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Male Kirtland's Warblers' patch-level response to landscape structure during periods of varying population size and habitat amounts

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ABSTRACT

Forest planners must evaluate how spatiotemporal changes in habitat amount and configuration across the landscape as a result of timber management will affect species' persistence. However, there are few long-term programs available for evaluation. We investigated the response of male Kirtland's Warbler (*Dendroica kirtlandii*) to 26 years of changing patch and landscape structure during a large, 26-year forestry-habitat restoration program within the warbler's primary breeding range. We found that the average density of male Kirtland's Warblers was related to a different combination of patch and landscape attributes depending on the species' regional population level and habitat amounts on the landscape (early succession jack pine (*Pinus banksiana*) forests; 15–42% habitat cover). Specifically, patch age and habitat regeneration type were important at low male population and total habitat amounts, while patch age and distance to an occupied patch were important at relatively high population and habitat amounts. Patch age and size were more important at increasing population levels and an intermediate amount of habitat. The importance of patch age to average male density during all periods reflects the temporal buildup and decline of male numbers as habitat suitability within the patch changed with succession. Habitat selection (i.e., preference for wildfire-regenerated habitat) and availability may explain the importance of habitat type and patch size during lower population and habitat levels. The relationship between male density and distance when there was the most habitat on the landscape and the male population was large and still increasing may be explained by the widening spatial dispersion of the increasing male population at the regional scale. Because creating or preserving habitat is not a random process, management efforts would benefit from more investigations of managed population responses to changes in spatial structure that occur through habitat gain rather than habitat loss to further our empirical understanding of general principles of the fragmentation process and habitat cover threshold effects within dynamic landscapes.

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1. Introduction

Forest planners must evaluate how spatiotemporal changes in habitat amount and configuration across the landscape as a result of timber management, natural disturbance, and other factors will affect species' persistence, especially for small, habitat-limited populations. Conservation concepts are often used as a guide despite the lack of empirical support at the broad spatial and temporal scales at which forest management is conducted (Harrison and Bruna, 1999; Schulte et al., 2006). Of particular value have been concepts derived from the process of habitat loss and fragmentation (Boutin and Hebert, 2002). Theories suggest that species' response to habitat loss is nonlinear where below a critical amount of habitat remaining in the landscape, populations of individual species decline more rapidly (Andren, 1994; With and King, 1999; Fahrig, 2003; Flather and Bevers, 2002). Below a threshold amount of 10–30% of original habitat remaining in a landscape, the abrupt changes in spatial configuration (e.g., decreasing patch size and increasing patch isolation; reduced connectivity) contributes to the decline in patch occupancy and abundance beyond what is expected from habitat loss alone (Andren, 1994; With and Crist, 1995; Fahrig, 2001; Flather and Bevers, 2002).

However, empirical evidence for the existence of a habitat amount threshold is weak (Fahrig, 2003). Further, the threshold in habitat amount can vary depending on the scale of the investigation (Mönkkoönen and Reunanen, 1999); the dispersal ability, habitat affinity, and reproductive rate of the species under consideration (With and Crist, 1995; Fahrig, 1998; With and King, 2001; Lindenmayer et al., 2005; Betts et al., 2007); landscape matrix quality (Mönkkoönen and Reunanen, 1999; Fahrig, 2001; Wiegand et al., 2005); and spatially across a species' geographical

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range (Rhodes et al., 2008). We have little understanding of how the temporal rate of habitat change (Keymer et al., 2000), and the regional population level (i.e., whether habitat is saturated or not) influences critical habitat threshold levels and habitat occupancy. Hence, it may be impossible to delineate clear or universal threshold responses for practical use (Lindenmayer and Luck, 2005; Groffman et al., 2006; Radford et al., 2005). Examining the qualitative pattern and form of population responses across a continuum of landscape structures rather that focusing on an exact habitat amount threshold would help planners apply the threshold concept to different landscapes and more species (Radford et al., 2005).

In the 1970s, forest managers were trying to reverse the population decline of the federally endangered Kirtland's Warbler (*Dendroica kirtlandii*). This long-distance migrant winters in the Bahama archipelago, and arrives on its breeding grounds throughout May and remains there until August–September. After controlling brood parasitism by Brown-Headed Cowbirds (*Molothrus ater*), the male population stabilized but failed to increase. Researchers determined that the breeding population was habitat limited (Probst, 1986; Probst and Weinrich, 1993). Fire suppression had greatly reduced the amount and extent of dense, young (5–23-year-old) jack pine (*Pinus banksiana*) forests found on the glacial outwash ecosystems in northern Michigan (USA) that the warbler almost exclusively uses for nesting. Using past research and island biogeography theory at the time, forest planners implemented a variety of management guidelines within 23 designated Kirtland's Warbler Management Areas (KWMAs; Probst, 1988; Byelich et al., 1976) including: (1) using large jack pine plantations to increase the amount of early succession jack pine forest by improving within-stand quality by increasing stem density, and the number and size of openings to more closely mimic wildfire-regenerated habitat, (2) reducing the isolation of small habitat patches by placing new, larger plantations near existing occupied habitat to enlarge blocks of habitat composed of stands of various ages within KWMAs, (3) clustering projects and staggering stand regeneration to encourage overlap in an area's use, and (4) maintaining 20% of each KWMA in each 10-year age class under a 50-year stand rotation base.

