

## S25-3 Contribution of site-dependence to regulation of population size: evidence and consequences for biological monitoring of populations

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**Abstract** Site dependence, the pre-emptive use of sites (e.g., breeding territories) that differ in suitability for survival and reproduction, is a little-studied negative feedback mechanism that can potentially regulate population size. Because its operation depends upon heterogeneity among sites, it can operate at both local and landscape scales. Field tests on a population of a parulid warbler (*Dendroica caerulescens*) showed that sites differed greatly in suitability and were occupied pre-emptively. More poor sites were also occupied when population size was large. Because site dependence operates across a range of spatial scales it is difficult to test. The challenges it creates for sampling include the following. First, sampling designs need to include a broad range of the heterogeneity in suitability found among sites. This requires sampling across relevant environmental gradients and terrain (e.g., elevation, moisture, etc.) that are not typically found within small study plots. Secondly, direct measures of site suitability, such as both territory-based measures of food abundance and measures of bird population density and site-specific demography, are required to distinguish site-dependence from other potential regulatory mechanisms such as crowding. Given these sampling requirements, it is not surprising that site dependence, as one of the multiple mechanisms regulating bird populations, remains poorly understood. Nevertheless, knowledge of site dependence and other regulatory mechanisms is essential for understanding avian population dynamics and for the conservation of bird populations.

**Key words** Site dependence, Sampling design, Habitat heterogeneity, Population regulation, Site demography, Site suitability, Population dynamics, Conservation

### 1 Introduction

Density dependent negative feedback on demographic rates is essential for population regulation (Murdoch, 1994). Multiple kinds of density dependent mechanisms, however, can generate the feedback necessary to regulate population size or density (Sutherland, 1996; Rodenhouse et al., 1997; Newton, 1998). These mechanisms fall into three classes: (1) those emphasizing the primacy of direct or indirect interactions among individuals (e.g., crowding, territoriality), (2) those generated from environmental heterogeneity (e.g., buffer-effect, source-sink, site-dependence), and (3) those arising from intrinsic differences among individuals, i.e., population structure (see Lømnicki, 1988; Sutherland, 1996; Rodenhouse et al., 1999).

Crowding mechanisms necessarily occur at local spatial scales because they are generated by direct interactions among neighbors (e.g., fighting) or indirectly via increases in nest predation or parasitism as population density increases. In contrast, regulatory mechanisms arising from environmental heterogeneity or population structure can occur across a wide range of spatial scales, from local to landscape. To date, studies of regulatory mechanisms have focused largely upon crowding effects due to interactions among individuals (Dhondt, 1992; Rodenhouse et al.,

1997; Bonsall et al., 1998) or on source-sink processes associated with environmental heterogeneity at regional spatial scales (Robinson et al., 1995; Donovan and Thompson, 2001). The site-dependence mechanism, in particular, has only recently been described (Rodenhouse et al., 1997, 1999, 2000; McPeck et al., 2001) and tested in the field (Rodenhouse et al., 2003).

Regulatory feedback via the site-dependence mechanism does not depend upon intrinsic differences among individuals or upon local interactions among them. Rather, it occurs when individuals pre-emptively use sites that differ in suitability for reproduction and/or survival (Rodenhouse et al., 1997; McPeck et al., 2001). Sites are areas occupied exclusively by individuals or breeding pairs, and species may be considered site-dependent when their reproduction or survival depends on the characteristics or quality of a site. The suitability of sites is typically determined by multiple characteristics, including food abundance, vegetation structure, risk of nest predation, etc. Sites for most bird species would be the breeding and wintering territories that they occupy. Pre-emptive occupancy means that the best sites are occupied first and that site holders are not usually displaced by conspecifics (Pulliam and Danielson, 1991).

Regulation by site-dependence can occur because, as population size grows, the average suitability of the sites occupied declines, reducing average reproductive performance and survival as proposed by Brown (1969), Holt (1985, 1987) and Dhondt et al. (1992). This negative feedback slows and stabilizes population growth (Rodenhouse et al., 1997; McPeck et al., 2001). Conversely, when population size declines, due to catastrophe or low breeding productivity, only the best sites are occupied, which results in higher average demographic rates and leads to population growth. Site-dependence, therefore, has two essential features: (1) environmentally-caused heterogeneity among sites in suitability for reproduction and/or survival, and (2) pre-emptive site occupancy, with the tendency for individuals to select initially or move subsequently to sites of higher suitability as they become available (Rodenhouse et al., 1997). The strength of site-dependent negative feedback, therefore, depends upon the distribution of site suitability, i.e., the proportions of sites of different suitability and how steeply site quality declines from the best to the poorest sites occupied.

