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Patch dynamics and the timing of colonization–abandonment events by male Kirtland's Warblers in an early succession habitat

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ABSTRACT

Habitat colonization and abandonment affects the distribution of a species in space and time, ultimately influencing the duration of time habitat is used and the total area of habitat occupied in any given year. Both aspects have important implications to long-term conservation planning. The importance of patch isolation and area to colonization–extinction events is well studied, but little information exists on how changing regional landscape structure and population dynamics influences the variability in the timing of patch colonization and abandonment events. We used 26 years of Kirtland's Warbler (*Dendroica kirtlandii*) population data taken during a habitat restoration program (1979–2004) across its historical breeding range to examine the influence of patch attributes and temporal large-scale processes, specifically the rate of habitat turnover and fraction of occupied patches, on the year-to-year timing of patch colonization and abandonment since patch origin. We found the timing of patch colonization and abandonment was influenced by patch and large-scale regional factors. In this system, larger patches were typically colonized earlier (i.e., at a younger age) and abandoned later than smaller patches. Isolated patches (i.e., patches farther from another occupied patch) were generally colonized later and abandoned earlier. Patch habitat type affected colonization and abandonment; colonization occurred at similar patch ages between plantation and wildfire areas (9 and 8.5 years, respectively), but plantations were abandoned at earlier ages (13.9 years) than wildfire areas (16.4 years) resulting in shorter use. As the fraction of occupied patches increased, patches were colonized and abandoned at earlier ages. Patches were abandoned at older ages when the influx of new habitat patches was at low and high rates. Our results provide empirical support for the temporal influence of patch dynamics (i.e., patch destruction, creation, and succession) on local colonization and extinction processes that help explain large-scale patterns of habitat occupancy. Results highlight the need for practitioners to consider the timing of habitat restoration as well as total amount and spatial arrangement of habitat to sustain populations.

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1. Introduction

Fundamentally, colonization and extinction events determine the distribution of a species in space and time (Gaston and Blackburn, 2002), especially those species that currently exist in patchy environments. Hence, colonization and extinction rates are often used to parameterize models investigating the effects of habitat loss and fragmentation on population dynamics, frequently within the context of metapopulation theory (Hanski, 1999; Levins, 1969). In these patch occupancy models, the rate of colonization is typically assumed constant because the set of occupied patches varies at stochastic steady state (Hanski, 1999). In real landscapes, however, disturbance and succession drive spatial and temporal variability in patch turnover and suitability (Pickett and White,

1985), which are not adequately incorporated in most models. Disturbance can eliminate or create new patches in the landscape at varying rates, while succession can change the suitability of a patch for the focal species altering local colonization and extinction dynamics through time.

Recently, considerable attention has focused on incorporating the rate of habitat turnover and patch age structure in theoretical metapopulation persistence studies (Amarasekare and Possingham, 2001; DeWoody et al., 2005; Ellner and Fussmann, 2003; Hastings, 2003; Keymer et al., 2000; Wilcox et al., 2006). For example, incorporating patch age distribution in patch occupancy models raised extinction thresholds (Johnson, 2000), while increasing rates of patch destruction resulted in declining colonization rates (Johst et al., 2002). Amarasekare and Possingham (2001) reported that the fraction of occupied patches at equilibrium declined when the rate of habitat succession occurred more rapidly than the species ability to colonize new patches. Although theoretical advances

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have been made within a patch occupancy context, more long-term empirical studies are needed to better understand how local colonization and extinction events may vary with patch dynamics and the population dynamics of the focal species simultaneously (Biedermann, 2004).

Studies to date have generally recorded changes in patch occupancy from presence–absence data collected across a few years, or between two points in time. Variation in colonization–abandonment events between these points in time are often attributed to habitat type, vertical structure, or habitat configuration (e.g., fragmentation) shifts within a region or landscape (e.g., Sirami et al., 2008; Matthysen et al., 1995; Villard et al., 1995). Few studies investigate how these factors may influence the timing of colonization and abandonment events between the two sampling dates (i.e., the inter-annual variation) even though temporal variability has been reported. For example, temporal variability in spring arrival times by migratory birds colonizing breeding habitat patches within a single year have been shown to vary depending on an individual's physiological condition as a consequence of winter range habitat quality (Forstmeier, 2002; Marra et al., 1998), the frequency at which a patch is occupied (Doran and Holmes, 2005), or regional population size (Tryjanowski and Sparks, 2001). Individual territories in fragmented patches were colonized at a slower rate by nuthatches (*Sitta europaea*) than territories in large forest patches (Matthysen and Currie, 1996). Groom and Grubb (2006) found patch isolation and size influenced the timing of patch recolonization and patch abandonment of woodlots by Carolina Chickadees (*Poecile carolinensis*) over a 6 months time period after birds were removed from the woodlots. Several years post-burn, bird species composition was found to be different in spatially separated fires due to variability in colonization patterns (Brotons et al., 2005). Thus, one may hypothesize that inter-annual variation of colonization and abandonment events may occur as well. However, to our knowledge, no long-term studies exist that examine the year-to-year variability in the timing of patch colonization and abandonment events for a migratory bird species within the context of changing regional landscape structure (i.e., patch dynamics context) and population dynamics.

