pairs.

To examine how the number of levels of territory suitability and the distribution of territories among those levels influenced the regulation of population size, we initially divided the 144 territories evenly among suitability levels, e.g., 72 for high suitability and 72 for low suitability in the two-level version of the model, 36 territories in each level for the four-level model, etc. The results of simulations indicated that population size reached a stable level in each deterministic model, i.e., all populations were regulated (Fig. 2A). Furthermore, population size did not continue to grow in an unbounded fashion, despite the continued use of sites of highest suitability, because high breeding productivity on the best sites was balanced by lower reproduction on sites of lower suitability, which were occupied increasingly as population
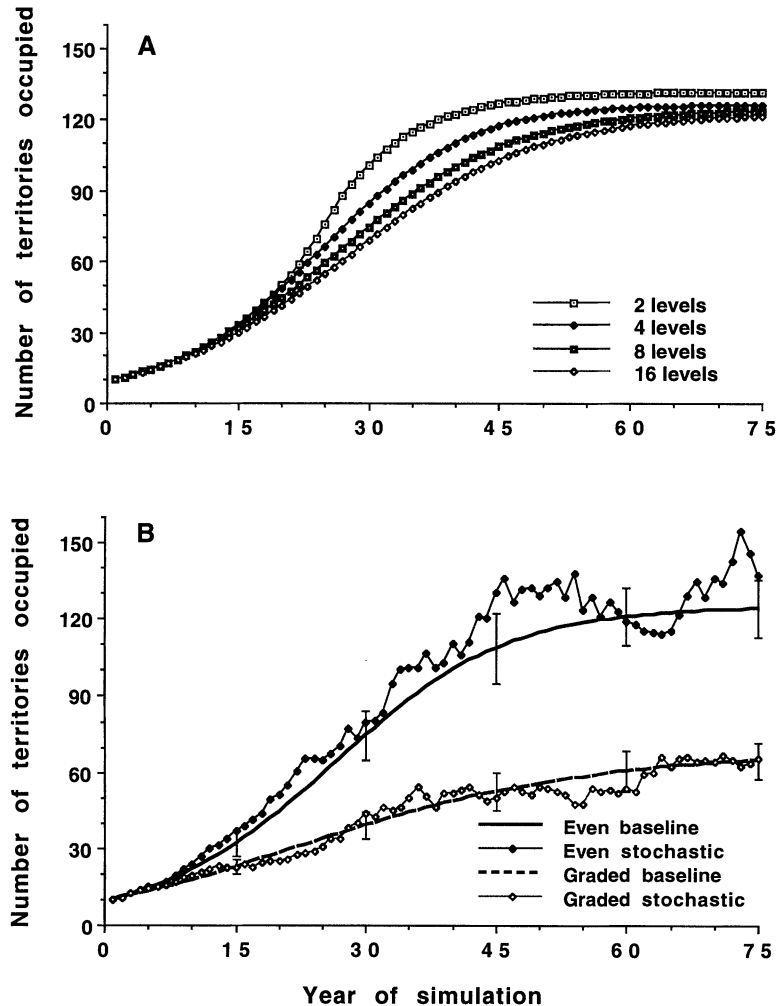
FIG. 2. (A) Growth of simulated Black-throated Blue Warbler populations when territories were divided among 2, 4, 8, or 16 levels of suitability for reproduction. Population growth reaches a stable level because of preemptive use of territories differing in suitability for reproduction (i.e., the best available are always occupied first). (B) Simulations of the eight-level model in which territories were distributed evenly among levels of suitability or in a graded manner, with more territories in levels of lower suitability. For each, a run with baseline values and one stochastic run are shown. The error bars on each simulation represent 1 SD of the mean, calculated from 20 runs of the stochastic model.

size expanded. Of course, site dependence could not be regulatory if all sites produced recruits in excess of replacement levels, or if no sites did, i.e., in rapidly increasing or declining populations. The former scenario is unlikely to occur for more than brief periods, but the latter may persist where site suitabilities have been lowered by environmental changes, such as those associated with habitat fragmentation (Herkert 1994, Robinson et al. 1995).

The number of levels of territory suitability influenced the shapes of the population growth curves and, to a lesser extent, the sizes at which each population stabilized (Fig. 2A), but models with 8 or 16 levels of suitability differed little. The two-level model had the highest stable population size because it included the largest number of the most suitable sites. However,

neither this model nor any of the others produced floaters (i.e., >144 breeding pairs). Thus, the number of most suitable sites available influenced stable population size, but was not in itself regulatory. The simulated populations were regulated entirely due to preemptive selection of territories that differed in suitability, not because all available sites were saturated and some females were unable to breed. No structural characteristic of the models precluded the production of floaters, and runs of the model with parameters altered from baseline values (i.e., increased fecundity or reduced mortality) did produce floaters (N. L. Rodenhouse, *unpublished data*).

Next, we repeated these simulations with stochastic variation in fecundity, nesting success, adult mortality, and juvenile survivorship (see Table 1 for means and

TABLE 1. Baseline values of four demographic parameters for sites of highest and lowest suitability, and sensitivity† of population size to variation in those parameters for a model simulating a Black-throated Blue Warbler population. Greater sensitivity values indicate greater influence of that parameter on population size.

| | Baseline values | | | | |
Parameter	High suitability	Low suitability	Mean	1 SD	Sensitivity value
Fecundity (no. eggs per female per season)	7.0	5.0	6.0	1.0	5.36
Nesting success (probability per nesting attempt)	0.60	0.40	0.50	0.05	3.72
Juvenile survivorship (from fledging to first breeding)‡	0.25			0.05	5.36
Adult mortality (annual probability)	0.40			0.05	4.57

† To determine sensitivity, each parameter (P) was varied $\pm 10\%$ of its mean value. The resulting values of the dependent variable (D) (population size) were used to calculate a sensitivity (S) value as: $S = [(D_i - D_d)/D_m]/[(P_i - P_d)/P_m]$, where D and P represented the values of the dependent and parameter variables, respectively, and i and d indicate the results from a run with a 10% increase (i) or decrease (d) relative to the mean (m) value of the parameter (see Jørgensen 1994:23).