These forest management activities as well as naturally occurring wildfires over the last two decades have spatially and temporally changed the amount and spatial configuration of suitable habitat across the warbler's primary breeding range (Probst and Weinrich, 1993; Bocetti, 1994; Probst et al., 2003; Donner et al., 2008). The warbler's population size and the species' regional spatiotemporal distribution across its breeding range in response to these dynamics has been described (Probst and Weinrich, 1993; Probst et al., 2003; Donner et al., 2008). However, the long-term management of Kirtland's Warbler also presents the opportunity to explore how changing landscape structure influences patch-scale responses.

In this paper, we investigate how the density of Kirtland's Warbler singing males changes in response to changes in patch and landscape structure related to forest management. Our specific objectives are to: (1) define past time periods that differed in the proportion of suitable habitat in the landscape and also differed in regional male population levels, and (2) determine if the relationship between average male density at the patch scale to patch attributes was similar across defined periods.

2. Methods

2.1. Study area

This study was conducted on 23 KWMAs, lands specifically managed for breeding Kirtland's Warblers in northern Lower Michigan by the United State Department of Agriculture, Huron-Manistee National Forests, Michigan Department of Natural Resources, and the United State Department of Fish and Wildlife Service. Management areas varied in size from approximately 1400 to 13,000 ha totaling 71,610 ha, and are dispersed across an area approximately 137 km × 130 km (Fig. 1). This area experiences large fluctuations in temperature because of its inland location and relatively high elevation; late spring and early fall freezes are common (see Kashian et al., 2003). KWMAs are primarily surrounded by public or commercial forested lands that are managed for forest products, wildlife, and recreation.

Kirtland's Warbler's historical breeding range and KWMAs are located mostly in the Grayling outwash plains characterized by landforms of outwash sands deposited by fast moving glacial meltwaters (Grayling Outwash Plain sub-subsection of the High-plains subsection; USDA Forest Service, Ecological Classification System) (Fig. 1). The dominant soils classify as Grayling sand at the series level, and are composed of well-washed coarse sands with less than 5% silt plus clay, generally lack weatherable minerals, and are well-drained. These poor quality soils facilitate jack pine dominance, and maintain a mixture of low shrubs [e.g., blueberry (*Vaccinium angustifolium*), juneberry (*Amelanchier* spp.), sweetfern (*Comptonia peregrina*)], grasses, sedges, and forbs that are important forage and nesting cover (Walkinshaw, 1983; Bocetti, 1994; Kashian et al., 2003; Probst and DonnerWright, 2003). The low shrub cover and the lower live branches of jack pine provide shelter and concealment for the warblers' ground nest, provide foraging places, and conceal nest access (Probst, 1988). Ground cover density varies from sparse areas with bare ground to dense patches (Bocetti, 1994; Probst and DonnerWright, 2003).

Historically, large fires perpetuated the jack pine ecosystem over the relatively flat topographic terrain (Kashian et al., 2003). Fire continues to be an important factor regenerating jack pines in this area, but due to fire suppression, the modern fire rotation interval is many times longer than in historical times, and less area is burned (Cleland et al., 2004). Managers use whole-tree harvesting followed by plantations, and unburned, natural regeneration to help maintain young jack pine forests on a short rotation throughout the KWMAs (Probst, 1988; Donner et al., 2008). Northern pin oak (*Quercus ellipsoidalis*), trembling and bigtooth aspen (*Populus tremuloides* and *P. grandidentata*), black cherry (*Prunus serotina*), and choke cherry (*P. virginiana*) are often scattered within the jack pine stands (Walkinshaw, 1983; Probst, 1988). Other major species on the outwash plains are red pine (*Pinus resinosa*), and white pine (*Pinus strobus*). Northern hardwood forests of sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), American basswood (*Tilia americana*), and white pine dominate surrounding moraines.

2.2. Suitable breeding habitat and patch attributes

Breeding habitat for the Kirtland's Warbler consists of primarily pure, even-aged stands of young jack pine trees typically 1.7–5.0 m in height, at least 20–25% tree canopy cover, and a minimum of 2000 stems/ha (Walkinshaw, 1983; Probst and Weinrich, 1993). Preferred habitat (i.e., those stands with the highest density of warblers) has more than 7500 stems/ha, between 35 and 65% canopy cover, and was historically regenerated after wildfires (Probst, 1988; Probst and Weinrich, 1993).

The suitability of a habitat patch is a function of age and the associated changes in sapling height, canopy cover, lower live branch height, and the development of understory plants required for nesting and fledgling cover. Specifically, self-pruning of the lower branches and the elimination of small openings as trees grow diminishes cover (Probst, 1988; Probst and Weinrich, 1993). In addition, the decline in the number of males with patch age may