Multiple density-dependence mechanisms regulate a migratory bird population during the breeding season

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The mechanisms regulating bird populations are poorly understood and controversial. We provide evidence that a migratory songbird, the black-throated blue warbler (*Dendroica caerulescens*), is regulated by multiple density-dependence mechanisms in its breeding quarters. Evidence of regulation includes: stability in population density during 1969–2002, strong density dependence in time-series analyses of this period, an inverse relationship between warbler density and annual fecundity, and a positive relationship between annual fecundity and recruitment of yearlings in the subsequent breeding season. Tests of the mechanisms causing regulation were carried out within the Hubbard Brook Experimental Forest, New Hampshire, during 1997–1999. When individuals from abutting territories were experimentally removed in a homogeneous patch of high-quality habitat, the fecundity of focal pairs nearly doubled, revealing a locally operating crowding mechanism. A site-dependence mechanism was indicated by an inverse relationship between population size and mean territory quality, as well as by greater annual fecundity on the sites that were most frequently occupied and of highest quality. These site-dependence relationships were revealed by intensive monitoring of territory quality and demography at the landscape spatial scale. Crowding and site-dependence mechanisms, therefore, acted simultaneously but at different spatial scales to regulate local abundance of this migratory bird population.

Keywords: population regulation; density dependence; migratory bird

1. INTRODUCTION

The size and density of many animal populations fluctuate as if regulated (Sinclair 1989; Murdoch 1994), yet whether they are in fact regulated remains controversial because the mechanisms generating regulation in nature are poorly understood (Turchin 1999; Hixon *et al.* 2002; Krebs 2002). Elucidating these mechanisms, however, is essential for predicting how populations will respond to environmental perturbations such as habitat fragmentation or climate change (Saether *et al.* 2000; Sillett *et al.* 2000; Sutherland & Norris 2002).

Regulation of population size can occur via multiple kinds of mechanisms that generate density-dependent, negative feedback on demographic rates (Lømnicki 1988; Sutherland 1996; Rodenhouse *et al.* 1997). These mechanisms fall into three classes: (i) those emphasizing the primacy of direct and indirect interactions among individuals (e.g. crowding, territoriality); (ii) those generated from environmental heterogeneity (e.g. source–sink, buffer effect, site dependence); and (iii) those arising from intrinsic differences among individuals. Past tests for regulation have almost invariably focused, mostly for practical reasons, on single mechanisms (Rodenhouse *et al.* 1999), even though it has been suggested that several negative feedback mechanisms may operate simultaneously (den Boer & Reddingius 1996; Polis *et al.* 1998).

Birds have featured prominently in studies of population regulation (Lack 1954; Newton 1998). However, most studies of population regulation in birds have focused on non-migratory, resident species (Newton 1998), even though migrants compose the majority of species and individuals in temperate zones (Sherry & Holmes 1995). What is needed, therefore, are long-term demographic studies of migrants that can be used to test density dependence, paired with intensive studies of the mechanisms causing regulation.