We stress that site-dependence is not an alternative to density dependence. Density dependence refers to the negative feedback that can be generated by a variety of mechanisms (Berryman, 1989), and site-dependence is one of those mechanisms (Rodenhouse et al., 2000). We prefer the name “site-dependence” rather than “sequential habitat occupancy” (Newton, 1998) or “habitat heterogeneity” (Both, 1998a), because site-dependence operates at the spatial scale of sites used by individuals or breeding pairs rather than habitats themselves, and because the negative feedback derives not just from heterogeneity among sites but from such heterogeneity combined with pre-emptive use of sites (Rodenhouse et al., 1997). Tests of site-dependence, therefore, need to focus on environmental heterogeneity and pre-emptive use, as well as on the relationship between population size and key demographic variables such as fecundity and survival.

In this paper, we review the evidence from tests of site-dependence, finding growing support for its operation as a regulatory mechanism. We also examine how sampling needs to be conducted to reveal the site-dependence process, as one of potentially several negative feedback processes that may be operating simultaneously to regulate population size (Rodenhouse et al., 1999). The data required to reveal the relative importance of multiple negative feedback mechanisms affecting population size will not be obtained or unravelled easily. We argue, nevertheless, that they are essential for understanding and projecting fluctuations in the size and density of bird populations, and so essential for the monitoring and conservation management of bird populations.

## 2 Methods

### 2.1 Study site

The research described here was conducted within the 3 000+ ha Hubbard Brook Experimental Forest (HBEF) in

north-central New Hampshire, USA. The Hubbard Brook valley contains an environmental gradient extending from an elevation of about 250 m to 850 m a.s.l., and is vegetated mostly by northern hardwoods, grading into boreal forests on the north facing slopes and along the ridges (Bormann and Likens, 1979). Research conducted over the past 40 years as part of the Hubbard Brook Ecosystem Study provides extensive information on the ecology of these northern hardwood forests (<http://www.hubbardbrook.org>), including their avifauna (Holmes and Sherry, 2001).

### 2.2 Study species

We have been investigating the demography of the black-throated blue warbler (*Dendroica caerulescens*) within the HBEF since 1982 (Rodenhouse and Holmes, 1992; Holmes, 1994; Holmes et al., 1992, 1996; Sillett and Holmes, 2002). From 1997 to 1999, we expanded this work to include multiple, spatially separated areas within the HBEF and undertook intensive study of environmental features of individual territories. The black-throated blue warbler is suitable for demographic studies because of the accessibility of its nests in the shrub stratum and because its abundance has been relatively stable in the HBEF, and regionally in New England, over at least the past 30 years (Holmes and Sherry, 2001; Peterjohn and Sauer, 1994). The black-throated blue warbler is a forest-interior species that is considered “area sensitive” (Robbins et al., 1989) and thus of conservation concern.

## 3 Results

### 3.1 Evidence for site-dependence in black-throated blue warblers

Based on Rodenhouse et al. (1997), conditions necessary for the operation of site-dependent regulation include: (1) differences among sites in suitability that affect reproduction or survival, and (2) pre-emptive use of sites, i.e., good sites are occupied more frequently or before those of lower suitability. Where these features occur, site-dependent negative feedback must be generated. In association with such feedback, an inverse relationship between population size and variance in demographic rates is also expected, because site-dependent feedback occurs without lowering the performance of individuals on the best sites (Both, 1998a).

Testing directly for site-dependent feedback — a positive relationship between population size and use of successively poorer sites — has its problems because of the difficulty in defining and measuring population size for species distributed across regionally variable landscapes and in multiple habitat types. It is possible, however, to use indices of population size such as density or abundance on plots that include wide differences in suitability to test this relationship; and we present such a measure below. Even so, whether the negative feedback generated by site-dependence is strong enough to regulate population size in the manner observed in the actual population can only be assessed by computer mod-

eling of population processes (Rodenhause et al., 1997; Bradbury et al., 2001) or by density perturbation experiments (Sutherland, 1996; Newton, 1998).

