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Kimberly A. With

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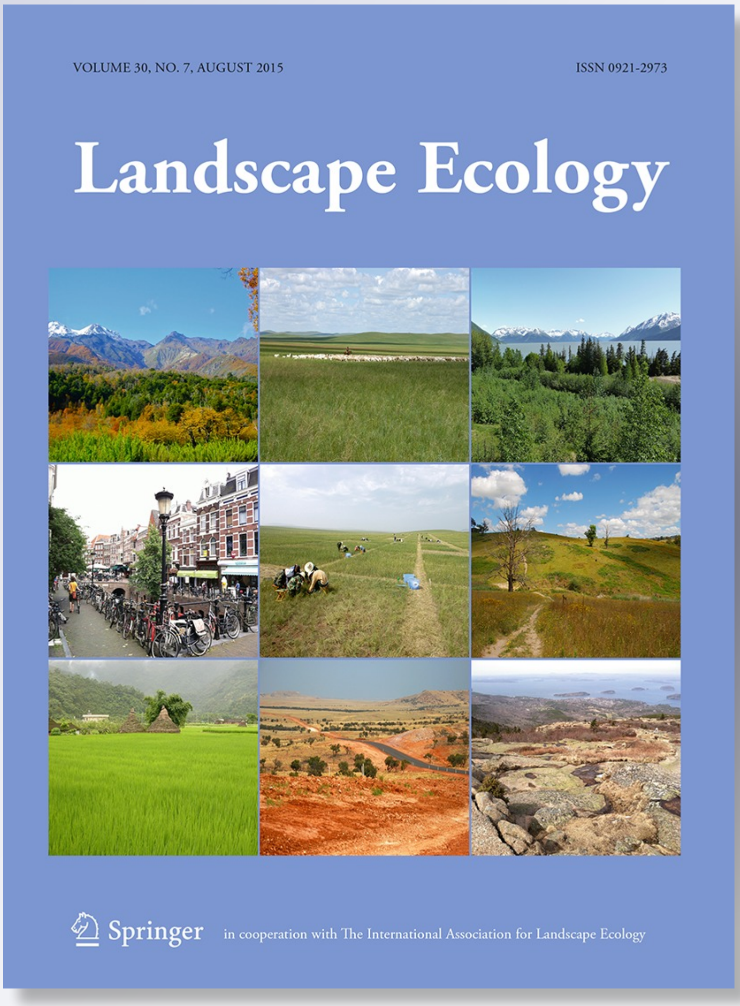

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RESEARCH ARTICLE

How fast do migratory songbirds have to adapt to keep pace with rapidly changing landscapes?

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Abstract

Context Landscapes are being transformed globally by human land use. Given the rate such changes are occurring, it is unclear how quickly species might need to adapt, whether genetically or behaviorally, especially in migratory songbirds that have declined in recent decades as a result of habitat loss and fragmentation.
Objective My objective was to determine via simulation modeling the rate at which a generic migratory songbird might need to mount an adaptive response to keep pace with current rates of habitat loss and fragmentation.
Methods Using a spatially-structured avian demographic model, I simulated an adaptive response to landscape change by reducing the degree of edge sensitivity in a fraction of the population each generation; songbirds are known to have lower success in habitat fragments owing to higher nest predation and brood parasitism rates. By adjusting the rate of this response, I determined how quickly populations would need to adapt to track the rate of landscape change and offset population declines.
Results Adaptive responses had the greatest effect when initiated quickly, within 3–5 generations, especially in landscapes undergoing extensive habitat fragmentation. Paradoxically, the rate of adaptive response had the greatest effect in landscapes undergoing more gradual rates of habitat loss (0.5–1 %/year) because populations were actually able to track these rates of landscape change demographically.
Conclusions Given these results, it seems unlikely that songbirds can evolve genetic responses quickly enough to offset current rates of landscape change, leaving behavioral adaptation (phenotypic plasticity) a more likely mechanism for responding to rapid landscape change.

Keywords Adaptive response · Edge effects · Habitat loss · Habitat fragmentation · Landscape dynamics · Phenotypic plasticity · Spatially-structured population model

Introduction

The transformation of landscapes by human land use is one of the most pervasive drivers of global environmental change, contributing to an unprecedented loss of biodiversity that is due, in large part, to the loss and fragmentation of species' habitats (Wilcove et al.