‡ Site suitability did not influence juvenile or adult survival in our model. However, this might occur. If it did, it would tend to increase differences among sites and, hence, strengthen regulation by site dependence.

standard deviations). Variation of each of these parameters was simulated as normally distributed, and the range of values generated by the stochastic simulations approximated those observed in the field (see Holmes et al. 1992, 1996). With these calculations, the range in fecundity was now 3–9 eggs per female per season; adult mortality ranged from 0.5 to 0.3 (i.e., 50–70% adult survival); juvenile survival was 15–35%, and the probability of nesting success was 30–70%. The variances of these parameters were simulated as uncorrelated, because the primary factors influencing them do not seem to be related empirically. For example, fecundity of Black-throated Blue Warblers is influenced by nest predators and by arthropod (food) abundance, both factors that vary independently of the bird populations (Holmes et al. 1992, Rodenhouse and Holmes 1992). In these simulations, regulation of population size persisted even when realistic levels of stochasticity were included (Fig. 2B).

To examine whether preemptive use of sites was key to site-dependent regulation of the simulated population, we conducted runs using the parameter values that would occur if individuals chose sites at random. Such selection of sites would generate an approximately constant value of fecundity that was the mean of the site suitabilities available (see Table 1). When parameter values representing random site selection were simulated, the population was not regulated and population size declined by 2% per year. When stochastic runs of this same model were simulated, only three of 20 simulations sustained populations at or above initial population size for 10 years, and all simulated populations were declining rapidly by year 20. These runs indicated

that preemptive site selection was essential for regulation by site dependence.

Finally, to examine how an uneven distribution of territories among levels of suitability influenced regulation, we conducted simulations using the eight-level model. When relatively fewer territories of high suitability were available, the size at which the population stabilized was lower, as expected, and the magnitude of fluctuations around the stable size was significantly smaller (Fig. 2B). That is, regulation was tighter (Bartlett's test of difference between the variances in stable population size for the even vs. graded, stochastic simulations: chi-square = 5.33, df = 1, P = 0.02). This increase in the tightness of regulation occurred, in part, because a narrower range of suitability levels was occupied when the distribution of territories was graded (six of eight levels) than when it was even (seven of eight levels).

We also conducted sensitivity analyses (Jørgensen 1994:23) of the eight-level stochastic model to determine if the model produced reasonable results in comparison to other modeling studies of small passerine birds. With baseline parameter values, we found that population size was most sensitive to changes in fecundity and juvenile survival, less sensitive to adult mortality, and least sensitive to nesting success (Table 1). These results are what would be expected for populations of small passerine birds (see Emlen and Pikitich 1989, Thompson 1993).

The key results of these simulations are that the number of levels of site suitability and the distribution of territories among those levels strongly affect both population size and the apparent tightness of regulation.

These findings imply that previous assessments of regulation involving similar mechanisms but only two levels of territory suitability, such as source–sink models (e.g., Wiens and Rotenberry 1981, Pulliam 1988, 1996), may have underestimated the potential of preemptive site selection in heterogeneous environments to regulate population size tightly. Furthermore, the strong ability of site dependence to regulate population size may preclude the high population sizes at which crowding mechanisms become prominent.

We conclude from the modeling results that site dependence, as we have described it, can generate a strong, negative feedback on demographic rates, which could regulate the size of this Black-throated Blue Warbler population. The negative feedback is generated at the spatial scale of sites selected by individuals (e.g., territories or predation refuges), as argued theoretically by Lande (1987) and Łomnicki (1988). Wherever some of these sites support reproduction or survival at a level above that needed for replacement of breeding adults, regulatory negative feedback can be generated when sites of lesser suitability are also used. The recruits that occupy the less suitable sites are provided by above-replacement-level reproduction on the most suitable sites, but the distribution of sites among levels of suitability determines the strength of the site-dependent negative feedback and, hence, its regulatory potential. Conceptual and mathematical arguments have been made for similar regulatory processes occurring at the scale of habitat types (see Brown 1969, Holt 1985, 1987, Pulliam 1988, 1996, Howe et al. 1991), but the focus of those studies has been on two or three habitat types, not on the continuous distribution of site suitabilities that may occur within, as well as among, habitat types. As shown here, the distribution of site suitabilities can strongly affect the regulation of population size for species that exhibit site dependence.

EMPIRICAL EVIDENCE FOR THE CONDITIONS OF SITE-DEPENDENT REGULATION

The regulatory potential of site dependence is influenced by the operation of two primary conditions: (1) heterogeneity among sites in their suitability for breeding and/or survival, and (2) preemptive site occupancy. We will examine the functional role of each of these features and the available evidence.

Heterogeneity of site suitability

Site-dependent regulation assumes the existence of an array of sites that differ predictably in their relative suitability for reproduction or survival. Such differences in the suitability of sites are the result of spatial and temporal heterogeneity in the distribution of environmental conditions and resources (Wiens 1976, Whittaker and Levin 1977, reviewed by Lord and Norton 1990). Because sites are selected from a complex environmental mosaic, they are expected to differ near-

ly continuously in suitability for reproduction and survival (Southwood 1977, Block and Brennan 1993), even within seemingly homogeneous habitat.

Evaluation of fine-scale environmental heterogeneity (e.g., sites occupied by individuals or pairs) is difficult because frequency distributions of site suitabilities are seldom obtained or reported. In the few cases in which the environmental causes or consequences of differences in site suitability for animals have been assessed, suitability has been found to vary substantially (e.g., Potts et al. 1980, Reichert 1981, Ligon and Ligon 1988, Beletsky and Orians 1989, Armitage 1991, Ens et al. 1992, Tye 1992, Widen 1994, Siikamaki 1995, Wauters and Lens 1995), with sites of greatest suitability sometimes comprising only a small proportion ($<10\%$) of all sites (e.g., Potts et al. 1980, Reichert 1981). Differences in suitability have been sought and found most commonly among habitat types (e.g., Brown 1969, Krebs 1970, Krebs and Perrins 1977, Zimmerman 1982, Yahner 1988, Andrén 1990, Halama and Dueser 1994, Donovan et al. 1995, Riddington and Gosler 1995, Svensson and Nilsson 1995, Holmes et al. 1996). Such differences among habitats probably are the consequence of different distributions of site suitabilities within these habitats.

Relative differences in site or habitat suitability often persist longer than the life-spans of most individuals (see Blancher and Robertson 1985, Beletsky and Orians 1987, Peterson and Best 1987, Ligon and Ligon 1988, Sherry and Holmes 1989, Groen 1993). Thus, locations of the most suitable sites are often predictable even if absolute suitability varies among years. For example, relative differences in the suitability of Blue Tit (*Parus caeruleus*) territories persisted for a decade (Dhondt et al. 1992); more suitable territories were occupied more frequently than less suitable ones in long-term studies of Nuthatches (*Sitta europaea*; Matthysen 1987, Nilsson 1987); and preferred territories were consistently occupied early each season in a 7-yr study of Great Reed Warblers (*Acrocephalus arundinaceus*; Bensch and Hasselquist 1991). Suitability is also predictable among territories preempted by invertebrates (Whitham 1978, Hart 1987, Krupa and Sih 1993).