We employed this approach in a study of a temperate–tropical migrant songbird, the black-throated blue warbler (*Dendroica caerulescens*). Regulation of our study population was demonstrated by several key findings. First, warbler abundance has remained relatively stable over the period 1969–2002 (figure 1*a*), and a time-series analysis of year-to-year changes in abundance indicates strong density dependence during this period (figure 1*b*). Second, annual fecundity is significantly negatively related with warbler density (figure 2), indicating density-dependent reproductive performance. Third, a stochastic projection matrix model, parameterized with field data for black-throated blue warblers, demonstrates that the negative feedback on annual fecundity is sufficient to regulate this population (Sillett & Holmes 2004). Finally, reproductive performance of black-throated blue warblers is positively related with recruitment of yearlings in the subsequent breeding season (Sillett *et al.* 2000), confirming the continuity of breeding season processes among years, as must occur for regulation by density-dependent fecundity in migratory species. While these findings demonstrate regulation of this warbler population, they do not
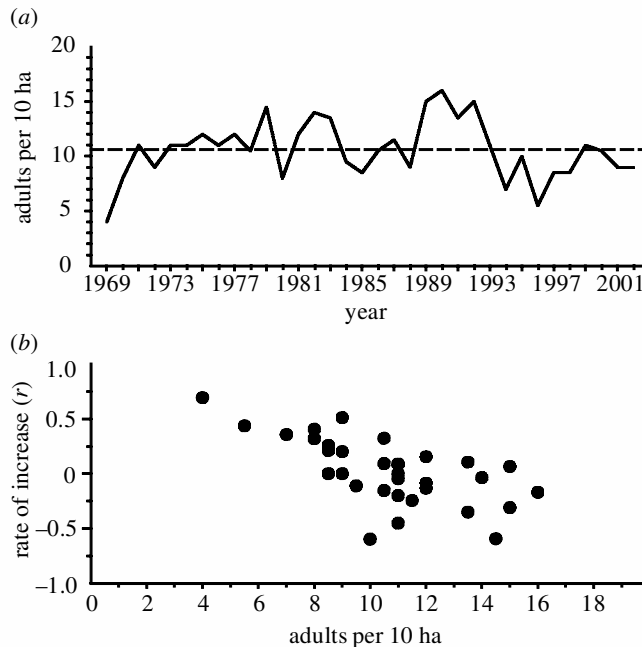
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Figure 1. Population trends of black-throated blue warblers within a 10 ha census plot at Hubbard Brook Experimental Forest, New Hampshire, USA. (*a*) The number of adults has remained relatively stable for at least three decades, 1969–2002. The dashed line indicates mean population density on the study area; the slope of linear regression was not significantly different from zero ($R^2 = 0.0001$, $p = 0.94$). (*b*) A parametric bootstrap test for density dependence in time-series data indicated that the population growth rate of this species, r (i.e. the log of the difference in abundance between year$_t$ and year$_{t+1}$), was negatively related with its density in year$_t$ on the 10 ha census plot ($T_{12} = -4.82$, $p = 0.0002$, 10 000 iterations). Thus, years of high warbler density are generally followed by decreases in abundance, while years of low density are generally followed by increases in abundance.

identify the mechanism(s) causing the density dependence.

Indeed, the density dependence illustrated in figure 2 could result from at least two mechanisms, one involving crowding and the other site dependence. In a crowding mechanism, the frequency or intensity of intraspecific agonism or of interactions with natural enemies, such as nest predators or parasites, increases as population density increases, lowering average annual fecundity for the population (Newton 1998). In a site-dependent mechanism (Rodenhouse *et al.* 1997; McPeek *et al.* 2001), pre-emption of territories by dominant individuals (as described by Pulliam & Danielson 1991) causes an increasing proportion of subordinate individuals to occupy successively poorer-quality sites (i.e. breeding territories for black-throated blue warblers) as population size increases, lowering average annual fecundity. Because site dependence results from a pre-emptive use of territories that differ in suitability for survival and/or reproduction (Rodenhouse *et al.* 1997; McPeek *et al.* 2001), we predicted that: (i) the sites used in all 3 years (good sites) would have better conditions for breeding and sustain greater reproductive performance than sites used in only 1 or 2 years (poor sites); (ii) warblers changing territories between years would shift to sites of higher quality; and (iii) population
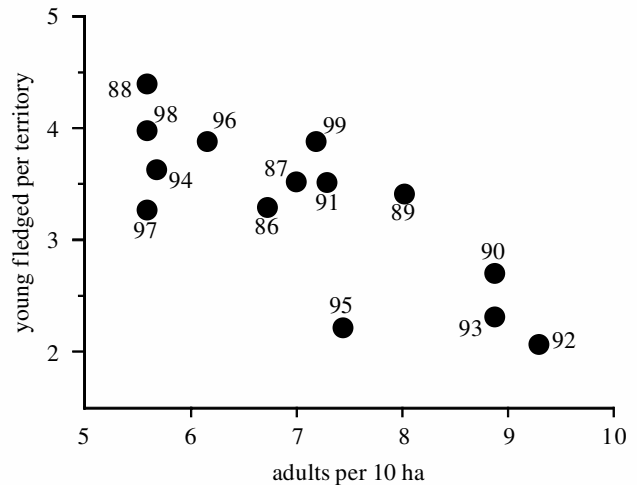
Figure 2. Annual fecundity of black-throated blue warblers declined as density of breeding adults increased on a 64 ha plot used for demographic studies at the Hubbard Brook Experimental Forest, New Hampshire, USA, 1986–1999. Numbers by points indicate year. First-order temporal autocorrelation in model residuals was not significant (Durbin–Watson $d > 1.61$, $p = 0.19$). $r = -0.76$; $p = 0.0015$.

size would be inversely related to mean territory quality. To elucidate the mechanisms of density dependence observed in our warbler population, we tested for the existence of both crowding and site-dependence mechanisms. We present experimental and empirical evidence that the study population is regulated by these mechanisms operating simultaneously but at different spatial scales during the breeding season.