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K. A. With (✉)
Laboratory for Landscape and Conservation Ecology,
Division of Biology, Kansas State University, Manhattan,
KS 66506, USA
e-mail: kwith@ksu.edu

1998; Brooks et al. 2002; Fahrig 2003; Fischer and Lindenmayer 2007; Hanksi 2011). Apart from the wholesale loss and fragmentation of habitat, there is also concern over the rate at which such changes are occurring. For example, global forest cover has declined by about 0.5 %/year during the last decade (2000–2012), although the annual rate of decline is considerably higher for some forest types (up to 3.1 %/year in subtropical forests) and in some countries currently undergoing intensive deforestation (e.g., ~2 %/year in Malaysia; Hansen et al. 2013). Even in the United States, where forests account for nearly a third of the land-surface area, forest cover has declined by about 0.8 %/year during this same period, with some forest types experiencing higher rates of decline (e.g., 1–2 %/year for subtropical humid and temperate oceanic forests; Hansen et al. 2013). Although most types of land-cover change in the United States have averaged 0.3–0.6 %/year over the last quarter of the 20th century (1973–2000; Sleeter et al. 2013), such seemingly low rates of change add up over time and can have cumulative impacts that may not be evident until a threshold has been crossed.

Although much research has sought to understand the various impacts of habitat loss and fragmentation on biodiversity, we are still left with the fundamental question of whether species will be able to respond quickly enough to keep pace with current or projected rates of environmental change. Species have several options for responding to environmental change, which has been succinctly summarized as "move, adapt, or die" (Reed et al. 2011). Species' range shifts (movements in space) and phenological changes in the timing of migration and reproduction (movements in time) are well-documented responses to recent climate change, for example (Parmesan 2006). Over the past 20–30 years, breeding birds in North America and Europe have shifted the northern limits of their distribution northward, by an average 2.4 and ~1–1.6 km/year, respectively (Thomas and Lennon 1999; Brommer 2004; Hitch and Leberg 2007). Similarly, many bird species have advanced the timing of their migration and breeding season in recent decades (Jonzén et al. 2006; Møller et al. 2010; Charmantier and Gienapp 2013). Although such shifts are presumably adaptive (Møller et al. 2007), they may well reflect phenotypic plasticity (adaptive behavioral responses) as opposed to evolutionary (adaptive genetic) responses to environmental change (Charmantier et al. 2008; Vedder et al. 2013). Still, range shifts and phenological advancements may not be enough; the long-term persistence of many species is in jeopardy unless populations can adapt in situ to environmental change, including that due to habitat loss and fragmentation (Reed et al. 2011).

The loss and fragmentation of breeding habitat have been implicated in the decline of many migratory songbirds, such as those breeding in the forests and grasslands of North America (Robbins et al. 1989; Böhning-Gaese et al. 1993; Peterjohn and Sauer 1999; Donovan and Flather 2002; Valiela and Marinetto 2007; With et al. 2008). Although habitat loss reduces the amount of breeding habitat, fragmentation shifts the patch-size distribution toward more patches of smaller size, which have a disproportionately greater amount of edge habitat relative to larger patches (Harris 1988; Saunders et al. 1991). Negative edge effects are a well-documented response to landscape fragmentation in many breeding songbirds, which manifests primarily in lower reproductive success in small habitat fragments owing to higher rates of brood parasitism (by brown-headed cowbirds, *Molothrus ater*) and nest predation near habitat edges (Robinson et al. 1995; Donovan et al. 1997; Flaspohler et al. 2001; Herkert et al. 2003; Stephens et al. 2003).

Given the negative fitness consequences of nest predation and brood parasitism on breeding songbirds (Pease and Grzybowski 1995; Schmidt and Whelan 1999; Lampila et al. 2005), there should be strong selective pressure in fragmented landscapes for the emergence of adaptive behaviors that mitigate these fitness costs. For example, some songbirds have developed adaptive responses to brood parasitism by brown-headed cowbirds, from abandoning nests that have been parasitized, to ejecting cowbird eggs from the nest, to burying eggs by building a new nest atop the old one (Rothstein 1975; Winfree 1999). Such behaviors are believed to reflect an evolutionary (genetic) response rather than behavioral plasticity (Hosoi and Rothstein 2000; Kuehn et al. 2014). Not all songbirds have evolved adaptive responses to cowbird parasitism, however; far fewer forest-nesting songbirds appear to have done so, for example (Rothstein 1975; Hosoi and Rothstein 2000). Brown-headed cowbirds historically occurred throughout the grasslands of North America, but were able to spread into the eastern United States during the 1800s as forests were cleared during European settlement (Lowther

1993). Although cowbirds now occur throughout the United States, cowbird parasitism may still represent a relatively novel threat to forest-breeding songbirds from an evolutionary standpoint, which may explain why so few of these species have developed adaptive strategies (an example of an evolutionary lag; Hosoi and Rothstein 2000).