Persistence of relative site suitabilities for even several years would be longer than the average lifetime of most small territorial vertebrates or invertebrates; hence, such differences in relative suitability would create selection pressure favoring site fidelity of individuals occupying good sites (Switzer 1993, Weatherhead and Forbes 1994). Indeed, traits of individuals such as site fidelity, dominance, and breeding experience could enhance environmentally caused differences in site suitability (Sæther 1990, Goodburn 1991, Bowers 1994, Forslund and Part 1995, Holmes et al. 1996). For example, individuals experiencing reproductive failure are less likely to return to a territory than successful individuals (e.g., Harvey et al. 1979,

Gavin and Bollinger 1988, Roth and Johnson 1993). This behavior probably accounts for the observations that older and more experienced individuals preferentially occupy territories of greatest suitability (i.e., with the highest probability of nesting success; e.g., Gauthreaux 1978, Matthysen 1990, Bensch and Hasselquist 1991, Holmes et al. 1996), and that inexperienced or less dominant breeders are relegated to less suitable sites (e.g., Zang 1982, 1988, Peterson and Best 1987, Sherry and Holmes 1989, Verboom et al. 1991). Thus, individual differences may augment the environmentally caused suitability of sites and thereby increase the likelihood of negative feedback via site dependence. However, such individual differences are not a prerequisite for the mechanism of site dependence, as we have shown by simulation modeling.

Preemptive use of sites

The fitness advantage of occupying a good site should strongly select for preemptive site selection (i.e., individuals always selecting the best unoccupied site; Pulliam and Danielson 1991). Evidence for preemption is found whenever good sites tend to be occupied before poor ones (e.g., Whitham 1978, Reichert 1981, Best and Rodenhouse 1984, Bensch and Hasselquist 1991, Ens et al. 1992), dominant (older, more experienced) individuals obtain the best territories (e.g., Knapton and Krebs 1974, Potts et al. 1980, Lanyon and Thompson 1986, Sherry and Holmes 1988, 1989, Armitage 1991, Verboom et al. 1991), or pairing success or site fidelity is greater on high- than low-suitability territories (Fretwell 1987, Roth and Johnson 1993, Holmes et al. 1996). The fact that intraspecific social dominance constrains distributions (e.g., Brown 1969, Gauthreaux 1978, Nilsson et al. 1982, Zang 1982, 1988, Sherry and Holmes 1989, 1995) or reproduction (e.g., Ens et al. 1992, Orell et al. 1994) of some age and sex classes also suggests that preemptive selection of territories may be widespread.

Ideal preemptive site selection has been demonstrated for a variety of species (Rosenzweig 1991), but direct tests of this theory for site-dependent species remain few (e.g., see O'Connor 1985, Pulliam and Danielson 1991, Holmes et al. 1996). Ideal-preemptive selection assumes that habitats differ in resource supply and, hence, in suitability for reproduction and/or survival. Where such differences occur, Fretwell and Lucas (1970) hypothesized that the most suitable habitats would be occupied first. Then, as population size increases, the density of individuals in this most suitable habitat rises, causing decreases in per capita resource supply and, therefore, in realized suitability for all individuals within that habitat. When the average suitability of the preferred habitat is reduced by crowding effects to the level found in the next most suitable habitat, the less suitable habitat should then begin to fill. Much support for this hypothesis exists (e.g., Krebs

1971, Morse 1976, Krebs and Perrins 1977, Wilcove and Terborgh 1984, O'Connor 1986, Clark and Weatherhead 1987, Morris 1989, Bernstein et al. 1991, Dhondt et al. 1992, Krohn 1992, Halama and Dueser 1994), but field tests have almost exclusively focused on patterns of habitat occupancy and not on the mechanisms generating these patterns.

The mechanisms usually assumed to generate such patterns involve individuals examining many sites, assessing their relative quality, and then choosing the best site for use, i.e., preempting that site (Pulliam and Danielson 1991). However, the outcome of preemptive selection, that the best sites are consistently occupied, whereas those of lesser suitability are not, could occur without such extensive examination of sites. This outcome is possible where individuals on good sites tend to survive longer or disperse less frequently than those on poor sites. Good sites with higher expected breeding success tend to be retained by experienced breeders, whereas poor sites supporting lower breeding success are frequently abandoned (reviewed by Switzer 1993). The longer occupancy of good sites, combined with the inability of subordinates to displace dominant individuals, would make poor sites the most frequently available to subordinate, inexperienced recruits. Evidence that such "apparent" preemptive selection occurs comes from species whose site fidelity is positively correlated with reproductive success (e.g., Roth and Johnson 1993).

A correlate of preemptive site selection is that individuals should shift to more suitable sites as they become available. Evidence for this comes from individuals shifting from floating to territorial status (Reichert 1981, Hoffman et al. 1985, Arcese 1987) and shifting among territories within, or more commonly between, breeding periods (e.g., for birds: Krebs 1971, Enoksson 1987, Peterson and Best 1987, Sherry and Holmes 1989, Bensch and Hasselquist 1991, Switzer 1993, Lawn 1994, Aebischer et al. 1995). Shifting by already settled individuals to better sites would have the effect of strengthening the site-dependent regulatory effect. This would be particularly true in declining populations with few recruits, because shifting would guarantee that the best sites were occupied and, thus, demographic rates would be higher at low population sizes. Even if individuals do not shift to territories of higher suitability, however, site-dependent regulation can still generate negative feedback on demographic rates as long as new recruits select the best available sites (i.e., site use is preemptive).