2. MATERIAL AND METHODS

The research was conducted within the 3160 ha Hubbard Brook experimental forest in north-central New Hampshire, USA. The Hubbard Brook valley contains an environmental gradient extending from an elevation of *ca.* 250–850 m above sea level, and is vegetated mostly by northern hardwoods, grading into boreal forests on the north-facing slopes and along the ridges (Bormann & Likens 1979). Weather stations ($n = 21$) are distributed across the altitudinal range from 253 to 747 m. From low to high elevation along this gradient, mean temperature during the breeding season declines by 2 °C, and leafing out of trees is delayed by about 10 days (N. L. Rodenhouse, unpublished data). The black-throated blue warbler was chosen as the study species for several reasons. First, reproductive success can be measured accurately because its nests are accessible in the shrub stratum (Holmes 1994). Second, extensive long-term demographic data exist for this species (see Sillett & Holmes 2002, 2004). Finally, black-throated blue warbler abundance has been relatively stable at Hubbard Brook and regionally in New England during at least the past 30 years (Holmes & Sherry 1988, 2001; Peterjohn & Sauer 1994).

To test for the operation of a crowding mechanism while controlling for territory quality, we manipulated warbler density in an area of relatively homogeneous, high-quality habitat. Annual fecundity was compared between two treatment groups during the 1997–1999 breeding seasons: a high-density control ($n = 9$ in 1997, $n = 12$ per year in 1998 and 1999) and a second group ($n = 4$ territories per year) where density was experimentally

reduced by removing all conspecifics on territories abutting randomly selected focal territories (Sillett 2000). Such a removal was possible because the territory space occupied by a black-throated blue warbler pair remains empty for an entire breeding season if both members of the pair are removed after the end of spring migration (Marra & Holmes 1997). Focal territories were randomly selected (after all black-throated blue warblers had arrived and settled) from the approximately 60 being monitored on a 150 ha study area. Control territories were always separated from focal territories by at least one intervening warbler territory, and prior to neighbour removal, focal territories were always separated from other focal territories by at least two intervening territories. All individuals were marked with a unique combination of coloured leg rings, and all nests of each pair were located and monitored until fledging.

To test for the operation of a site-dependence mechanism, we examined reproductive success and site quality on 53 randomly selected black-throated blue warbler territories spanning a wide range of habitat qualities along the 600 m elevational gradient in the Hubbard Brook valley. Food availability, nest predator abundance, vegetation structure and reproductive success were intensively monitored on each territory from 1997 to 1999. Nest predator abundance was quantified by conducting four 5 min point counts of diurnally active predators (primarily eastern chipmunks *Tamias striatus*, red squirrels *Tamiasciurus hudsonicus* and blue jays *Cyanocitta cristata*) during each of four biweekly periods from late May to July ($n = 16$ censuses per territory per year). Vegetation density was quantified at five randomly selected, 394 m² circular plots per territory ($n = 5$ points per territory). In each plot, the number of leaves intersecting four vertical 3 m × 3 m planes, positioned at ground level, was quantified. Food abundance was quantified in the same biweekly periods, described above, by visually surveying lepidopteran larvae and spiders on understory leaves of American beech *Fagus grandifolia*, hobblebush *Viburnum alnifolium* and striped maple *Acer pensylvanicum* at randomly selected points within each territory. At each point, 800 leaves were sampled per plant species; the length of each caterpillar and spider detected was recorded, and prey lengths were converted to biomass using length–weight regressions (Rodenhouse & Holmes 1992). Territories were selected in the first year of the study, and their characteristics were monitored annually from 1997 to 1999, whether or not each territory site was occupied. All individuals were ringed, and annual fecundity was quantified for each pair.