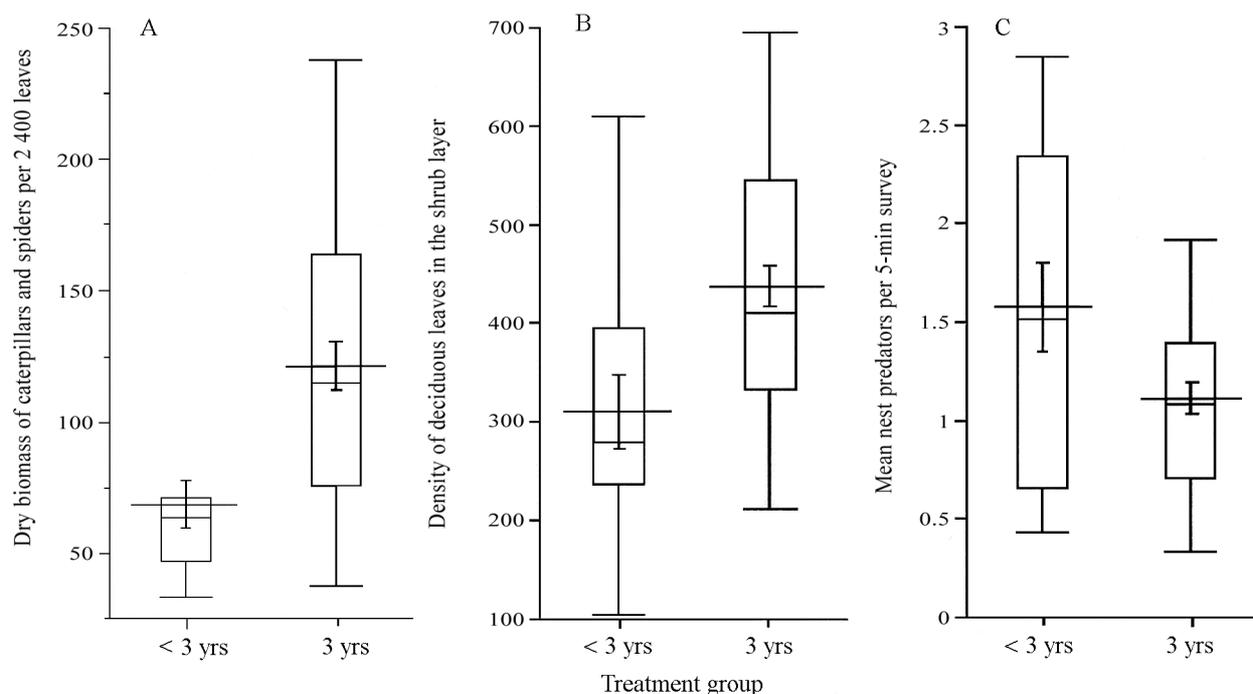
Our studies of black-throated blue warblers revealed pre-emptive use of sites, i.e., sites used only periodically were of lower suitability than those always occupied. Sites used in all three years of the study had 82% greater abundance of caterpillars and spiders clinging to leaves, 47% greater density of deciduous leaves in the shrub layer, and 28% fewer nest predators (Fig. 1). These large differences in the suitability of the sites used would suggest a potentially strong role for site-dependence in population regulation if they were reflected in annual fecundity — the number of young produced per territory per season. Indeed, territories occupied by black-throated blue warblers in all three years produced about twice the number of young per year as those occupied for less than three years (a mean of 4.1 vs. 1.9 young per territory per season; Fig. 2).

We also found evidence of site-dependent negative feedback in an inverse relationship between the total abundance of black-throated blue warblers on all of our study plots and the best predictor of site quality for black-throated blue warblers: mean density of deciduous leaves in the shrub layer (Rodenhause et al., 2003). Leaf density in the shrub layer is the best predictor of territory quality (Steele, 1992)

because it varies less within and among years than food abundance and nest predator density. In summary, we found that black-throated blue warblers pre-emptively used sites that differed in suitability for reproduction and that the suitability of the sites occupied was inversely related to population size, as is expected where site-dependent negative feedback occurs (Rodenhause et al., 1997).