Predation is the main cause of nesting failure in most bird species, however (Martin 1993). Nest predation thus has far greater fitness consequences than brood parasitism, and should therefore play a larger role in shaping the adaptive responses of breeding songbirds to habitat loss and fragmentation. In grassland birds, for example, most nests fail because of nest predation (>75 %), whereas brood parasitism has no discernible effect on overall nest survival, even though nearly half of some species' nests are parasitized (e.g., Rahmig et al. 2009; Ludlow et al. 2014). Furthermore, nest predation typically results in the complete loss of the clutch or brood, whereas brood parasitism causes only a reduction in the number of host young produced (typically, by 1–2 offspring; Rahmig et al. 2009; Ludlow et al. 2014). Still, brood parasitism and nest predation may act synergistically, especially when cowbirds behave like nest predators (e.g., by removing or destroying enough host eggs to cause nest abandonment; Zannette et al. 2007). Birds can mitigate these sorts of negative edge effects through a variety of mechanisms, such as by shifting nest placement based on prior experience with nest predators (adaptive behavioral response) or by evolving (adaptive genetic response) different nest-site preferences and avoiding habitat edges altogether (Martin 1998; Forstmeier and Weiss 2004; Chalfoun and Martin 2010; Halupka et al. 2014).

Whether migratory songbirds can employ adaptive responses quickly enough to offset population declines driven by current rates of habitat loss and fragmentation is uncertain. Given the paucity of empirical studies on adaptive responses to different rates of environmental change, we can at least address this question via simulation modeling to gain a first approximation of what rates of adaptive change might be necessary to offset population declines in landscape undergoing habitat loss and fragmentation. I therefore applied a spatially-structured avian demographic model to explore what rate of response would be needed for a generic migratory songbird to adapt to negative edge effects, such as increased nest predation or brood parasitism, in landscapes subjected to different rates of habitat loss and fragmentation. In this model, the adaptive response of the population is treated phenomenologically, as a reduction in the species' edge sensitivity (a function that relates nest success to patch edge-to-area ratios). If an adaptive response (a reduction in edge sensitivity) must take place at unrealistically high levels to offset population declines, then it stands to reason that songbirds are unlikely to be able to adapt quickly enough to rapid environmental change, such as that wrought by anthropogenic habitat loss and fragmentation.

Methods

Model overview

As the details and behavior of this dynamic spatially-structured avian demographic model (dSSAD) have been described in detail elsewhere (With and King 2001; Schrott et al. 2005a), I will provide only a general overview here. Basically, dSSAD implements an avian demographic model on a dynamic landscape in which the loss of habitat occurs at a specified rate (0.5, 1.0, or 5.0 %/year) and degree of fragmentation over time. Habitat loss and fragmentation are modeled as a correlated disturbance through the use of fractal neutral landscape models (With 1997), which permit control over both the amount (h) as well as the fragmentation (i.e., the pattern of loss, H) of habitat on the landscape ($\mathrm{H} = 0$ gives a highly fragmented habitat distribution, whereas $\mathrm{H} = 1$ produces a clumped habitat distribution; see Fig. 1 in With and King 2001).

At the start of each run, the simulation model was initialized to give a stationary population ($\lambda = 1.0$), with a stable size and age distribution, on a landscape with 100 % habitat ($h = 1.0$). Annual changes in the population size and growth rate (λ) occur as a result of habitat loss and fragmentation, and are described by an age-structured matrix population model parameterized from a demographic life table. Unlike most traditional avian demographic models, the age-specific birth rate b_x (the expected number of female produced per female at age x) is an explicit function of the distribution of breeding habitat in dSSAD (With and King 2001; Schrott et al. 2005a). In other words, b_x is both patch- and landscape-dependent, and is therefore an output of the model rather than a species-specific constant as in most demographic models.

The spatial dependency in b_x comes about because of the assumed negative relationship between nest success (a major contributor to female fecundity, which is used to calculate b_x) and the patch edge-to-area ratio (i.e., nest success is lower in small patches owing to negative edge effects). Although not all species exhibit a negative response to habitat edges (i.e., some exhibit a neutral or even positive response; Ries et al. 2004), many forest-breeding songbirds in the eastern and Midwestern United States do, especially in extensively fragmented landscapes that have high edge contrast created by agriculture, in which brown-headed cowbirds may act as both predator and brood parasite (Donovan et al. 1997; Cox et al. 2012). I therefore focus on adaptive responses to negative edge effects in this analysis. The rate at which nest success declines in response to increasing patch edge-area ratio is given by the edge sensitivity of the species (Fig. 1). Species with high edge-sensitivity experience a high probability of nest failure in small patches (or, more accurately, a higher proportion of nests in these patches fail within the model). Because a landscape is made up of individual patches, b_x is ultimately assessed over all females in all patches of the landscape, and is thus sensitive to the degree to which the landscape has been fragmented (fragmentation creates many small patches with greater edge, which lowers nest success within those patches, resulting in a lower overall b_x for the landscape; With and King 2001). Because habitat loss and fragmentation are modeled as a dynamic process, b_x changes over time (b_t) and is therefore time-dependent as well.