3. RESULTS

Our test of the crowding mechanism revealed that the mean number of young fledged annually per territory was significantly greater in the reduced-density treatment than in the control (figure 3). This difference in mean annual fecundity, 1.9 young per territory, was probably not influenced by variation in site suitability because territory quality did not differ significantly between treatments (Sillett 2000). These experimental results indicated that interactions with neighbours, and presumably competition for resources at a local, neighbourhood scale, had a direct, density-dependent effect on the number of young fledged per territory (Sillett 2000). Neither experimental nor observational data indicated a crowding effect of parasites or predators in our study system. Brood parasitism by cowbirds (*Molothrus ater*) does not occur in the unfragmented forests at Hubbard Brook (Holmes & Sherry
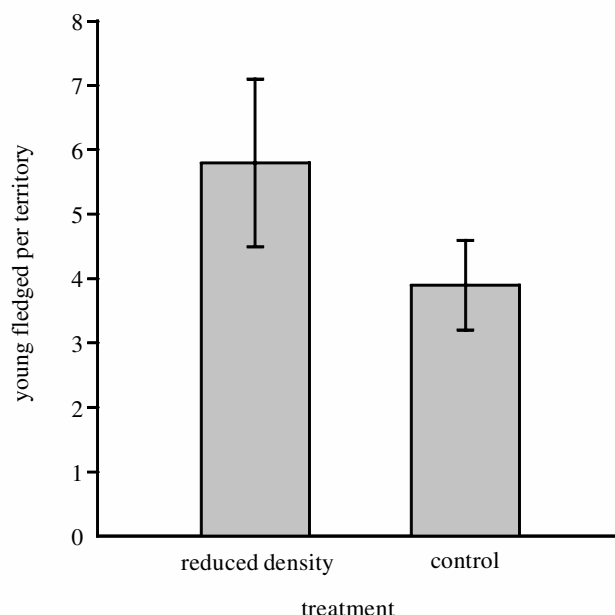

Figure 3. Annual fecundity of black-throated blue warblers occupying territories with neighbours experimentally removed ($n = 12$) was higher than that of control pairs ($n = 33$). Bars give means ± 1 standard error. Data were analysed using a three-factor analysis of variance with year (1997–1999), male age class (adult and yearling) and density treatment as independent variables. Only treatment (shown here) and male age (older males produced more fledglings than younger males) had statistically significant effects on fecundity. Neither the main effect of year nor any interaction terms were statistically significant. $F_{1,33} = 5.03$; $p = 0.03$.

2001; Sillett & Holmes 2004). Predation on eggs and nestlings reduces nesting success but does not change with local bird density (Sillett & Holmes 2004) and thus has little, if any, regulatory effect via a crowding mechanism on our study population.

The results of our investigation of site dependence were consistent with each of our three predictions. First, we found that good sites (i.e. those occupied in all 3 years) had 82% higher food biomass, 47% greater density of deciduous leaves in the understory and 28% fewer nest predators than poor sites (figure 4a–c), and that these differences in site characteristics corresponded to a significant difference in the annual fecundity of warblers occupying those sites. Warbler pairs occupying good territory sites fledged almost twice as many young as pairs on poor territory sites (figure 4d).