EVIDENCE OF SITE-DEPENDENT REGULATION FROM FIELD STUDIES

The model and arguments we have presented demonstrate theoretical support for site-dependent regulation and for its underlying assumptions. But does this mechanism actually function in nature? Many studies

have considered aspects of this proposed mechanism, although none has provided a comprehensive test. For example, numerous studies identify how the occupation of suboptimal habitat (or in a few studies, sites) by some individuals influences one or more demographic rates. In studies of birds, Krebs (1970) found that the proportion of Great Tits (*Parus major*) nesting in lower quality habitats (i.e., ones characterized by low clutch sizes) increased from ~35% to 50% as population size increased from ~30 to 90 pairs. Although he reported that this effect was too small to regulate population size, our simulations suggest that grouping territories dichotomously into good and poor "habitats" may obscure the effect of site-dependent regulation. Dhondt et al. (1992) reported that the average clutch size of Blue Tits (*Parus caeruleus*) also declined as population size increased, due to the addition of territories on which clutch size was persistently low. Andrén (1990) suggested that differences in the quality of jay (*Garrulus glandarius*) territories, due to differences in nest predation, might regulate his study population, and Ferrer and Donazar (1996) reported density-dependent fecundity in Spanish Imperial Eagles (*Aquila adalberti*) that was generated by spatial heterogeneity, i.e., "source" territories produced, on average, more than four times more chicks than "sink" territories. In taxa other than birds, Reichert (1981) found that spiders on more suitable territories could have as much as 13 times the reproductive success of those on less suitable ones. She concluded, however, that territoriality limits, but does not regulate, the population size of her study species. Lord and Roth (1985) identified high-quality habitats as those used repeatedly by yellow jacket (*Vespula maculifrons*) colonies, and they found that production of queens by colonies in these areas was significantly greater than in areas used only once. Wauters and Lens (1995) found that more female red squirrels (*Sciurus vulgaris*) occupied poor-quality territories when population size was greatest, and that females on poor territories had significantly higher rates of breeding failure than those on better ones. Their long-term study also revealed that heterogeneity in territory quality and crowding effects, i.e., reductions in the quality of even the best territories when population sizes peak, can simultaneously generate negative feedback on demographic rates. In none of these studies, however, was regulation analyzed quantitatively or explicitly.

The best quantitative and experimental evidence to date that site dependence could be regulatory comes from the study of Potts et al. (1980) of Shags (*Phalacrocorax aristotelis*). They reported an inverse relationship between the average suitability of nest sites occupied and population size. Only 4% of nest sites were of highest suitability, and more sites of low suitability were used as population size increased. Sites of low suitability were occupied primarily by young breeders that had low breeding success. However, after a catastrophic reduction of population size, young birds used sites of highest suitability and increased their breeding productivity by 71% indicating the importance of sites per se. Potts et al. (1980) demonstrated by simulation that the use of nest sites of low suitability was a major factor slowing the growth of this Shag population.

The only other quantitative assessment of the impact of territory suitability and selection on population regulation is a modeling study conducted by Pulliam et al. (1992). They simulated a closed sparrow population occupying territories of low, medium, and high suitability. Excess individuals produced on territories of high suitability dispersed until an unoccupied, suitable territory was encountered. Individuals dispersing greater distances had a greater probability of dying during dispersal; thus, dispersal mortality depended explicitly on population size. Territory selection was preemptive because individuals occupying territories could not be displaced by dispersing individuals, and territory holders did not disperse from territories of high suitability. Pulliam et al. (1992) found that the simulated population tended to stabilize at a small size relative to the total number of territories available, and that individuals became concentrated in territories of highest suitability. These results seem consistent with our proposal that spatial heterogeneity in territory suitability, combined with even simple preemptive site selection, can regulate population size tightly. However, the cause of regulation in their model is not clear, because two potentially regulatory mechanisms were confounded: site-dependent regulation and population size-dependent dispersal mortality.

Results of the field studies reviewed demonstrate that preemptive use of sites differing in suitability can generate negative feedback on demographic rates, and quantitative analyses of the mechanism (Potts et al. 1980) and theoretical considerations (Pulliam et al. 1992, and this study) suggest that it may be strong enough to regulate population size.

IMPLICATIONS OF SITE-DEPENDENT REGULATION

Density-free regulation of population size

One of the most intriguing features of site-dependent regulation, as we have described and modeled it, is that it is density free. Because density may be measured in multiple ways (Lewontin and Levins 1989), it is important to note that we define the term "density" in this paper as the number of individuals per unit area, the typical definition in ecology textbooks (see Ricklefs 1990:331, Krebs 1994:707, Begon et al. 1996:223) and measurement in field studies (e.g., Dhondt et al. 1992, Massot et al. 1992). Our models are density free because they contain no direct structural link between population density and demographic rates, as is found in conventional models of density-dependent mechanisms (e.g., logistic models), and because the area oc-

cupied in our simulations is assumed to expand or contract as population size changes (for examples, see O'Connor 1985, 1986). Furthermore, the concept of site dependence is density-free because site preemption precludes crowding effects from lowering the demographic traits of individuals on either high- or low-suitability sites, at least over a wide range of densities (see Getty 1981, Lømnicki 1988, Pulliam and Danielson 1991 for similar arguments). By the process of preemption, site holders gain exclusive use of sites and achieve the level of survival or reproduction intrinsic to those sites, which is independent of the number of occupied neighboring sites. Thus, the fitness advantage of preemption, and hence its prevalence, may occur precisely because preemption can preclude the detrimental effects of crowding, which tend to occur only at or near saturation of available habitat (Sinclair 1989, Murray 1994). Even at population densities above saturation, floaters (e.g., nonterritorial individuals) might have no impact on site holders (e.g., Smith 1978, Reichert 1981, Zack and Stutchbury 1992; but see Wauters and Lens 1995). Where neither floaters nor neighbors impact site holders, population regulation, when it occurs, must necessarily be independent of local population density.

Although the suitability of all sites within a habitat is often assumed to decline progressively as more sites are occupied in an ideal-free or an ideal-despotic manner (Fig. 3, Scenarios 1 and 2), such reductions tend to occur only at or near saturation of available habitat (Sinclair 1989, Murray 1994) and may be precluded entirely by preemptive use of sites. Where preemption occurs, population size can vary independently of local crowding, across a wide range of spatial scales and environmental conditions, particularly when available habitat is unsaturated. One possible result is that, as population size increases in an unsaturated habitat, sites of equal or lower suitability and equal size may be added that are not adjacent to occupied sites Fig. 3, Scenario 3), and thus have no influence on other individuals' reproduction or survival, either directly or indirectly. Note that neither the number of neighbors nor the size of territories adjacent to the territory marked "×" in Fig. 3, scenario 3, changes when new sites are added, suggesting no change in local crowding effects. A second possibility is that population size increases independently of local crowding where interactions between adjacent territory holders have no impact on reproduction or survival (Fig. 3, Scenario 4), as hypothesized by Lømnicki (1988) and Pulliam and Danielson (1991). Finally, a third possibility is that sites of progressively lower suitability and larger size (e.g., Verboom et al. 1991, Tye 1992) are added as population size grows (Fig. 3, and Scenario 5). In this latter scenario, the density of individuals actually decreases (per unit of area occupied) as population size increases, demonstrating the counterintuitive possibil-

ity that negative feedback on demographic rates can occur even as local population density declines!