Of special conservation concern has been the recorded decline for many neotropical migrant bird species that prefer disturbance-mediated early successional habitat (Brawn et al., 2001; Thompson and DeGraaf, 2001). Due to the rapidly changing landscape, these species may be more sensitive to temporal changes in their habitat than to spatial structure (Keymer et al., 2000) making these species good candidates for investigating variability in inter-annual patch colonization and abandonment events. The endangered Kirtland's Warbler (*Dendroica kirtlandii*) is one such neotropical migrant that requires a constant supply of newly-formed habitat through disturbance to compensate for disappearing habitat through succession (Probst et al., 2003). The Warbler breeds exclusively in young jack pine (*Pinus jacksiana*) forests found on nutrient poor, sandy soils in primarily northern Lower Michigan and scattered locations throughout Michigan's Upper Peninsula, Wisconsin, and Ontario (Petrucha and Carlson, 2007; Probst et al., 2003). As part of the Kirtland's Warbler Recovery Plan (Byelich et al., 1985), a network of essential habitat areas was established in the lower peninsula of Michigan where timber harvesting and plantations are used to supplement wildfires in regenerating adequate amounts of young jack pine forests on a rotational basis (Kepler et al., 1996; Probst and Weinrich, 1993). Through these forest management activities and the succession of jack pine forests, the breeding areas have become a dynamic mosaic of patches that differ spatially and temporally in age, size, and regeneration type across the landscape (Donner et al., 2008; Probst and Weinrich, 1993). These temporal changes provide an opportunity to investigate the importance of patch attributes and

landscape factors on year-to-year local colonization–abandonment events.

In this paper, we use 26 years of regional male population census data and temporally referenced landscape data to: (1) examine the influence of patch characteristics on the timing of patch colonization and abandonment events (i.e., patch age) and longevity of patch use, and (2) determine whether the timing of patch colonization and abandonment events correlates with the rate of habitat influx and population size (i.e., fraction of occupied patches) on the landscape.

2. Material and methods

2.1. Kirtland's Warbler ecology

The Kirtland's Warbler nests in the early stages (5–23 years old) of primarily pure, even-aged stands of jack pine trees typically 1.7–5.0 m in height. Marginal habitat has at least 20–25% tree canopy cover, and a minimum of 2500 stems per hectare (Probst and Weinrich, 1993; Walkinshaw, 1983), which is often found with unburned, natural regeneration. Optimal habitat (i.e., those stands with the highest density of Warblers) has more than 7500 stems per hectare, between 35% and 65% canopy cover, and was historically regenerated after wildfires (Probst, 1988; Probst and Weinrich, 1993). Patterns of patch occupancy of larger breeding areas show Warbler numbers will rapidly increase in an area for 3–5 years, stabilize during the next 4–7 years, and decline for the next 3–5 years as the area declines in suitability (Bocetti, 1994; Donner et al., 2009; Probst, 1986). Thus, the suitability of a habitat patch is a function of age and the associated habitat changes that occur with aging (succession). Specifically, as the saplings grow in height, percent canopy cover increases and self-pruning of the lower branches begins thereby diminishing small herbaceous understory plants important for nesting and fledgling cover (Probst, 1988; Probst and Weinrich, 1993; Probst and Donner-Wright, 2003).

2.2. Study area

We restricted the study area to jack pine patches within the boundaries of 23 Kirtland's Warbler Management Areas (KWMA), lands specifically managed for Kirtland's Warblers within their historical breeding range in northern Lower Michigan (Fig. 1). Patches outside KWMA were included under specific conditions (see below). Management areas varied in size (approximately 5–120 km²) averaging 32 km², and are dispersed across a region approximately 137 km × 130 km covering 71,610 ha. The KWMA 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 KWMA are located mostly in outwash sands (i.e., Grayling series) deposited by glacial meltwaters. These soils are composed of well-washed coarse sands with less than 5% silt plus clay, generally lack weatherable minerals, and are well-drained. The low nutrient soils promote 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 provide important forage and nesting cover for Kirtland's Warblers (Bocetti, 1994, Kashian et al., 2003, Probst and Donner-Wright, 2003; Walkinshaw, 1983). The low shrub cover and the lower live branches of jack pine provide shelter for the Warblers' ground nests, provide foraging places, and conceal nest access (Probst, 1988; Walkinshaw, 1983).

Historically, large fires perpetuated the jack pine ecosystem over the relatively flat topographic terrain (Kashian et al., 2003).