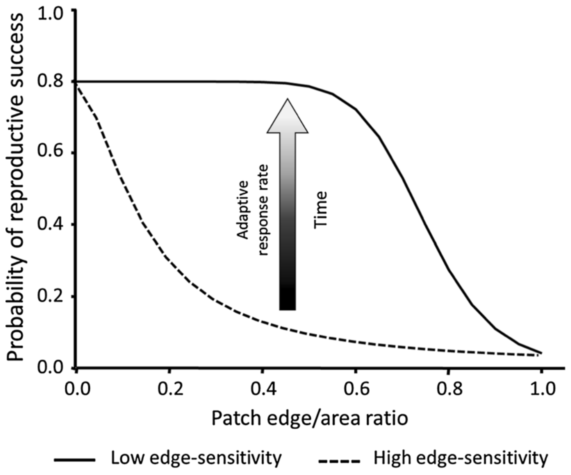

Fig. 1 Adaptive response to habitat loss and fragmentation is modeled as a directional change in edge sensitivity within the population over time (i.e., from high to low edge-sensitivity). Edge sensitivity quantifies the effect of patch geometry (edge-to-area ratio) on songbird nesting success within habitat fragments. Because some degree of nesting failure occurs regardless of patch size, maximum success is set at 0.8 (at best, 80 % of nests succeed in large patches with little edge). The ARR is the number of generations it takes for populations to switch from high to low edge-sensitivity

The maternity function b_t is combined with age-specific survivorship to create a life table for the population. Annual survival probabilities were defined for two age classes: juveniles ($s_0 = 0.3$) and adults ($s = 0.6$). These rates of survivorship are typical for many Neotropical migratory songbirds (Karr et al. 1990; Anders et al. 1997) and are therefore commonly used in avian demographic models (Donovan et al. 1995; With and King 2001; Schrott et al. 2005a, b). The life table is used to parameterize an age-structured matrix population model that projects the number of females in the population forward 1 year. This new population and the landscape at time $t + 1$ are used to calculate the maternity function b_{t+1}, and this cycle is repeated for the duration of the simulation (200 years). At each time step, the population's finite rate of increase λ is given by the solution to the characteristic equation (Lande 1988):

$$\lambda^{\alpha} - s\lambda^{\alpha-1} - bl_{\alpha} = 0 \qquad (1)$$

where $\alpha \geq 1$ is the age of sexual maturity (1 year) and $0 < s < 1$. The age of last reproduction is assumed here to be 8 years, consistent with the maximum longevity of many small passerines (e.g., *Dendroica*, *Oporornis*, *Vermivora*, *Vireo*, *Wilsonia*; Beauchamp 2010). The population is declining when $\lambda < 1.0$ and is increasing when $\lambda > 1.0$.

At each time step ($t + 1$), nesting females are assigned to patches stochastically, with the probability that an individual female nests in a particular patch given by an incidence function, J_A (based on a species with low area-sensitivity; cf. Table 1 and Fig. 1 in Schrott et al. 2005a). Area sensitivity has much less effect on the model results than edge sensitivity (With and King 2001; Schrott et al. 2005a). Females returning to the breeding ground are assigned to patches until all females are settled or all potential nesting sites in all patches are occupied. If there is not enough habitat remaining on the landscape for all returning females, the surplus birds become non-breeding "floaters." Within patches, nest success is determined by the edge-sensitivity function, although this probability is applied stochastically to each nest in a patch (i.e., some fraction of nests for a given patch failed based on the edge-sensitivity function). The location of individual nests within patches, such as their relative distance to the edge, is not actually mapped and recorded. Successful nests fledge the entire clutch (assumed here to be a uniform distribution of 4–5 eggs). The sex ratio of fledglings is determined stochastically according to the population's sex ratio (assumed to be 1:1). The model also assumes a closed population with no net immigration or emigration. While this assumption may appear unrealistic for migratory bird populations, it has the advantage here of isolating the response of the focal population due to dynamic landscape change in the absence of any "rescue effect" from immigration (e.g., With et al. 2006).