### 3.2 Evidence for site-dependence in other bird species

Several studies indicate that heterogeneity among sites occupied by breeding pairs contributes to population regulation in other bird species (e.g., Andr n, 1990; Dhondt et al., 1992; Komdeur, 1992; Ferrer and Donazar, 1996). There is also evidence of significant differences in site suitability and pre-emptive use of sites. None of the studies, however, assessed whether the negative feedbacks were strong enough to be regulatory. Blanco et al. (1998) found density dependent clutch size in a population of red-billed choughs (*Pyrrhocorax pyrrhocorax*): mean clutch size decreased as population density increased. Because this pattern was associated with an increase in the variance of clutch size, they attributed it to “habitat heterogeneity” rather than a crowding mechanism. Pre-emptive use of territories was reported by Kruger and Lindstrom (2001a) in a study of the northern goshawk (*Accipiter gentilis*); territories that were occupied earlier and more frequently, i.e., pre-emptively, had larger



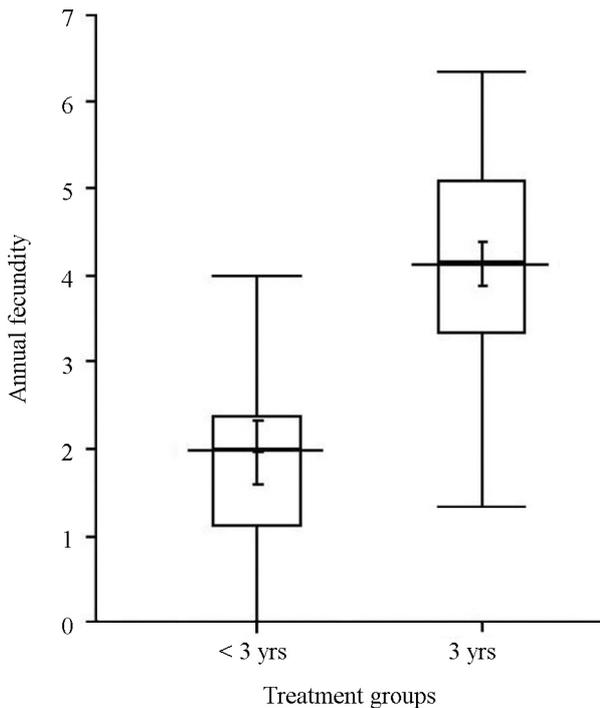
**Fig. 1 Environmental characteristics of black-throated blue warbler (*Dendroica caerulescens*) territories within the Hubbard Brook Experimental Forest**

These differed between “good” territories, those occupied during all three years of the study (labelled 3 yrs), and “poor” territories, those occupied in two or fewer years (< 3 yrs). Good sites were characterized by significantly (A) more food for Black-throated Blue Warblers (mg dry biomass of caterpillars and spiders/2,400 leaves; Median test,  $\chi^2 = 8.37$ ,  $n = 13$ ,  $m = 35$ ,  $P = 0.004$ ), (B) greater density of deciduous leaves in the shrub layer ( $t$ -test,  $t = -3.05$ ,  $df = 51$ ,  $P = 0.004$ ), and (C) lower abundance of nest predators (median number observed per 5 min census; Median test,  $\chi^2 = 3.80$ ,  $n = 14$ ,  $m = 37$ ,  $P = 0.05$ ) (after Rodenhause et al., in review). Box plots depict the mean (horizontal line extending outside of the box), standard error of the mean (short whiskers), median (horizontal line within the box), quartiles (box), and 10 and 90% deciles (long whiskers).

brood sizes. Similarly, in a study of an expanding population of ospreys (*Pandion haliaetus*), Lohmus (2001) found that nest sites closer to foraging areas and near more lakes were occupied first as population size increased. This pattern of habitat selection resulted in greater breeding productivity on these better territories and average productivity declined as population size increased, as would be expected in a site-dependent mechanism.

Alternatively, some studies reported no strong role for site-dependence. Both (1998b) found that female great tits (*Parus major*) seemed to adjust clutch size to changes in population density rather than in accord with habitat heterogeneity. Although an excellent study in many ways, it included no direct measures of habitat heterogeneity (or suitability), and breeding sites within habitats were assumed to be of similar suitability. All differences in clutch size within habitats were therefore attributed to differences among individual females rather than partitioned among individuals and the suitability of their breeding sites. A study of the common buzzard (*Buteo buteo*), however, found that characteristics of individuals, particularly breeding experience, were more important than habitat quality in determining annual fecundity (Kruger and Lindstrom, 2001b).