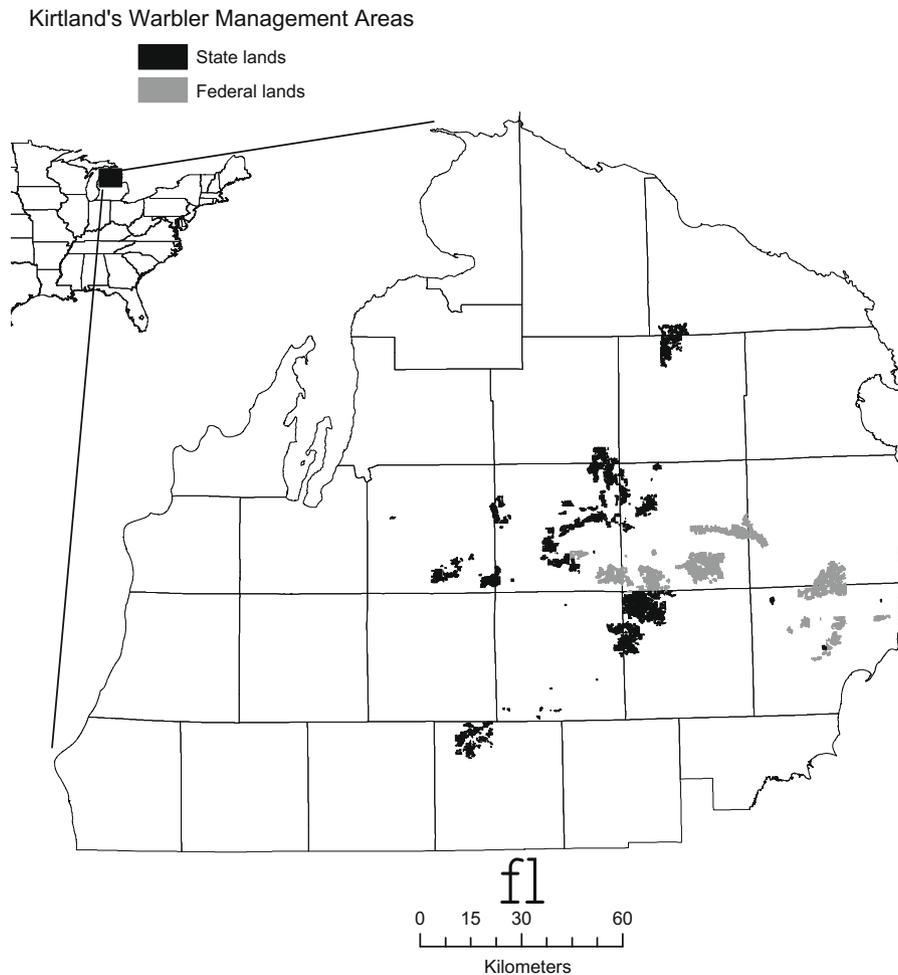


Fig. 1. Location of Kirtland's Warbler Management Areas within their primary breeding range, northern Lower Michigan, USA.

Fire continues to be an important factor regenerating jack pine across the landscape, but due to fire suppression, fire now burns a smaller proportion of the landscape and at longer intervals compared to historical periods (Cleland et al., 2004). Forest managers clearcut stands of jack pine, and use unburned, natural regeneration or plantations to help maintain young jack pine forests on a short-rotation timber harvesting basis throughout the KWMA (Donner et al., 2008; Probst, 1988). Northern pin oak (*Quercus ellipsoidalis*), trembling and bigtooth aspen (*Populus tremuloides* and *Populus grandidentata*), black cherry (*Prunus serotina*), and choke cherry (*Prunus virginiana*) are often scattered within the jack pine stands (Probst, 1988). Other common species on the poorly drained sections of the outwash plains are white pine (*Pinus strobus*) and red pine (*Pinus resinosa*). Northern hardwood forests of sugar maple (*Acer sacharrum*), beech (*Fagus grandifolia*), American basswood (*Tilia americana*), white pine and eastern hemlock (*Tsuga canadensis*) dominate the moraines.

2.3. Response variables

We used patch age at colonization and abandonment based on the patch's year of origin (i.e., year planted or burned or harvested and left to naturally regenerate) to model the timing of colonization and abandonment as a function of three patch variables [patch size, nearest distance to an occupied patch, and habitat type (defined under Section 2.4)] and two landscape variables [fraction of suitably-aged patches occupied and the rate patches within KWMA became suitably-aged (defined under Section

2.4)]. We calculated the number of years a patch was occupied to model the duration of patch use as a function of the three patch variables.

We used the results from the annual Kirtland's Warbler official census to identify occupied patches from 1979 to 2004. The census is coordinated under the direction of the Kirtland's Warbler Recovery Team, and is used to count all singing males within the known breeding range in northern Lower Michigan and the eastern and central Upper Peninsula of Michigan. Annually, federal and state forest management stands 3–23 years old are identified and surveyed for singing males between sunrise and 11:00 EDT from June 6 to 15 (Probst et al., 2005; Ryel, 1981). Methods are standardized to minimize sources of variation important to monitoring programs (Ryel, 1981). The male population was estimated at 211 in 1979 increasing to 1808 males by 2008 (MDNR press release 2009, Petrucha and Carlson, 2007).

Few Kirtland's Warblers nest outside KWMA boundaries due to a general lack of large, high-density jack pine areas located on outwash sands; however, it does occur. Because of the historical preference for wildfire-regenerated patches, this habitat regeneration-type was checked regularly outside of the KWMA by the official census. Therefore, we included occupied wildfire-regenerated patches outside KWMA in the analysis. Occupied patches outside KWMA that were not systematically checked for male presence (i.e., forestry plantations and unburned, natural regeneration areas) but were subsequently found to have been colonized were used in the patch abandonment analysis; the patch was checked annually for male presence once it became occupied.

We excluded patches occupied in 1979 from the colonization analysis because they may have been occupied the previous year. Likewise, if a patch was occupied in 2004, it was excluded from the patch abandonment analysis because it may have been occupied the following year. Only patches colonized and abandoned between 1979 and 2004 were included in the duration of patch use analysis. We used 288 occupied patches in the patch colonization analysis, 199 patches in the patch abandonment analysis, and 165 patches in the duration of patch use analysis.

2.4. Predictor variables

We measured patch and landscape variables from merged geographical vector coverages of managed breeding habitat within the KWMA, which are maintained independently by the Huron-Manistee National Forest and the Michigan Department of Natural Resources as part of the habitat management program. Because 2-year old stock was used for planting federal and state lands, we adjusted the year of origin for jack pine plantations by 2 years to make the age structural components more similar between plantations and the other regeneration types (Donner et al., 2008). Adjacent management stands of the same regeneration type that had year of origin within 1 year were merged to form jack pine patches that were functionally a single patch. Patch year of origin was the earlier date.