The adaptive response of species to fragmentation is modeled here as a decrease in edge sensitivity of the population over time; that is, a directional shift from high edge-sensitivity to low edge-sensitivity (Fig. 1). A population dominated by birds with high edge-sensitivity will initially decline as the landscape undergoes habitat loss and fragmentation, but the rate of decline should stabilize once birds "adapt" (i.e., birds become less edge-sensitive) and begin to make up a larger proportion of the population. The specific evolutionary mechanisms or behaviors that might give rise to this sort of adaptive response are thus not being modeled directly here; the response is purely a phenomenological one, which is sufficient for the objectives of this analysis. In other words, it is the potential for an adaptive response to landscape change, and not the specific mechanisms by which such adaptive changes might occur, that is of interest here.

Model simulations

Modeling dynamic landscape change

At the start of each simulation, the landscape was initialized at 100 % breeding habitat. Habitat was then removed at one of three rates ($r = 0.5$, 1.0, and 5.0 %/year), which bracket the annual rates of decline observed in real landscapes, although the lower rates (0.5–1 %/year) are more typical (Hansen et al. 2013; Sleeter et al. 2013). Habitat loss occurs as a fixed percentage, such that the total amount of habitat lost over t years is $h_t = 100 - rt$ (e.g., $h_t = 80$ % for $t = 20$ and $r = 1.0$). In the simulations that follow, a full-factorial analysis was conducted for populations in landscapes undergoing an intermediate degree of fragmentation ($H = 0.5$), as prior research revealed that this landscape scenario exhibited the greatest range of variability in population responses (Schrott et al. 2005a). Nevertheless, a subset of simulations was also conducted in highly fragmented ($H = 0.0$) and clumped ($H = 1.0$) landscapes to gain additional insights into the interaction between fragmentation and the rate of adaptive response (Supplemental Table 1).

Habitat loss was implemented at rate r until a threshold amount of habitat ($h_{\min}$) was reached, which is both species- and landscape-dependent. The values for $h_{\min}$ were obtained from a previous study that identified a population vulnerability threshold to dynamic landscape change (Schrott et al. 2005a). As defined in that study, population growth rates begin an accelerated decline toward extinction at the vulnerability threshold, such that population recovery is difficult or impossible past this threshold (Schrott et al. 2005b). It is thus necessary to halt habitat loss at a point just before the vulnerability threshold in the simulations (i.e., at $h_{\min}$) as otherwise populations would go extinct regardless of the adaptive response rate (ARR) (Schrott et al. 2005b).

Adaptive response to landscape change

To assess the rate of response needed to offset population declines caused by habitat loss and fragmentation, I varied the ARR to reflect different levels of penetrance in the population; that is, the number of generations it should take for the adaptive behavior(s) to spread throughout the entire population (ARR = 3, 5, 10, 20, 40, or 80 generations). The rate of adaptive response was thus based on a fixed percentage of the population that shifted from high edge-sensitivity to low edge-sensitivity each year (14.5, 8.7, 4.4, 2.2, 1.1, or 0.5 % of population/year; Fig. 1). Generation time (G) for the population was calculated following Gotelli (1995) as:

$$G = \frac{\sum_{x=0}^{k} l(x)b(x)x}{\sum_{x=0}^{k} l(x)b(x)}, \quad (2)$$

where x is the age class, l is the survivorship rate, b is the female fecundity rate, and k is the maximum longevity of a bird. The generation time for the hypothetical songbird being modelled here was thus 2.3 years.

In this first set of simulations, the adaptive response was assumed to emerge immediately within the population (i.e., in the first generation), and thus was initiated during the second time step (year) of the simulation (since 1 generation = 2 years). Habitat loss occurred at a fixed rate (r) until the specified habitat limit (h_{min}) was reached ($50 \le h_{\mathrm{min}} \le 90$; Supplemental Table 1), at which point the simulation continued to run up to a total of 200 years (~87 generations) to overcome any initial transient dynamics. Ten runs were performed for each factor combination ($r \times$ ARR) for a given landscape scenario ($h_{\mathrm{min}} \times$ H; Supplemental Table 1), and the average over all 10 runs was used to characterize population trends over time (standard errors were all <0.01 and are not shown in figures).

Because simulations were initialized with stationary populations ($\lambda = 1$), all populations decline as habitat is removed during the simulation. A simple comparison of population sizes or growth rates (λ) is therefore not especially informative in this context (i.e., all populations have $\lambda_t < 1$). Instead, a population index that related the population size at each time step to the initial population size was used, as in previous applications of the dSSAD model (Schrott et al. 2005b; With et al. 2006). I therefore examined the relative change in this population index over time for populations with an adaptive response (for each ARR) compared to control populations that lacked an adaptive response. This provides a convenient means of summarizing the magnitude of the effect for a given rate of adaptive response.