From these studies, it is apparent that site-dependence



**Fig. 2** Fecundity of the black-throated blue warbler (*Dendroica caerulescens*) within the Hubbard Brook Experimental Forest

More young were fledged per pair per year (annual fecundity) on good sites (occupied for 3 years) than poor sites (occupied < 3 years):  $t$ -test,  $t = -4.94$ ,  $df = 42$ ,  $P < 0.0001$  (after Rodenhouse et al., in review). Box plots depict the mean (horizontal line extending outside of the box), standard error of the mean (short whiskers), median (horizontal line within the box), quartiles (box), and 10 and 90% deciles (long whiskers).

ence operates in some species and situations but not in others; most of the studies tested for this mechanism, nevertheless, have found evidence of it. What is not yet clear is whether any generalizations about its operation are possible. For example, is site-dependence likely to be stronger in some habitats than others (e.g., stronger in habitats with patchy resource distribution) or for some types of birds (e.g., open-cup nesting birds or species with larger territory sizes such as raptors). We suggest that there is not enough evidence yet to make such distinctions. The mechanism, however, warrants further study, in part because the nearly ubiquitous occurrence of extensive heterogeneity among sites creates a potentially strong role for this mechanism. Few studies, however, have tested the site-dependence mechanism explicitly, the primary reasons for which are probably that testing for it requires territory-specific sampling of environmental characteristics and demography at a spatial scale that encompasses a broad range in site suitability, both of which require levels of extensive and intensive sampling that are difficult to achieve in field studies.

### 3.3 Regulation of population size via multiple mechanisms

All of the recent studies that have tested for site-dependent processes have also assessed the relative importance of multiple negative feedback mechanisms. Except for ours, each of the studies reviewed above (Both, 1998a; Guillermo et al., 1998; Kruger and Lindstrom, 2001a, 2001b; Lohmus, 2001) concluded that one mechanism was predominant. The results for black-throated blue warblers, however, suggest that not only was site-dependence operating but crowding as well. Sillett (2000) found that when the pairs abutting focal territories were removed permanently, the mean number of young fledged annually by pairs experiencing reduced local density was nearly twice that of control pairs. These findings lead us to propose that site-dependence and crowding mechanisms can operate simultaneously because they operate at different spatial scales (Rodenhouse et al., 2003). Crowding operates at the scale of individuals and their neighbors, while site-dependence occurs on a larger (i.e., regional) spatial scale which includes a broad range in site suitability.

Furthermore, it is possible for either mechanism alone to regulate population size. Crowding reduced annual fecundity to only about 3.9 young per pair, which is replacement-level reproduction for this population (Sillett and Holmes, in review), and hence, would eventually halt population growth. Use of poor suitability sites in some years — a site-dependence mechanism — further lowered annual fecundity to 1.9 on the lowest quality sites, which is well below estimated replacement level (Rodenhouse et al., 2003).

### 3.4 Sampling to reveal site-dependent regulation

Ours is one of few studies reporting multiple negative feedback mechanisms operating within the same population, and this finding was perhaps due to a unique sampling protocol. Hence, we consider here the types of

sampling needed to detect and quantify the operation of site-dependence and other negative feedback mechanisms potentially contributing to regulation of population size or density. The goals of sampling in studies of demography and population regulation are to test hypotheses relevant to specific mechanisms of regulation and to obtain estimates of demographic parameters that can be used in population modeling (Johnson, 1995). The latter is essential for determining whether any negative feedback is strong enough to regulate population density or size.

*What variables should be sampled?* For detecting site-dependence, those features of the site that affect basic demographic parameters, such as fecundity, survivorship, immigration and emigration should be sampled, as should annual fecundity and survival as well. For our study species, long term monitoring coupled with experiments have revealed that vegetation structure, food availability, predator abundance and weather conditions are the features of sites that most influence reproductive success (Rodenhouse and Holmes, 1992; Steele, 1992; Reitsma, 1990; Sillett et al., 2000). The key environmental features affecting demography, however, are likely to differ among bird species and perhaps locations.

When sampling reproductive performance, it is essential to measure the annual fecundity of pairs (number of young produced per sites per season) and not simply the success of individual nests, for example as given by Mayfield estimates (see Powell et al., 1999; Murray, 2000; Thompson et al., 2001; Nagy, 2002). Sampling only nesting success requires the assumption that the sample of nests is randomly distributed among pairs on sites of different suitability and across the breeding season. Such an assumption is unlikely to be true and is seldom tested.