Habitat type was classified into three regeneration types: wild-fire, plantation, and unburned, naturally-regenerated jack pine patches. We used the Euclidean distance to the next nearest occupied patch using patch centroids to measure patch isolation for the year the patch was colonized and abandoned. For the duration of patch use analysis, we used the average distance to the nearest occupied patch; distances were measured for each year the patch was occupied.

Each patch was attributed with temporally referenced landscape-scale variables estimated for the year the patch was colonized and abandoned. We calculated the fraction of suitably-aged patches occupied, and the rate patches within the KWMA became suitably-aged (new patches/total suitable patches on the landscape; hereafter referred to as habitat influx) from 1979 to 2004. Suitably-aged habitat was defined as jack pine patches 5–23 years old and ≥ 12 ha, based on the use of jack pine habitat by males (Probst and Weinrich, 1993) during the period 1979 through 2004 (Donner et al., 2008). Our finding that males were using patches smaller than previously reported for the Kirtland's Warblers (32 ha; Mayfield 1960, Probst and Weinrich, 1993; Walkinshaw, 1983) is most likely due to these patches being positioned within larger complexes of suitably-aged jack pine habitat or younger clearcuts making them more attractive to the Warblers.

2.5. Statistical approach

We used linear models and generalized additive models (Wood, 2006) to model the timing of colonization and abandonment to the patch- and landscape-scale variables. Duration of patch use was modeled as a function of patch-scale variables only. We used generalized additive models to determine if linear models (i.e., ordinary least squares regression) were adequate for modeling the data; this was done to avoid overfitting the data with complex nonlinear terms because we did not know the form of the nonlinearities. Models were fit using the 'mgcv' package in the R software environment using a penalized thin plate regression spline basis to represent the smooth functions (Wood, 2006). In GAMS, the response is modeled as the additive sum of smoothed functions of covariates (i.e., nonparametric functions) allowing the response to follow any smooth curve rather than being constrained to a parametric form. However, parametric relationships (such as linear relationships)

can also be modeled in this framework. There was no evidence that nonlinear terms were needed to model patch age at colonization or duration of patch use as a function of the explanatory variables; estimated degrees of freedom from the generalized additive models for the continuous variables were at or near 1.0. In contrast, nonlinear relationships were found between patch age at abandonment and the predictor variables, so the timing of patch abandonment was modeled using generalized additive models. For the linear models, patch age at colonization was log-transformed, and patch duration of use was square-root transformed to better meet normality assumptions. Patch age at abandonment was modeled as a Gaussian-distributed response variable with a log link function. In all cases, examination of the residual spatial structure of the global models by empirical semivariograms showed no spatial autocorrelation (i.e., spatial correlation structure) in the model errors (Fortin and Dale, 2005).

We used Akaike's Information Criterion corrected for sample size (AICc) for model selection (Burnham and Anderson, 2002). An *a priori* candidate set of 17 models that incorporated patch characteristics and landscape-scale covariates was developed to model variation in the timing of patch colonization and abandonment, and duration of patch use (Appendix A). We compared candidate models using the differences in AICc scores (Δ_i). Models within two AICc units of the minimum were considered competitive models. We report the model with the fewest parameters that fell within the set of competitive models to avoid overfitting the data; this model was generally the model with the minimum AICc. Akaike weights (w_i) are presented to indicate the relative likelihood of the model given the data and candidate set of models tested (Burnham and Anderson, 2002). The relative importance of each explanatory factor was determined by summing w_i over the subset of models that included each variable (Burnham and Anderson, 2002). We also report adjusted R^2 values for the linear models, and deviance explained for the generalized additive models. Factor significance was assessed at 0.05.

3. Results

3.1. Timing of patch colonization

Mean patch age at colonization was 9.2 years (± 2.8 SD, range = 4–20). The timing of patch colonization was related to patch size, distance to an occupied patch, habitat regeneration-type, and the fraction of occupied patches in the landscape (Table 1). This model has a probability of 0.46 of being the best model out of all models considered. Patch size, habitat type, and distance had importance value weights of 1.0 compared to 0.99 for fraction of occupied patches and 0.53 for the rate of habitat influx.

Large patches were colonized at younger ages and patches farther from another occupied patch were colonized at older ages. In addition, plantations and wildfire-regenerated patches were colonized at earlier ages than unburned, naturally-regenerated patches. Mean patch age at colonization among habitat regeneration-types was 11.6 (± 2.9 SD) for unburned, naturally-regenerated patches compared to 9.0 (± 2.7 SD) and 8.5 (± 2.7 SD) years for plantation and wildfire-regenerated patches, respectively. At the landscape-scale, patches were colonized earlier when the fraction of occupied patches in the landscape increased.

3.2. Timing of patch abandonment

Mean patch age at abandonment was 14.5 years (± 3.7 SD, range = 5–24). The timing of patch abandonment was related to patch size and the landscape-scale variables of fraction of occupied patches and rate of new, suitably-aged patches in the landscape.

Table 1

The selected best linear models relating patch age at colonization and the duration of patch use by male Kirtland's Warblers in northern Lower Michigan, 1979–2004 to patch and landscape explanatory variables as determined by AICc.