Because the intensity of competition for sites may increase as the number of individuals competing for those sites increases (Sinclair 1989), it could be argued that site dependence is not density free. If such competition were to result in the reduction of site size and fitness of site holders, this would indeed be an example of a crowding mechanism. Such crowding mechanisms may occur in some circumstances, e.g., in spatially constrained populations such as those concentrated by the provision of nest boxes (e.g., Stenning et al. 1988, Torok and Toth 1988, Perrins 1990), and those confined to islands (e.g., Grant 1986, Arcese et al. 1992) or habitat fragments (e.g., Wauters and Lens 1995). However, if competition occurs only at the time of territory establishment, it may have little or no effect on site size or on the subsequent fitness of site holders. This is illustrated as scenarios 3 and 4 in Fig. 3. Even at or above saturation densities, the size of sites need not decline as competition for sites intensifies, because preemption could force some individuals to be floaters, entirely excluded from available habitat. Thus, for species that occupy sites preemptively, local population density may be a poor and even misleading indicator of regulatory feedback.

The focus on density, and hence crowding effects, in most studies of population regulation (see Begon et al. 1996:223) may have precluded the examination of regulatory negative feedback arising from density-free mechanisms such as site dependence for several reasons. First, the study plots used to measure density are often located in the most homogeneous and favorable habitats available (e.g., our long-term studies; Holmes et al. 1986, 1992, 1996), which reduces the range of site suitabilities examined and, thus, makes regulation by site dependence difficult to detect. Second, density can be measured in various ways (Lewontin and Levins 1989), but regulation will only be detected when using that measure of density appropriate for a particular organism and environment. For example, density measured as the number of individuals per unit area may adequately measure negative feedback for only some types of organisms (e.g., scramble competitors) in some habitats (e.g., saturated habitats). However, this measure of density may be inadequate to elucidate regulation associated with changes in the number of individuals per total area available to the population. Third, plot-based measures of density can only detect processes operating at the fixed and arbitrary scale of the study plot, which may not be the scale at which population regulation operates, as we will discuss next. Thus, how one samples a population and measures its density is crucial for assessing whether or not regulation is occurring and for identifying the process(es) involved.

Smaller population size   **Larger population size**

Habitat A   Habitat A

Habitat B   Habitat B
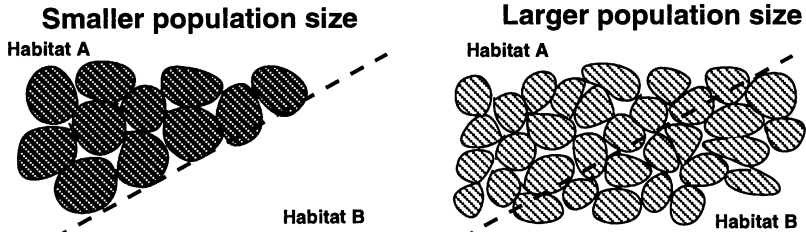
Scenario 1. Ideal-free distribution of territory suitability. Increased population size results in individuals on all sites experiencing increased density, smaller territory size, and decreased site suitability (high suitability on the left becomes medium on the right), whether habitat suitability is high (to the left of the dashed line, labelled Habitat A) or low (Habitat B).

Habitat A   Habitat A

Habitat B   Habitat B
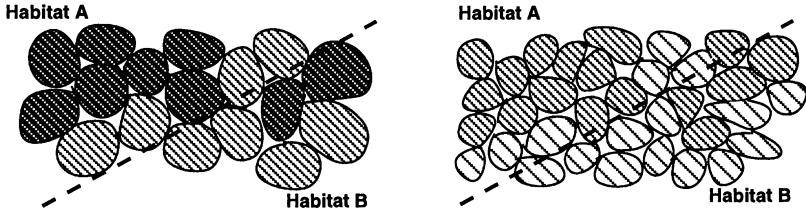
Scenario 2. Ideal-despotic distribution of territory suitability. Increased population size results in individuals on all sites experiencing increased density, smaller territory size, and decreased site suitability. Unlike scenario 1, however, despotism results in some individuals experiencing higher suitability than others, in this particular case, at both smaller and larger population sizes. Like scenario 1, suitability declines for all site holders as population size increases.

Scenario 3. Site dependence by the addition of noncontiguous sites of low suitability. Increased population size results in decreased *average* suitability per site by the addition of noncontiguous sites, which are of relatively reduced (medium rather than high) suitability, and which do not affect the suitability of previously occupied sites such as the site marked with an x.
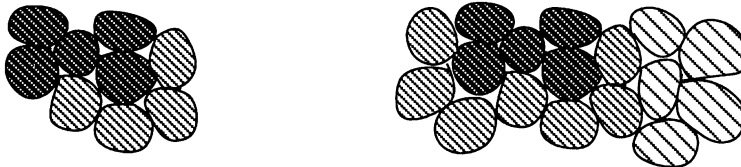
Scenario 4. Site dependence by the addition of contiguous sites of low suitability. Increased population size results in decreased *average* suitability per site by the addition of contiguous sites, which are of relatively reduced (medium or low) suitability, and which do not affect the suitability of previously occupied, contiguous sites because of site preemption.
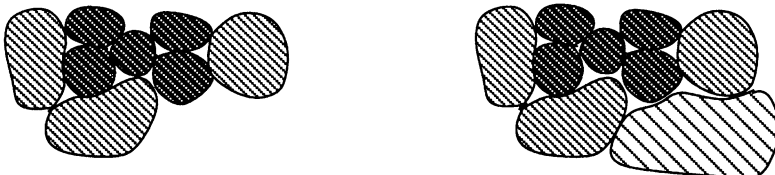
Scenario 5. Site dependence by the addition of larger sites of low suitability. Increased population size leads to both decreased *average* suitability per site, by the addition of relatively low-suitability sites, and also to decreased average density as measured by number of site holders per occupied area. This scenario illustrates the potential independence of regulation from population density (but not from population size).