Second, returning males that shifted territory locations during 1997–1999 moved to sites of higher suitability than they held the previous year. Eleven males switched territory sites between 1997 and 1999. Based on one-tailed results from paired *t*-tests, the territories to which these males shifted had greater food biomass (118.12 ± 15.39 versus 88.79 ± 11.39 mg dry biomass of caterpillars and spiders per 2400 leaves; $t_9 = -2.65$, $p = 0.01$), greater density of deciduous leaves in the shrub layer (389.55 ± 32.41 versus 321.82 ± 38.59; $t_{10} = -2.02$, $p = 0.04$), and almost significantly fewer nest predators (1.05 ± 0.23 versus 1.40 ± 0.21 mean predators per 5 min survey; $t_9 = 1.64$, $p = 0.07$) compared with the birds' first territories.
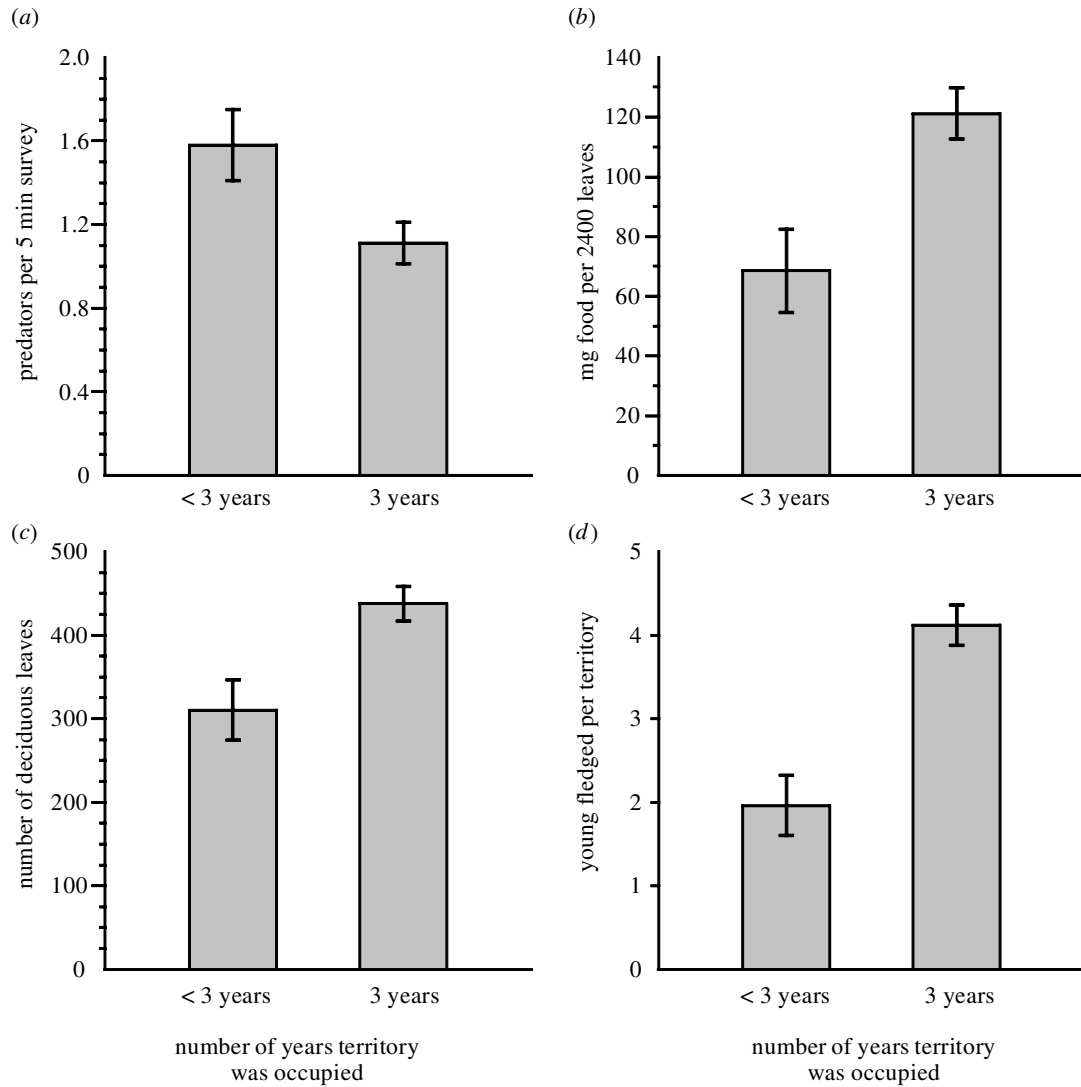
Figure 4. Territories occupied during all 3 years of the 1997–1999 study (good sites) had significantly (*a*) lower abundance of nest predators, (*b*) more food and (*c*) greater density of deciduous leaves in the shrub layer than territories occupied for less than 3 years (poor sites). (*d*) Good sites also fledged significantly more young per year than poor sites. Bars give means ± 1 standard error. Data were analysed with one-factor analyses of variance and were transformed, when necessary, to meet model assumptions. (*a*) $F_{1,49} = 4.04$, $p = 0.05$; (*b*) $F_{1,40} = 13.81$, $p = 0.0005$; (*c*) $F_{1,51} = 9.30$, $p = 0.004$; (*d*) $F_{1,47} = 24.37$, $p < 0.0001$.