Predictor variable	Patch colonization			Years patch occupied		
	β (SE)	t-Value	p-Value	β (SE)	t-Value	p-Value
Patch size	–0.09 (0.02)	–4.78	<0.001	0.35 (0.06)	5.62	<0.001
Distance to occupied patch	0.01 (0.001)	3.27	0.00	–2.0e–05 (9.2e–6)	–2.34	0.02
Habitat type:						
Wildfire	–0.25 (0.07)	–3.74	0.00	0.92 (0.22)	4.26	<0.001
Plantation	–0.18 (0.05)	–3.44	0.00	0.40 (0.17)	2.54	0.01
Fraction patches occupied	–0.80 (0.23)	–3.56	0.00	–	–	–
Adjusted R^2	19.3			29.1		
w_i^a	0.46			0.94		

^a Akaike weight for the model.

This model has a probability of 0.59 of being the best model out of all models considered. Patch size and rate of habitat influx had importance value weights of 1.0 compared to 0.93 for fraction of occupied patches. Both distance to an occupied patch and habitat regeneration-types had lower weights of 0.41.

In the model, larger patches were abandoned at older ages (Fig. 2a). There were nonlinear relationships between patch age at abandonment and the landscape-scale variables. Patches were abandoned at earlier ages as the fraction of occupied patches neared 0.30 (Fig. 2b). Above this fraction, the average patch age at abandonment was 13.2 years (3.2 SD) compared to 14.4 (3.7 SD) when there were fewer patches occupied. Patches were abandoned at older ages when the influx of new habitat patches in the landscape was at low and high rates (Fig. 2c). Average patch age at abandonment when the rate of new patches was <0.30 was 15.1 years (SD 3.4) and 15.2 (SD 4.4) years old when the rate of new, suitably-aged patches in the landscape was >0.60. Patches were abandoned at an average age of 13.7 years (3.4 SD) when the rate of new patches in the landscape was between 0.30 and 0.60.

3.3. Duration of patch use

Duration of patch use was related to all three patch variables (Table 1). This model had a probability of 0.94. Larger patches, and patches closer to another occupied patch were used for longer periods of time. Wildfire-regenerated patches were used on average 8.2 years (± 4.3 SD; $n = 23$) compared to 4.9 (± 3.1 SD; $n = 127$) and 2.6 (± 1.8 SD; $n = 18$) years for plantation and unburned, natural regeneration habitat, respectively. Patch size and habitat regeneration-type were relatively more important explanatory variables with variable weights of 1.0 compared to 0.94 for distance to another occupied patch. Nearly one-third of the patches were used only 1–2 years ($n = 48$; 29.1%), and were primarily plantation ($n = 36$) and unburned, natural regeneration ($n = 11$), <80 ha ($n = 40$), and >1 km from another occupied stand ($n = 32$).

4. Discussion

Many bird populations exhibit variable spatial distributions through time with many seemingly suitable areas not occupied in any given year (see Scott et al., 2002). Reasons for these large-scale patterns have focused on habitat selection mechanisms (Doran and Holmes, 2005; Fretwell and Lucas, 1970; Morris, 2003; Pulliam and Danielson, 1991), dispersal ability and body size of species, population size (see Gaston and Blackburn, 2002), and metapopulation dynamics (Hanski, 1999). We applied a metapopulation and patch dynamics framework to study long-term colonization and abandonment events by the Kirtland's Warbler

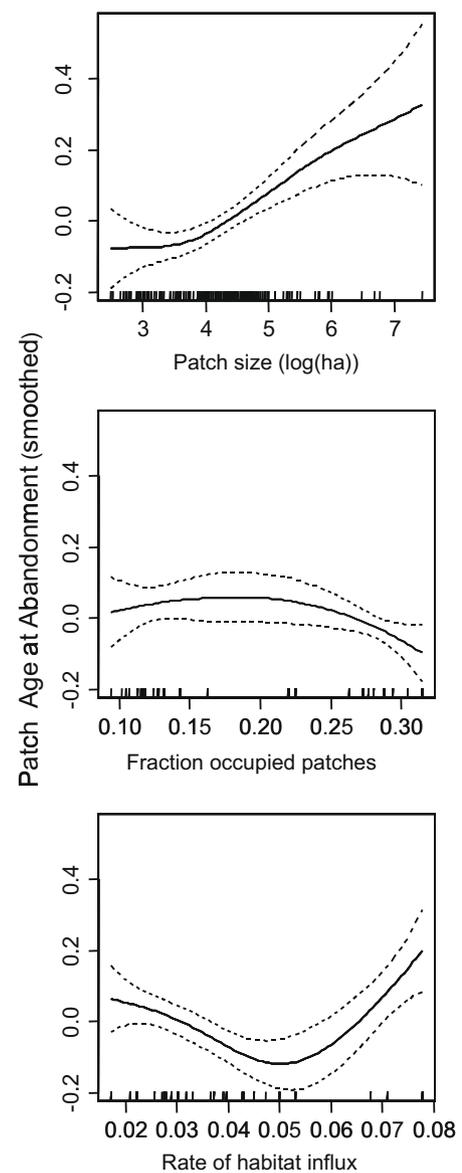


Fig. 2. Smoothed functional response of patch age at abandonment by male Kirtland's Warbler, 1979–2004, to patch- and landscape-scale continuous variables using generalized additive mixed models with a penalized thin plate regression spline fit. Solid lines represent the smooth function; dashed lines represent the approximate 95% confidence intervals. Patch age at abandonment is standardized. Note axis scales are not uniform across variables.