In a second set of simulations, I also assessed the effect of delaying the onset of the adaptive response for different lengths of time, in terms of the number of generations the population was exposed to habitat loss and fragmentation before an adaptive response was initiated (i.e., delays of 1, 3, 5, 8, or 10 generations = ~2, 7, 12, 18, or 23 years). These trials were all conducted in landscapes of intermediate fragmentation (H = 0.5), in which the rate of habitat loss (r = 0.5, 1, or 5 %/year) was varied (Supplemental Table 2). Ten replicate time-series were run for each factor combination. As before, treatment effects were characterized in terms of the relative difference between control populations and those exhibiting an adaptive response.

Results

Effect of the adaptive response rate relative to the rate of landscape change

Adjusting the ARR relative to the rate of landscape change produced three types of dynamics within these simulated songbird populations (Fig. 2; Supplemental Table 1): (1) *Little-to-no effect* (relative change < 20)—Although population sizes were greater than in control populations that lacked an adaptive response, the magnitude of the effect was rather small. The ARR had little-to-no effect if populations were only briefly exposed to habitat loss and fragmentation (<10 years; Supplemental Table 1), especially if habitat loss occurred too rapidly relative to the demographic response (5 %/year; Fig. 2 and Supplemental Table 1). In either case, the population suffered little erosion of demographic potential (b_{L}), so population growth rates were not yet impacted by habitat loss and fragmentation (or, at least, did not appear to be affected, in the case of demographic lags). The rate of adaptive response therefore had little-to-no effect in these scenarios; (2) *Little-to-moderate effect* (relative change 21–100)—Effect sizes increased gradually but consistently, as a "staircase" (1 %/year; Fig. 2) that continued to grow larger over time (relative change ≤100 at 200 years). The greatest effect sizes were observed when populations adapted rapidly (3–5 generations) to habitat loss and fragmentation (1 %/year; Fig. 2). As this dynamic was observed in populations that had been subjected to about two decades of habitat loss and fragmentation, populations have experienced some degree of demographic erosion (b_L has been reduced), such that an adaptive response can have a moderate effect on offsetting population declines if it spreads rapidly through the population (i.e., within 3–5 generations); and, (3) *Great-to-very great effects* (relative change >100)—The ARR had the greatest effect in populations that had been subjected to long-term, low-

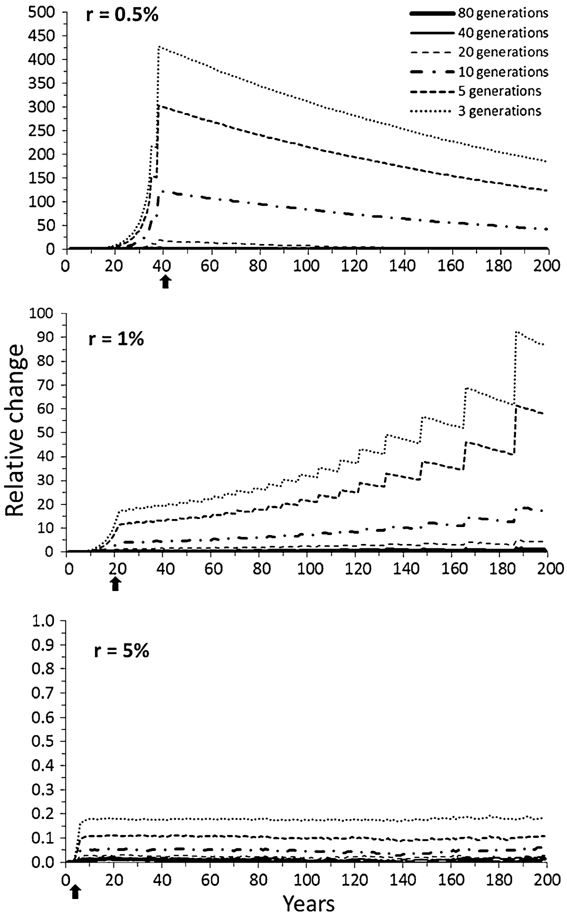

Fig. 2 Adaptive response by simulated songbird populations to different rates of landscape change ($r = 0.5$, 1, or 5 %/year). The magnitude of the adaptive response is assessed in terms of the relative change in the population index compared to a control population that lacks an adaptive response (see text for explanation). Shown here are representative results for populations within landscapes subjected to a 20 % loss of habitat and moderate degree of fragmentation (H = 0.5). Depending on the rate of habitat loss (r), populations were thus exposed to either 40, 20 or 4 years ($\sim$17.4, 8.7 or 1.7 generations) of habitat loss, respectively (*black arrows* mark the point at which no more habitat loss occurs in each landscape scenario)