Site suitability   ▓ High   ◨ Low   ⊢————————⊣
               ▨ Medium   ☐ Suitable   1000 m
                               but unused
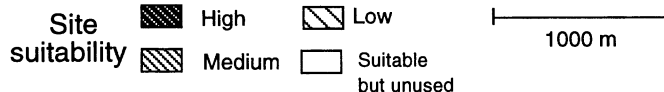
Spatial scale of population regulation

Site-dependent regulation may operate over a broad range of spatial scales and is largely independent of the spatial location of suitable sites, as represented in our models. This occurs because site size (e.g., territory diameter) is often small relative to natal or adult dispersal distances (Greenwood and Harvey 1982, Weatherhead and Forbes 1994, Villard et al. 1995); therefore, dispersal distance determines the spatial scale at which site-dependent regulation operates (Fig. 4). In all but highly fragmented habitats or in sparse populations, it is likely that tens to thousands of territories will occur within the area that could be reached by dispersing individuals, particularly juveniles that disperse the longest distances (we recognize that actual dispersal distances can depend, in part, on the spatial configuration of suitable habitat types; see Fahrig and Merriam 1994, Haas 1995). Spatial variability in environmental conditions makes it likely that good and poor sites, potentially even from different subpopulations, will occur within dispersal distance of most species (Fig. 4). Hence, site-dependent regulation is expected to be largely insensitive to the location of sites, i.e., whether good sites are clumped or randomly scattered among sites of lesser suitability is irrelevant, as long as natal or adult dispersal among these sites is possible (see also Bjornstad and Hansen 1994). It is interesting to note that, where the spatial scale of regulation matches that of dispersal, the scales of regulation and the genetic structure of populations would also coincide.

Although it seems reasonable to conclude that the spatial scale of regulation is determined by species' dispersal distances (Holt 1985, Lande 1987, De Roos et al. 1991, Morris 1992, Fahrig and Merriam 1994), surprisingly, this may not occur whenever crowding effects generate regulation. Crowding effects tend to be highly local and, therefore, may affect most individuals only in saturated habitats or in dense aggregations of individuals. Under such conditions, the spatial scale of regulation would be determined primarily by the size of the saturated habitat or aggregation, not by dispersal distances.

Multiple limiting factors are integrated by site-dependent regulation

Limiting factors put a ceiling on population size (Newton 1992) or in some way reduce breeding pro-
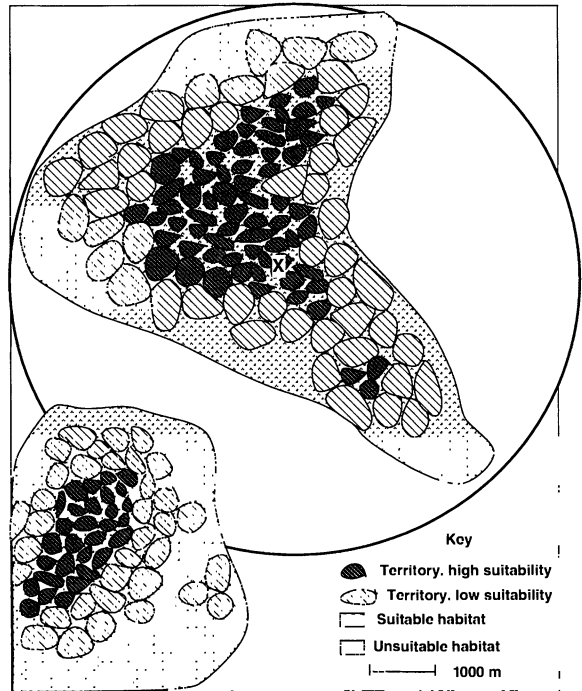

FIG. 4. The spatial scale of site-dependent regulation of population size is determined by adult and natal dispersal distances. The large dark circle indicates dispersal distance from the territory marked with an X. Within the distance reached by dispersal are numerous territories of different suitability and a separate subpopulation. Territory suitability is indicated by stippling and size. Territory suitability probably varies continuously, but it is shown here in two levels for convenience and clarity.

ductivity or survival (Sinclair 1989). Numerous biotic or abiotic factors can limit population size, including breeding sites, food, predators, parasites, or weather conditions (Sinclair 1989), and these factors can operate sequentially or sometimes interactively (e.g., Smith et al. 1991, Arcese et al. 1992, Newton 1994, Pulliam and Haddad 1994). Site-dependent regulation integrates these multiple limiting factors because their combined effects determine site suitability. Certainly, the impact of different environmental factors on site suitability varies among years, and identifying the few factors that are most frequently or intensely limiting may be critical for management purposes. However, the negative feedback generated by site dependence

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FIG. 3. Scenarios of population regulation involving different potential changes in density with increasing population size. All scenarios generate negative feedback because average per capita (or per site) suitability declines between a smaller population size (left-hand series of panels) and a larger population (right-hand panels). Scenarios 1 and 2 represent conventional ideal-free and ideal-despotic habitat selection (Fretwell and Lucas 1970), whereas scenarios 3–5 represent alternative ways in which site-dependent regulation may operate. Habitats are not identified in scenarios 3–5 because the site dependence mechanism focuses on differences among sites, not habitats. Site suitability probably varies continuously in nature but is represented by only three levels here for simplicity; floater individuals are also excluded for simplicity but could be included in any of these scenarios.
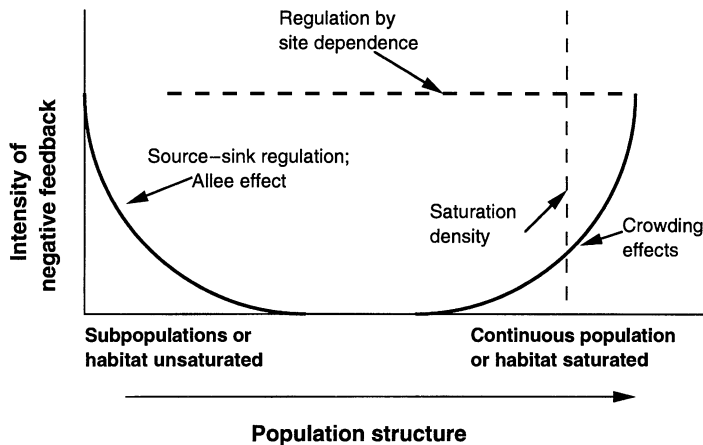
FIG. 5. The intensity of negative feedback generated by different mechanisms of population regulation depends on population structure. Source–sink regulation functions for populations with well-defined subpopulation structure (clumped); crowding effects occur primarily for populations that are rare (i.e., Allee effect) or that saturate locally available habitat. At or near saturation density, site dependence may function concomitantly with crowding mechanisms. Regulation by site dependence potentially occurs over all population structures where site suitability is continuously distributed. Idealized relationships are presented; the actual intensity of negative feedback will depend upon the environmental conditions of the species considered.

arises from the operation of all of the biotic and abiotic factors acting together to determine suitability of individual sites occupied by organisms.