population because of the species' patch-oriented distribution across the landscape in response to habitat management and natural disturbances, and because of the strong effects of succession on habitat suitability. Colonization and extinction probabilities within stochastic patch occupancy models generally are held constant because many years of data are needed to provide information on the variability of these model parameters instead of the few years of census data usually available (Etienne et al., 2004). However, colonization and extinction processes may not be constant for real populations, especially if these populations exist within temporally dynamic systems such as successional habitats or within systems experiencing landuse changes where patches are being created or destroyed annually (Etienne et al., 2004). Our results provide empirical support for the temporal influence of patch dynamics (i.e., patch destruction, creation, and succession) and population size on local colonization and extinction events that help explain large-scale patterns of habitat occupancy over a long time period. We found that the rate of habitat influx and regional population size as well as local patch characteristics influenced the inter-annual timing of patch colonization and abandonment events by male Kirtland's Warblers over 26 years. These findings show that patch and landscape-scale factors can influence not only the length of time each individual patch is occupied, but also the total area of habitat occupied by a species in any given year, which have important implications to long-term conservation planning.

Within the classical metapopulation context where the landscape is considered static, the probability of a patch becoming occupied (i.e., colonized) is associated more with isolation factors, while extinction probability (i.e., abandoned) is associated more with patch size (Hanski, 1999). When patch occupancy is considered within a temporal context where the landscape is dynamic as in this study, we found patch size and habitat regeneration-type (i.e., patch quality) were equally important as isolation in explaining patch age at colonization. These results are similar to what is generally expected under spatially realistic metapopulation theory where colonization rate of an empty patch is a function of its distance from an occupied patch and size (modified by quality) (Ovaskainen and Hanski, 2004).

However, habitat quality was not important to the timing of abandonment in our study. Habitat quality can affect extinction probability if quality produces variable density from patch to patch (Ovaskainen and Hanski, 2004). Given historical variability in male Kirtland Warbler densities among habitat regeneration-types, we were expecting habitat quality to be an important factor explaining patch age at abandonment (i.e., higher quality habitat would be abandoned at later ages). However, male densities among the regeneration types became more similar during the later years of the study (Probst et al., 2005). Donner et al. (2009) found regeneration type was an important factor explaining male density only during the early period of the study when the regional population and amount of total habitat in the landscape were low; it was not an important factor in subsequent periods. The spatial distribution of the population during the early study years more closely resembled a metapopulation structure than during the later periods when the regional male population and amount of habitat increased in the study area. Thus, the degree to which habitat quality modifies patch size in the extinction process may depend on the relationship between regional population size and total habitat amounts.

Temporal changes in habitat availability and population size may also influence the colonization process beyond the well documented influence of patch geometry. Reported habitat use patterns show Kirtland's Warblers occupied wildfire-regenerated habitat over available plantation and unburned, naturally-regenerated habitat in the early 1980s (Probst, 1988; Probst and Weinrich,

1993), temporally shifting their distribution across the breeding range in response to the availability of wildfire-regenerated habitat during the late 1980s and 1990s (Donner et al., 2008), and used wildfire-regenerated habitat for longer periods of time (this paper). Thus, one would expect wildfire-regenerated habitat to be colonized at younger ages and abandoned at later ages under habitat selection theory (Morris, 2003). As wildfire-regenerated habitat became scarce due to succession, however, the increasing male population dispersed into primarily available plantation habitat in the mid-1990s (Donner et al., 2008), which could account for the similar age (i.e., younger age) at patch colonization between wildfire-regenerated and plantation habitat found in this study. Because the regional population continues to increase, the future timing of abandonment for the currently occupied plantations may also become similar to that seen for wildlife-regenerated patches, especially with no large wildfire-regenerated patches upcoming and managers' current focus on creating larger plantations within landscape-scale complexes of suitable habitat. Our finding that marginal unburned, natural-regenerated habitat as defined in this study, is colonized at older ages and occupied for fewer years supports other studies that have found marginal habitat is used only when a more preferred habitat is not available (Donner et al., 2008; Probst and Weinrich, 1993).

Combining patch dynamics and metapopulation dynamics in a modeling approach, Amarasekare and Possingham (2001) found fewer patches were occupied at equilibrium when the rate of habitat succession occurred more rapidly than species were able to colonize. We did not find a relationship between the rate of habitat influx and colonization events in this system (i.e., patch age at colonization was not older as would be expected if habitat influx was occurring more rapidly than the population could use). The absence of a strong temporal trend or extended periods of large habitat influxes may explain this finding. Instead, there were several pulses of rapid increases in upcoming, suitably-aged habitat in our study system (Fig. 3a). Conversely, the fraction of occupied patches displayed an increasing trend through time (Fig. 3b) with increasing population (Donner et al., 2008), which most likely accounted for the observed effect on the timing of colonization. Our results suggest regional population size plays a more important role in the timing of colonization events for this species than the rate of habitat influx. This supports the model of colonization within a metapopulation framework where colonization rate of the focal patch is a function of all occupied patches (Ovaskainen and Hanski, 2004).