level habitat loss and fragmentation (>20 years at 0.5 %/year; Fig. 2). The population's demographic potential has been more seriously eroded in these scenarios, as the rate of landscape change is slow enough to be tracked by the population. Not surprisingly, then, these are the scenarios in which the rate of adaptive response can have the most effect. Still, the greatest effects manifest only when the adaptive response spreads fairly rapidly through the population (<10 generations; Fig. 2). Even then, the effect size peaks and begins to decline gradually over time as the population reaches an equilibrium with the new landscape. For example, if a total of 20 % habitat is removed at a rate of 0.5 %/year over a 40-year period (Fig. 2), the effect size increases up to that point (40 years), and then slowly begins to decline as population size converges on a new equilibrium (although still not reached in the 200 years simulated by the model).

Effect of adaptive response to habitat fragmentation

The ARR had greater (and earlier) effects in landscapes undergoing moderate-to-severe fragmentation (H = 0.0–0.5), with the greatest relative change seen in populations that mounted a rapid ("Fast") response within 3–5 generations (Fig. 3; Supplemental Table 1). Given that the adaptive response was modeled as a decrease in edge sensitivity, it stands to reason that this type of response would have the greatest effect in landscapes that were actually being fragmented (i.e., where the amount of edge increased).

Effect of delaying adaptive response to landscape change

Delaying the onset of the adaptive response had the predictable result of mitigating the effect size attained by the population (Supplemental Table 2). In nearly all cases, this simply reinforced the results of the first set of runs; adaptation had to be initiated within 3–5 generations ($\sim$7–12 years) to offset population declines in response to habitat loss. Depending on the rate at which habitat is lost, this may entail a loss of as little as 10–30 % habitat over just a few decades (20–40 years). As before, the adaptive response has little effect in landscapes undergoing rapid habitat loss ($r = 5$ %/year), because of the short time over which populations were exposed to habitat loss and the lagged demographic response to rapid landscape change.

Discussion

The results of this analysis suggest that migratory songbirds affected by negative edge effects will need

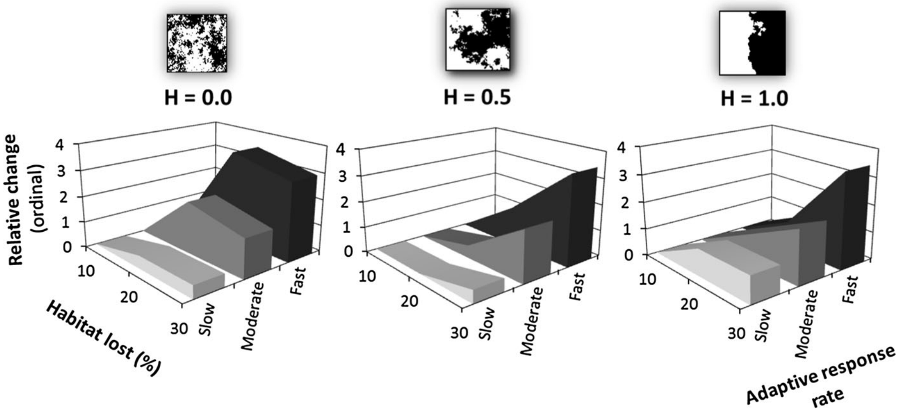

Fig. 3 Effect of habitat fragmentation (H) on the adaptive response of songbird populations to habitat loss. The magnitude of the population response, relative to a control that lacked an adaptive response, is presented as an ordinal scale: 1 = little-to-no effect (<20 relative change); 2 = little-to-moderate effect (21–100 relative change); 3 = great effect (101–200 relative change); and, 4 = very great effect (>200 relative change). The adaptive response rate has likewise been categorized as "Fast" (3–5 generations), "Moderate" (10–20 generations), or "Slow" (40–80 generations) to simplify the presentation