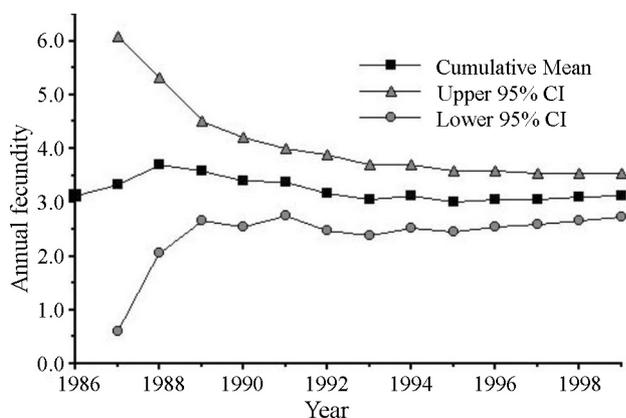
Quantifying survivorship is essential to parameterize the demographic models needed for testing whether den-

sity dependent feedbacks are strong enough to be regulatory. Estimates of survival for young in the nest, juveniles and adults are needed for population modeling. However, estimating juvenile survivorship for species with extensive natal dispersal, which includes many migrants such as the black-throated blue warbler, is notoriously difficult (Anders et al., 1997; Thompson et al., 1999; Sillett and Holmes, 2002).

*Sample size* Sample sizes for hypothesis-testing can be determined from preliminary data by examining the power of the test (Zschokke and Lüdin, 2001); and sample sizes should be as large as are needed to minimize the variance of parameter estimates. For example, variance in annual fecundity of black-throated blue warblers was consistently reduced by sampling additional years, even over a 14 year period (Fig. 3). Similarly, relatively large sample sizes are needed to characterize distributions of site characteristics that are often non-normal. For example, distributions of two of the three variables that we used to characterize site suitability for black-throated blue warblers were not normally distributed. The abundance of nest predators on sites (Shapiro-Wilks test,  $W_{50} = 0.93$ ,  $P = 0.004$ ) and the biomass of food for birds (Shapiro-Wilks test,  $W_{47} = 0.90$ ,  $P = 0.0005$ , for samples of caterpillars and spiders clinging to leaves), were both strongly non-normal.

Because the likelihood of mistakenly classifying a non-normal distribution as normal increases as sample sizes become smaller, it may be necessary to take relatively large samples of sites to correctly describe the distribution of site suitability. We sampled 48 sites to determine the distribution of site suitability as measured by food biomass. When subsamples of 20 sites were selected randomly from this total, only half (5 of 10 subsamples) of the resulting distributions for food biomass could be distinguished from normal, indicating that sample sizes larger than 20 would be necessary to characterize this variable accurately. Precise characterization of the distribution of site suitability is essential because it is the distribution of site suitability that determines the regulatory strength of site-dependence (Rodenhouse et al., 1997; McPeck et al., 2001).

*Spatial scale of sampling* It is unlikely that the distribution of site suitability will be adequately represented by focusing on small study plots, as is usually done (also Brown, 1969; Watkinson and Sutherland, 1995; Smith et al., 1996). To reveal the full range of site suitability, the 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 — and this implies measuring “territory” suitability even in some locations and years when a formerly occupied territory, for example, is not occupied. Because of the few studies of site-dependence to date, it is not clear how broad an area must be sampled. Determining what spatial scale is appropriate is extremely difficult for most studies of populations, but especially for migratory bird species that disperse widely across multiple habitat types.



**Fig. 3** Variance in mean annual fecundity of black-throated blue warblers (*Dendroica caerulescens*) on the long-term study plot within the Hubbard Brook Experimental Forest

Variance was reduced with each new sample point (year) added to the data set throughout the 14-year sampling period. The means and confidence intervals displayed are cumulative, i.e., each year with a confidence interval includes the data for all years that came before it.