Third, we found that population size (i.e. the abundance of black-throated blue warblers on all of the study plots combined) was significantly negatively correlated with the best predictor of mean territory quality—the density of deciduous leaves in the shrub layer ($r = -0.999$, $p = 0.01$). The density of deciduous leaves is the best predictor of territory quality for our study species (Steele 1992) because it varies less within and among years than food abundance and predator density, which were also inversely correlated with population size but not significantly so (food abundance: $r = -0.909$, $p = 0.27$; predator density: $r = -0.238$, $p = 0.85$). This finding indicates that sites of lower quality were used only when population size was large, which is essential for the operation of site dependence.

4. DISCUSSION

Our tests of crowding and site dependence suggest that both mechanisms operate simultaneously to regulate population size in the following manner. As population size grows, sites of highest suitability become the foci of high-density aggregations in which average fecundity is reduced locally via crowding. Additional increases in warbler abundance result in individuals spreading out and occupying sites of successively lower suitability, further reducing mean fecundity for the population. In the scenario described above, both crowding and site dependence operate, but over different spatial scales. Crowding operates in a high-quality, high-density habitat, at the scale of individuals and their neighbours, while site dependence occurs on a larger (i.e. landscape) spatial scale, which includes a broad range in site suitability.

Regulation via multiple negative-feedback mechanisms occurring at multiple spatial scales has not previously been reported, probably because studies of population regulation in birds are almost invariably carried out on single study plots with results reported as plot averages. Such studies can detect density dependence, which may or may not be sufficient for regulation (see Newton 1998 for examples). However, they are likely to reveal crowding mechanisms only, because the single plots chosen are

often of uniformly high suitability. Furthermore, by focusing on plot means instead of the sites and the performance of individuals, all possibility of detecting site dependence is lost. We concur with Sutherland & Norris (2002) that focusing studies at the individual level is most likely to reveal the mechanisms of population regulation. We add that it will be possible to examine the widest range of density-dependence mechanisms if the individuals chosen for study use sites spanning the broadest possible range of the environmental conditions, as was done in the present study.

Events and conditions during the non-breeding period no doubt also contribute to fluctuations in the size of breeding populations of migratory species, such as the black-throated blue warbler (Sherry & Holmes 1995; Sillett *et al.* 2000). However, our research indicates that processes operating during the breeding period are sufficient for regulation of our study species. Modelling of the population dynamics of black-throated blue warblers shows that the negative feedback on reproductive output can regulate local abundance at the densities observed (Sillett & Holmes 2004). Furthermore, when reproductive success was high, more yearlings were recruited into the breeding population in the following year (Sillett *et al.* 2000). Such a correlation would be unlikely if the population were strongly regulated during the non-breeding period.

Events on winter quarters and during migration that dramatically limit demographic rates could at times overwhelm the regulatory processes we have documented here, and thus could have a greater influence on warbler population dynamics than density-dependent fecundity. Indeed, winter limitation of migratory bird populations has been suggested by several authors (see, for example, Terborgh 1989; Rappole & McDonald 1994; Sherry & Holmes 1996; Latta & Baltz 1997). Furthermore, density-dependence processes such as site dependence may be occurring in wintering areas (Latta & Faaborg 2002). Nevertheless, our results suggest that the black-throated blue warbler population sampled at Hubbard Brook probably is not, at present, strongly limited during the non-breeding period. This species may be tolerant of disturbance to its winter quarters because it occupies a variety of habitat types, including primary forest, secondary woodlands and human-modified habitats such as rural settlements and coffee farms (Wunderle & Waide 1993; Sherry & Holmes 1996).

Temperate–tropical migrant songbirds have been the focus of much research because of population declines in some species (Martin & Finch 1995). Nevertheless, even basic demographic information is lacking for most species, and little is known about how events during different seasons interact to affect bird abundance (Sherry & Holmes 1996; Marra *et al.* 1998; Sillett & Holmes 2002; Webster *et al.* 2002). The results presented in this paper demonstrate that populations of these species can be regulated by events and conditions during breeding, specifically by both density-dependent fecundity generated from local crowding and site dependence operating at a regional spatial scale. The operation of site dependence, in particular, emphasizes the importance of sustaining not just the amount but also the suitability of habitats used by breeding songbirds. Therefore, processes that threaten the suit-

ability of breeding habitat either directly or indirectly, such as forest fragmentation (Robinson *et al.* 1995) or climate change (Rodenhouse 1992; Sillett *et al.* 2000), must be considered threats to migratory songbird populations.

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