to respond quickly, within 3–5 to 10 generations (~7–12 to 23 years), if they are to keep pace with typically observed rates of landscape change (e.g., $r = 0.5$–1 %/year). Because the adaptive response was modelled as a reduction in edge sensitivity over time (i.e., from high to low edge-sensitivity), this type of response was closely tied to landscape structure, and thus should have been highly sensitive to landscape change. There are apparently limits to this sensitivity, however. In previous research utilizing this spatially-structured avian demographic model, populations were found to exhibit a lagged response to rapid landscape change (5 %/year), such that populations did not appear to be affected by habitat loss and fragmentation (Schrott et al. 2005a). In those scenarios, the demographic response of the population had effectively become decoupled from the landscape, making it appear that the population could tolerate a greater degree of habitat loss than it actually could. Although a demographic assessment of extinction risk did not reveal that these populations were at high risk, they inexorably went extinct within the 20 years it took to lose all habitat (i.e., when habitat was lost at a rate of 5 %/year; Schrott et al. 2005a). It thus follows that if populations are not affected by habitat loss and fragmentation (or do not appear to be affected), then the sort of adaptive response modelled here (a decrease in edge sensitivity) will have little apparent effect on the population (Supplemental Table 1). Nevertheless, the potential for such lagged responses to rapid landscape change is an important finding, for it highlights when and why populations may be unable to respond to habitat loss and fragmentation. In this case, demographic lags may also compromise the ability of species to mount an adaptive response to rapid landscape change.

Although the adaptive response was modelled phenomenologically here, a directional shift in edge sensitivity could be driven by either behavioral or genetic mechanisms that help to mitigate increased rates of nest predation and brood parasitism that contribute to negative edge effects. If migratory songbirds affected by negative edge effects have to mount an adaptive response within 20 years to keep pace with landscape change, as suggested by the results of this model analysis, it seems unlikely that this can occur as a microevolutionary (genetic) response. For example, adaptive responses to brood parasitism by brown-headed cowbirds, which pose a particular threat to North American songbirds in fragmented forest landscapes, are believed to have a genetic basis, and yet, prolonged contact with cowbirds (>10^2–10^3 years) appears to be necessary before adaptive responses (e.g., rejection of cowbird eggs by the host) will spread through a population (Hosoi and Rothstein 2000; Kuehn et al. 2014). Species may thus exhibit an evolutionary lag in response to more recent and rapid landscape changes, which could account for the lack of adaptive response to cowbird parasitism in most forest songbirds and even in some grassland species that have had a longer history with cowbirds (Rothstein 1975; Hosoi and Rothstein 2000; Peer et al. 2000). In addition, Neotropical migratory songbirds are believed to exhibit regional source-sink dynamics (i.e., metalandscape connectivity), in which immigration rates (and presumably gene flow) are asymmetrical among landscapes that differ in the amount and fragmentation of forest cover (Donovan et al. 1995; With et al. 2006). Any adaptive response to cowbird parasitism that emerged in fragmented landscapes, which are likely to be population sinks for forest-nesting songbirds (Donovan et al. 1995; With and King 2001), would thus be swamped by immigrants from source populations in unfragmented landscapes that lack cowbird parasitism.

Adaptation to brood parasitism represents only one type of response by songbirds to habitat loss and fragmentation, however. Predation is the greatest cause of nest failure in most species, and thus songbirds often undergo multiple nesting attempts in an effort to produce just one successful brood during the breeding season. Altering nest placement is a common strategy for dealing with nest predation (Lima 2009), and could therefore help songbirds mitigate edge sensitivity in fragmented landscapes. For example, birds may exhibit a "win-stay, lose-switch" strategy in response to nest predation (Nowak and Sigmund 1993). If a nest has been depredated, songbirds may alter the location of subsequent nests to reduce predation risk, such as by nesting higher off the ground, shifting to areas or habitats that afford greater nest concealment (e.g., more vegetation cover) or lower predation pressure, or by simply moving a greater distance away to re-nest after a nest has been depredated (Forstmeier and Weiss 2004; Peluc et al. 2008; Chalfoun and Martin 2010). Although nest-site selection is clearly adaptive and may therefore be under selection (i.e., a genetic adaptation; Martin 1998), many of these sorts of strategies are believed to represent behavioral adaptations (i.e., phenotypic plasticity) that enable breeding songbirds to cope with a variable and unpredictable predation-risk landscape (Lima 2009; Chalfoun and Martin 2010; Halupka et al. 2014).

Conclusions

Although microevolutionary changes are necessary for adapting to environmental change in the long-term, behavioral (phenotypic) plasticity permits a more rapid response to changing environmental conditions in the short-term (Van Buskirk 2012; Vedder et al. 2013). Behavioral plasticity itself likely represents an adaptive (genetic) response to environmental heterogeneity (Van Buskirk 2012), which may therefore encompass landscape changes due to habitat loss and fragmentation. Behaviorally plastic responses, such as shifts in habitat use and nest placement that can mitigate a species' edge sensitivity to nest predation and brood parasitism, are clearly adaptive and have been documented to occur both within and between breeding seasons in many songbird populations. Adaptive shifts in nest placement thus provide a possible mechanism by which edge-sensitive songbirds could achieve the sort of rapid response predicted by the model, given current rates (0.5–1 %/year) of landscape change.

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