Site dependence integrates the multiple environmental events and conditions operating during different phases of the breeding cycle or affecting different ages or stages of individuals. For example, food abundance and nest predation may limit breeding productivity of migratory birds (Martin 1992, Rodenhouse and Holmes 1992), whereas stochastic events such as storms may reduce population sizes during migration (e.g., Whitmore et al. 1977, Zumeta and Holmes 1978) or over winter (Baillie and Peach 1992). Such mortality would be partially compensated for by the occupation of only the most suitable territories (e.g., with more food and lower probability of nest predation) during the subsequent breeding season, leading to greater average demographic rates for the smaller population.

COMPARISON OF SITE-DEPENDENT REGULATION WITH OTHER REGULATORY MECHANISMS

Site dependence vs. crowding

Site-dependent regulation of population size differs from that caused by effects associated with crowding in several important ways. First, site-dependent regulation can occur over a broad range of spatial scales as just discussed, because the negative feedback required for population regulation is not tied to direct or indirect local interactions among site holders. In contrast, crowding mechanisms occur via increased costs of territory defense, social stress, or resource competition with neighbors, or via decreased rates of survival due to enhanced parasite-related morbidity or predation (see Martin 1988, Møller et al. 1990, Armitage 1991, Kempenaers and Dhondt 1992, Loye and Carroll 1995); these are inherently local in origin and effects. Such direct (e.g., agonistic) or indirect (e.g., via attracting predators) interactions among individuals, which can generate negative feedback on demographic rates, are not necessary for site dependence.

Second, site dependence potentially generates negative feedback over a broader range of population structures (Fig. 5) than do crowding mechanisms. Crowding-related negative feedback may only occur when populations are at or near saturation density, or when individuals are aggregated for other reasons, i.e., when most individuals in a population are interacting directly or indirectly with neighbors (Sinclair 1989, Murdoch 1994), but site dependence lacks these constraints. However, site dependence and crowding could contribute simultaneously to regulatory negative feedback when density approaches saturation (Fig. 5; see Wauters and Lens 1995).

Third, site dependence and crowding differ in how negative feedback alters demographic rates. For crowding, conspecifics generate density effects by their direct or indirect interactions. For site dependence, however, multiple limiting factors of the local environment generate differential suitability of sites for reproduction and survival. These differences in site suitability, in turn, create the potential for site-dependent regulation.

Site dependence vs. limitation by territoriality

Site-dependent regulation is not the same as limitation of breeding density by territoriality (or buffer effects), because it does not require the saturation of suitable habitat to generate negative feedback. Site-dependent regulation potentially occurs whenever the number of sites used by a population increases, because these additional sites are assumed to be of lower suitability than those previously occupied. Thus, site-dependent negative feedback can occur for all population sizes, including small populations far from saturation. In contrast, territoriality limits population *density* only when suitable habitat is at or near saturation (Brown 1969, Łomnicki 1988), and it does not limit population *size* because the number of floaters is, theoretically, not limited (Brown 1969, Newton 1992). Although territoriality and buffer effects can each be regulatory, we argue that site dependence, with its focus on individuals

seeking to maximize individual fitness in heterogeneous environments, is a more general mechanism that subsumes these others.

Site dependence vs. source–sink regulation

Populations composed of source and sink subpopulations located in different habitat types, as hypothesized by Wiens and Rotenberry (1981), can be regulated by the largely directional (from source to sink) dispersal of individuals from habitat types that are net sources of individuals (i.e., reproduction exceeds mortality) to sinks that are maintained by immigration from source areas (Pulliam 1988, 1996). In addition to differential reproduction among subpopulations, Pulliam (1988) included crowding effects in source–sink regulation by making habitat suitability directly dependent upon subpopulation density in an ideal-free or ideal-despotic manner (after Fretwell and Lucas 1970). Pulliam and Danielson (1991) extended the concept of source–sink regulation. First, they assumed that habitat selection is ideal-preemptive. According to this concept, the occupation of lesser quality sites has no effect on the reproduction or survival of those using higher quality sites. Second, they hypothesized an exponential distribution of site qualities within habitat types. These two concepts, preemptive site selection and the distribution of site suitabilities, have been incorporated into site-dependent regulation, and we extend the work of Pulliam and Danielson (1991) by explicitly assessing how each of these concepts potentially contributes to regulation.

Site-dependent regulation differs from source–sink regulation in several ways. First, site-dependent regulation focuses on individuals. For example, it emphasizes their ability to assess and compete for sites, their reproductive potential on specific sites, and their dispersal tendency. In contrast, source–sink regulation focuses on subpopulations within habitat types of different suitability. We argue that the individual level is the appropriate focus for the regulatory process because reproduction and survival, and hence the regulatory mechanism, operate at this level, particularly for species that select sites preemptively. An increasing number of studies demonstrate the insights that can be gained from such individual-oriented approaches (e.g., Armitage 1991, De Roos et al. 1991, Pulliam et al. 1992, Murdoch 1994, Wolff 1994, Goss-Custard et al. 1995, Uchmanski and Grimm 1996). Of course, knowledge of habitat suitability is extremely useful for management purposes, and it can be calculated by averaging individual site suitabilities within habitat types.

Second, site dependence is independent of local density as we have described, whereas the suitability of sites within source and sink habitats is often assumed to be influenced by crowding effects (e.g., Kawecki 1995, Watkinson and Sutherland 1995), following Pulliam's (1988) original formulation. Third, suitability,

according to site dependence, can be assessed independently of reproductive success or survival (e.g., using food or predator abundance), avoiding the tautology of defining site suitability in the same demographic terms used to measure site suitability. According to site dependence, differences among sites are the consequences of environmental differences. In contrast, source and sink habitats are defined by net recruitment (i.e., the outcome of births, immigration, deaths, and emigration). Consequently, identifying a source or sink habitat provides no mechanistic understanding of sources or sinks. Fourth, the scale of site-dependent regulation is linked explicitly to dispersal distances rather than to the distribution and size of habitat types supporting different subpopulations.

We conclude that, for site-dependent species, source–sink regulation represents a special case of site dependence, in which sites are strongly spatially structured into habitats of qualitatively different types. We draw this conclusion because (1) characteristics of habitats derive from those of the sites they contain, (2) dispersing individuals of a single population may often reach and settle in multiple habitat types, and (3) site suitability probably varies within most habitat types.