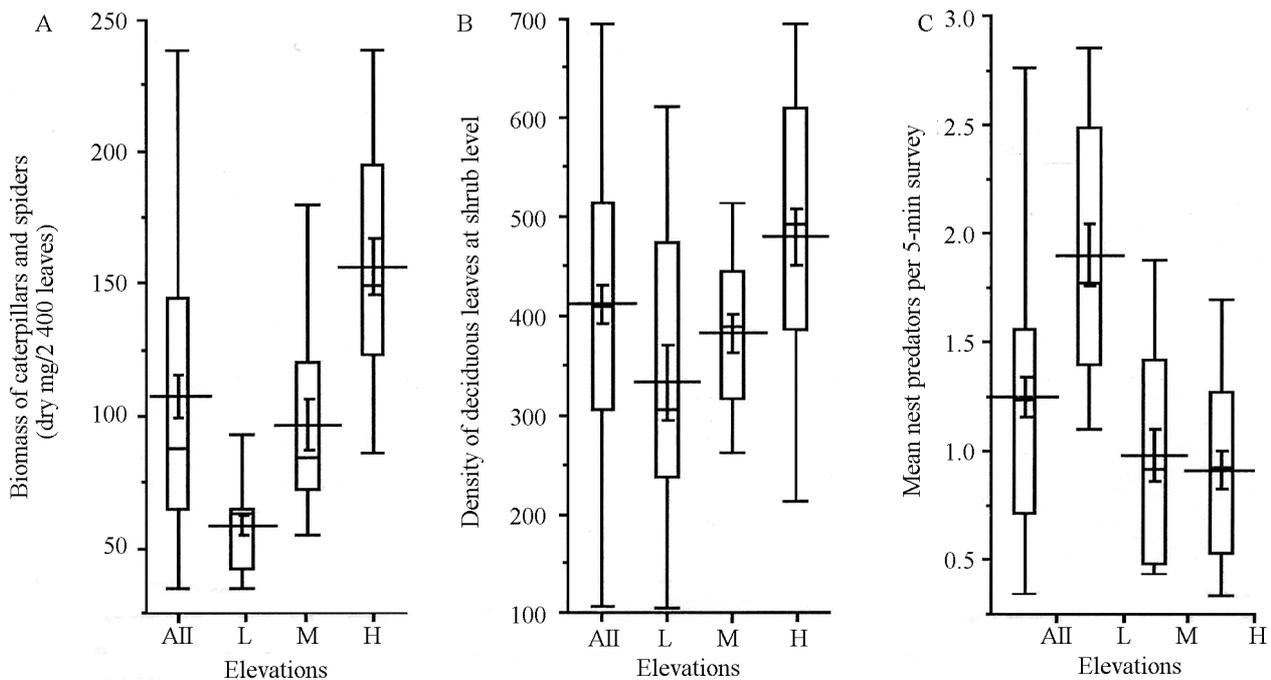
It is likely, however, that the appropriate spatial scales will be influenced by natal and adult dispersal distances which can differ greatly among species. In our study of black-throated blue warblers, we sampled across a 600-m elevational range, representing about 6.5 km distance on the ground, to include as broad a range of site suitability as could be found within the HBEF. We found that this extensive range of conditions was necessary because of disparate trends in suitability as measured by different variables. Food biomass and leaf density on sites, for example, increased from low to high elevation (Fig. 4). Moreover, nest predator abundance on sites differed between low and higher elevations. It is obvious from Fig. 4 that sampling sites at only one of any of the main elevations would have represented variation in site suitability inadequately across the region.

**Sampling to detect multiple mechanisms** A sampling design that will detect multiple negative feedback mechanisms (e.g., crowding, site-dependence and population structure) is ideal, because some evidence suggests that more than one mechanism may operate in some systems (Rodenhouse et al., 1999, in review; den Boer and Reddingius, 1996). A sampling design allowing this would include a random sample of sites spanning the environmental conditions used by the population. Often it will be convenient to work in study areas rather than on single isolated territories, but if this is done, then the sites sampled should be randomly selected from those available in the

area to avoid the problem of pseudoreplication.

All individuals should be marked uniquely and their ages determined as accurately as possible so that population structure can be monitored and considered in statistical analyses. Crowding-related interactions among neighboring pairs or territorial pairs and floaters can easily be detected by observing the behavior and demographic performance of individuals within much smaller areas (e.g., 10 s of ha) than are needed for sampling site suitability. Hence, it might be profitable to select locations along an environmental gradient (e.g., by elevation or population density) to carry out such measures, so that site specific measures of suitability are made across the full range of sites used when population density is high and low.