As we expected, patch abandonment was delayed when the rate of habitat influx was low suggesting males remain in patches longer in the absence of more suitable habitat. However, our results showed patch abandonment was delayed during high rates of habitat influx as well. This nonlinear pattern may best be explained by the temporal relationship between population size and available habitat during the large influx of habitat. Due to the lack of suitable habitat in the early 1980s, the low, but stable male population was distributed in primarily six aging wildfire areas (>18 years old; Donner et al., 2008; Probst and Weinrich, 1993). Once the large influx of habitat from a large burn event became suitably-aged in the late 1980s, males redistributed out of these aging areas into the developing habitat (Donner et al., 2008; Probst and Weinrich, 1993) resulting in older patch ages at abandonment. Another large influx of habitat became suitably-aged in 2002–2003, but during this time, the total amount of suitable habitat available declined slightly from 2001 levels (i.e., appearing habitat did not compensate for the amount of habitat that became unsuitably-aged), and the male population was still increasing (Donner et al., 2008). Patches 8–13 years old that typically have higher male densities were potentially becoming saturated; 71–73% of the male population found in these patches from 2001 to 2002. Once developing

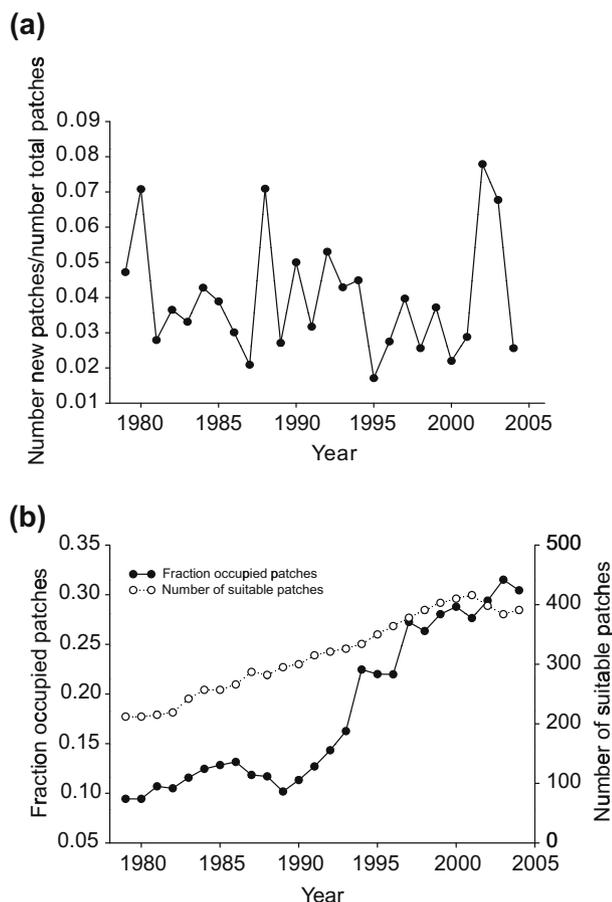


Fig. 3. Temporal trends of: (a) the rate of new habitat appearing on the landscape and (b) the fraction occupied patches within the Kirtland's Warbler primary breeding range, northern Lower Michigan, 1979–2004.

habitat became suitable, males abandoned several large plantations in the peripheral KWMA and a wildfire-regenerated area that were aging; no males were found in patches >17 years old by 2003 while 15–17 males were in patches 18–24 years old in 2001–2002. Our results support the importance of broad-scale variables such as population size and total area of habitat to the extinction process found in simulation metapopulation models for species in dynamic successional or transient habitats (Hodgson et al., 2009; Pellet et al., 2007).

Of particular interest, especially for metapopulation dynamics is the influence that individual behavior such as site fidelity and conspecific attraction may have on observed patterns of patch occupancy. Site fidelity is the tendency to return to an established breeding site (Dobkin et al., 1988; Villard et al., 1995), and conspecific attraction occurs when individuals use the presence of other individuals to direct their movement among patches (Muller et al., 1997; Smith and Peacock, 1990). Older Kirtland Warbler males have been found to display stronger site fidelity than younger males and will return to breeding sites in maturing habitat (Walkinshaw, 1983; Probst and Donner, pers. obs), which most likely extends the number of years used (i.e., increasing the age of patch abandonment) for some patches, especially the larger wildfire-regenerated patches that may have small pockets of suitable habitat within the larger, aging patch. Additionally, the few years of patch use for nearly one-third of the occupied patches suggests males may be vacating suitable patches to resettle near other males. Kirtland's Warblers tend to form loose breeding 'colonies' throughout their breeding range (Walkinshaw, 1983). In colonially breeding birds with strong site fidelity, Matthiopoulos et al. (2005)

found that the colonization process slowed and full occupancy of suitable habitat is prevented under local density dependence. This delayed colonization will cause a metapopulation to follow a step-like trajectory because individuals must overcome their site fidelity instincts to colonize new areas, but the delay is temporary. The fraction of occupied patches across our study period showed a large jump in the mid-1990s (Fig. 3b) when the population was expanding (Donner et al., 2008). One may expect the timing of colonization to occur at earlier ages after this jump as the population grew and reported densities increased (Probst et al., 2005; Donner et al., 2009), while the timing of colonization would occur at later ages (i.e., be delayed) prior to the jump due to lower density pressures when site fidelity and conspecific attraction may be more influential. Patch colonization was earlier post-1995 (8.8 years old) compared to 9.8 years old prior to the jump. To what degree site fidelity affects colonization and abandonment events in this system, however, is unknown, but the influence this behavior has on patch occupancy deserves more empirical investigation.