TESTING SITE-DEPENDENT REGULATION

No study to date has tested simultaneously, or for any one species, all of the components of site-dependent regulation. However, even partial tests can contribute to knowledge of the regulatory role of this mechanism (see Andrén 1990, Dhondt et al. 1992, Wauters and Lens 1995). Additional partial tests might be possible by using long-term data sets that include site-specific information on occupancy, breeding productivity, or survival. However, existing data sets that include environmental data usually do so for large spatial scales, such as habitats, rather than for sites of individuals. Thus, additional tests of the relationships between the environmental characteristics of sites and the demographic consequences for their holders will be needed to test this mechanism explicitly.

The assumptions of site-dependent regulation are readily testable and could be falsified in a variety of ways. For example, the mechanism would be rejected: (1) if predictable differences in site suitability could not be identified; (2) if differences in site suitability, as measured by environmental variables, failed to predict differences in demographic traits; or (3) if the frequency of occupation of sites differing in suitability did not differ from random. Large, stochastic demographic or environmental variation might limit the operation or detection of each of these relationships. If so, site dependence might not be regulatory, and populations could be limited by stochastic events acting independently of population size. Alternatively, regulation might be occurring at the metapopulation scale (Murdoch 1994).

Evidence in support of site-dependent regulation would include: (1) sites differing in relative suitability, particularly within habitats, and (2) sites of progressively lower relative suitability being occupied as local population size increases, lowering average demographic rates. Such relationships probably cannot be tested adequately by focusing on small study plots, as is usually done (see also Brown 1969, Watkinson and Sutherland 1995, Smith et al. 1996). Rather, the individual sites studied should be selected in a stratified random manner to represent a large portion of the range of environmental conditions used by a population. For territorial vertebrates, studies at spatial scales determined from natal and adult dispersal distances, and spanning the wide range of conditions created by environmental gradients (e.g., elevation, moisture) would be particularly informative.

Experimental manipulations of population size or density, as well as those of environmental characteristics of sites, if feasible, would provide even more critical tests of the mechanism. Such experiments could help to distinguish site dependence from crowding mechanisms. For example, removal of neighbors should boost breeding productivity or survival of focal individuals if crowding effects are important, but not if site dependence alone is operating. Quantitative assessment of the regulatory potential of each mechanism could then be explored by using simulation models, structured to represent alternative mechanisms and parameterized with field data.

CONCLUSIONS

Regulation of local population size for site-dependent species may be explained by individuals preemptively using sites that differ in suitability for reproduction and survival. The distribution of site suitabilities required for such site-dependent regulation is generated by spatial and temporal variability in environmental factors that influence reproduction and/or survival. Preemptive selection of sites from this environmental mosaic matches the most fit individuals with the sites of greatest suitability. For some species, crowding effects may coincide with site-dependent regulation under conditions of habitat saturation or aggregation of individuals. However, results of our simulation models suggest that site dependence alone can regulate population size tightly, and that the mechanism theoretically operates across a broad range of spatial scales. We suggest that site-dependent regulation should apply widely in vagile organisms, considering the prevalence of site dependence, preemptive site selection, and occupation of heterogeneous environments by these taxa.

ACKNOWLEDGMENTS

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APPENDIX

TABLE A1. Baseline values for parameters of the models used to simulate a population of Black-throated Blue Warblers breeding in northern hardwoods forest, New Hampshire, USA.

Parameter	Variable	Mean	Range†	1 SD	Units
Initial adults	$N_{i,t}$	20			no. individuals
Nesting success	n	0.5	0.4–0.6	0.05	probability of a nest surviving to fledging
Adult mortality	m	0.4		0.05	annual probability of adult mortality
Juvenile survival	s	0.25		0.05	survival probability from fledging to first breeding
Fecundity	f	6.0	5.0–7.0	1.0	no. eggs produced per breeding season

† Range is given only for the parameters that were partitioned to create different levels of site suitability (see text).

Each simulation model used to examine site dependence within a population was composed of three major subunits: (1) production of fledglings, which differed among sites; (2) recruitment and mortality of adults for the entire population; and (3) annual allocation of adults to breeding sites of differing suitabilities. Each model had a time step of one year (i.e., all rates are annual rates) and simulations were done by using STELLA II® simulation software (see Peterson and Richmond 1993). Generalized equations for these models are given below; values for the parameters are found in Table A1. The models, including the Stella II diagrams and equations, are available by request from the senior author.

1) Production of fledgings was simulated as

$$I_{i,t} = I_{i,t-1} + E_t - M_t - F_t$$

where $I_{i,t}$ was the number of immatures (eggs and nestlings) in sites of suitability i at time t, E_t was the number of eggs laid during the breeding season on these sites, M_t was the number of individuals dying as immatures, and F_t was the number of immatures surviving to fledgling. E_t, M_t, and F_t are defined in turn:

$$E_t = P_i f_i$$

where P_i was the number of pairs occupying sites with suitability level i, and f_i was the level of fecundity realized on those sites;

$$M_t = (I_{i,t-1})(n_i)$$

where n_i was the annual probability of nesting success for sites of suitability i; and

$$F_t = (I_{i,t-1})(1 - n_i).$$

2) Annual recruitment and mortality of adults was

$$N_t = N_{t-1} + R - D$$

where N_t was the total number of adults in all sites during year t, R was the annual number of recruits, and D was the mean annual number of adults dying;

$$R = \sum F_i s \quad \text{for } i = 1, \ldots, k \text{ levels of suitability,}$$

where s was the rate of juvenile survival, i.e., the probability of survival from fledging, to first breeding, and

$$D = N_{t-1} m$$

where m was the annual rate (i.e., probability) of adult mortality.

3) The number of pairs allocated to each of k levels of site suitability was determined by filling each level sequentially from highest to lowest. "If, then, else" statements were used for this purpose. Thus,

$$P_1 = \text{if } P_T > P_{\max,1} \quad \text{then } P_{\max,1} \quad \text{else } P_T$$

and for all lower levels,

$$P_i = \text{if } P_T > P_{\max,i} \quad \text{then } \min[(P_T - P_{\max,i}), P_{\max,i}] \quad \text{else } 0$$

for $i = 2, \ldots, k$ levels of suitability, where $P_T = N_t/2$, because the total number of pairs breeding in all sites was assumed to be half of the number of breeding adults, and $P_{\max,i}$ was the preselected maximum number of sites allocated to the ith level of site suitability. Min[ ] in Stella II returns the smaller of the two values within the brackets. Total number of breeding sites for all simulations was 144, which were allocated to the different levels of suitability. If numbers of pairs exceeded 144, all individuals in excess of this maximum were considered nonbreeding floaters.