Crowding effects may not easily be revealed by monitoring, particularly during short time periods and if the population is tightly regulated. Therefore, density manipulations are helpful and they have been done by enhancing (e.g., Alatalo and Lundberg, 1984; Brawn, 1987) or reducing (e.g., Dhondt et al., 1992; Both, 1998a; Sillett, 2000) density of conspecifics. Indeed, strong inferences of the occurrence and operation of any mechanism can only be achieved with manipulations of the appropriate variables; hence, this should be incorporated into study designs whenever possible. Because of the inherent variability of natural systems, particularly in areas of low suitability, long-term studies in which characteristics of site suitability for marked



**Fig. 4** Environmental characteristics of black-throated blue warbler (*Dendroica caerulescens*) territories along an altitudinal gradient within the Hubbard Brook Experimental Forest

Characteristics differed in means and variability at different elevations: low (L), middle (M) and high (H). In addition, the patterns observed across elevations differed among the variables sampled, where A = dry biomass of caterpillars and spiders per 2,400 leaves, B = density of deciduous leaves in the shrub layer, and C = mean abundance of nest predators per 5-min survey (for methods, see Rodenhouse et al., in review). Box plots depict the mean (horizontal line extending outside of the box), standard error of the mean (short whiskers), median (horizontal line within the box), quartiles (box), and 10 and 90% deciles (long whiskers).

populations and population density are measured will provide the most complete information, allowing time for both monitoring under a range of conditions and experimental manipulation of the study system. Such studies of expanding or contracting populations as those of Lohmus (2001) may be particularly informative.

## 4 Discussion

Despite extensive study of density dependence (Newton, 1998; Turchin, 1999), the specific mechanisms by which “density” affects demographic rates are not at all clear for most populations. Attempts to reveal these mechanisms must confront many challenges, because numerous factors affect demographic rates, making them highly variable and making multiple density dependent mechanisms possible. Furthermore, these multiple mechanisms may be operating at very different spatial scales. In our study system, we have shown that both crowding and site-dependence mechanisms are in operation, although their relative importance along with other mechanisms is yet to be determined. Moreover, whether the operation of site-dependence, in particular, is widespread is far from clear because of the dearth of tests; most studies to date have not collected the data needed to assess the operation of multiple mechanisms.

To illustrate this point, typical studies of population regulation are much like that of Wiklund (2001) studying the merlin (*Falco columbarius*). This is an excellent long-term study that includes experimental and monitoring components, and provides much insight into population processes in the study species. In particular, population density and survival were found to be food limited, population dynamics were density dependent, and the population expanded into suboptimal habitat whenever population size was large. However, these findings could result from either a crowding or site-dependent mechanism or both. Here the density dependence mechanism(s) underlying population processes in the merlin were not addressed.

In our opinion, it is important to distinguish such mechanisms because the regulatory mechanisms of the population generate its dynamics, determine its equilibrium level and are necessary for making specific conservation recommendations. In site-dependent regulation, the equilibrium population size and dynamics are determined by the distribution of site suitability, e.g., the proportion of sites of highest quality and how steeply site quality declines from best to poorest. Moreover, site-dependence can theoretically regulate population size at levels below habitat saturation (Rodenhouse et al., 1997; McPeck et al., 2001). With a crowding mechanism, in contrast, such limitation and regulation can only occur when suitable habitat is at or near saturation (Murray, 1994; Hixon et al., 2002). Equilibrium in such cases is determined by the total amount of habitat relative to population size, and dynamics are determined by the intrinsic rate of natural increase in the population and the strength of the negative feedback due to crowding.

Differences in how equilibrium in population size and

its dynamics are determined have clear conservation implications. Knowledge that site-dependence is operating focuses conservation efforts on site suitability at the local level and, particularly, on sustaining the suitability of the best sites (Rodenhouse et al., 1999; McPeck et al., 2001). Under a crowding regime, however, the local population is at or near carrying capacity and is performing as well as can be expected. One would expect any improvements in site quality to be countered by crowding-related reductions in performance. Hence conservation efforts should in this case shift toward expanding the total amount of habitat available.

In sum, determining whether one or more negative feedback mechanism is regulating population size or density is key to understanding avian population dynamics and conservation. This is because knowledge of these mechanisms and their interactions helps to clarify how demographic performance is affected by behavioral responses in specific environments (also Sutherland, 1996). Such information allows identification of the environmental variables that are key to managing and conserving species. At present, however, there are too few studies that assess the prevalence or relative importance of the multiple regulatory mechanisms that may be operating. We suggest that only by designing and conducting studies that include site-specific information on suitability and on annual fecundity and survival of marked individuals can site-dependence be adequately tested, evaluated and identified as one of the multiple mechanisms that regulate populations.

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