In this study, variable site factors (physiography, microclimate, soil) can influence growth rates of jack pine across the breeding range and within large patches that may influence the use of patches (Kashian and Barnes, 2000; Walker et al., 2003). For instance, Kashian et al. (2003) found early colonization of habitat patches on landforms within the easternmost management areas were colonized often at younger ages (≤ 5 years old). These management areas have a relatively warmer macroclimate due to lake effects resulting in more favorable growing conditions (i.e., based on annual jack pine height growth) than habitat located on the outwash plains landforms in the center of their breeding range, so habitat suitability was attained at younger ages. Post-examination of these patches, which were primarily plantations, show colonization occurred from 1986 to 1997. This time period was characterized by a rapidly growing (i.e., fraction of occupied patches increasing) and expanding Warbler population, and a slowing of new habitat patches appearing on the landscape (Donner et al., 2008). These factors may also help explain the earlier patch ages at colonization for these patches. Thus, jack pine growth is likely a higher-order constraint on the timing of colonization, but the temporal shifts in population size (i.e., fraction of occupied patches) and the rate of habitat influx are other large-scale processes influencing the timing of colonization for this species. Although Kashian et al. (2003) did not explicitly test for patch size effects on length of patch occupancy, our finding that larger patches were used longer by males supports their assertion that large areas containing more landform types (each with differential jack pine growth rates) would lead to longer patch occupancy by breeding Kirtland's Warblers.

4.1. Conclusion

Wildlife conservation and restoration programs often focus on habitat amount and spatial arrangement to strategically position patches on the landscape to maximize the potential for colonization or create large enough areas to lower the probability of extinction (Scott et al., 2001). However, our study shows that local colonization and abandonment events can be influenced by temporal shifts in population size and large-scale patch dynamics from disturbance (e.g., forest management) and succession in addition to local patch attributes. Our findings have implications for the management and conservation of early-successional species or for those species that rely on transient habitats. Conservation programs for these species become complex due to the relatively short time period in which habitat is suitable. The unpredictability of continued funding and of natural disturbances such as wildfire events, as is the case for Kirtland's Warbler, to create habitat further confounds habitat management programs for these species.

The age-related variability in patch colonization and abandonment reported in this study highlights the need for practitioners to consider the timing of future habitat management projects within the larger context of population size in relation to total available habitat as well as spatial structure considerations to maximize habitat use. Deciding where and when to place conservation efforts is difficult, and arguably more difficult for species in dynamic successional habitats, but the effectiveness of local actions may be helped by recognizing the importance of broad scale factors such as we report here on patchily distributed species. We encourage more empirical research to determine if the timing of patch colonization and abandonment patterns found in this study are found for other bird species in early successional systems, or in systems where the habitat network is being created or destroyed rather rapidly by changing landuse.

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Appendix A

Candidate set of *a priori* models used in the models examining the timing of patch colonization and abandonment, and the duration of patch use by male Kirtland's Warblers in their northern Lower Michigan breeding range. Only the patch variables were included in the *a priori* models for the duration of patch use analysis.

Category	Models
Null model	intercept
Patch variables	patch size isolation (distance to nearest occupied patch) habitat (wildfire, plantation, and unburned, natural regeneration) patch size + isolation + habitat patch size + habitat + size * habitat isolation + habitat + isolation * habitat patch size + isolation + patch size * isolation
Landscape (annual) variables	fraction occupied patches (fracocc) rate of new patches on landscape (rate) fracocc + rate + fracocc * rate
Patch and landscape variables	patch size + isolation + habitat + fracocc patch size + isolation + habitat + rate patch size + isolation + habitat + fracocc + rate patch size + fracocc + rate isolation + fracocc + rate habitat + fracocc + rate

References

- Amarasekare, P., Possingham, H., 2001. Patch dynamics and metapopulation theory: the case of successional species. *J. Theor. Biol.* 209, 333–344.
- Biedermann, R., 2004. Modelling the spatial dynamics and persistence of the leaf beetle *Gonioctena olivacea* in dynamic habitats. *Oikos* 107, 645–653.
- Bocetti, C. 1994. Density, demography, and mating success of Kirtland's Warblers in managed and natural habitats. PhD Dissertation. Ohio State University, Columbus, Ohio.
- Brawn, J.D., Robinson, S.K., Thompson III, F.R., 2001. The role of disturbance in the ecology and conservation of birds. *Ann. Rev. Ecol. Syst.* 32, 251–276.
- Brotos, L., Pons, P., Herrando, S., 2005. Colonization of dynamic Mediterranean landscapes: where do birds come from after fire? *J. Biogeogr.* 32, 789–798.
- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Inference: A Practical Information-Theoretic Approach, second ed. Springer, New York.
- Byelich, J., DeCapita, M.E., Irvine, G.W., Radtke, R.E., Johnson, N.L., Jones, W.R., Mayfield, H., Mahalak, W.J. 1976 (revised 1985). Kirtland's Warbler recovery plan. USDI Fish and Wildlife Service. Twin Cities, Minnesota.
- Cleland, D.T., Crow, T.R., Saunders, S.C., dickmann, D.L., Maclean, A.L., Jordan, J.K., Watson, R.L., Sloan, A.M., Brososfske, K.D., 2004. Characterizing historical and modern fire regimes in Michigan (USA): a landscape ecosystem approach. *Landscape Ecol.* 19, 311–325.
- DeWoody, Y.D., Feng, Z., Swihart, R.K., 2005. Merging spatial and temporal structure within a metapopulation model. *Am. Nat.* 166, 42–55.
- Dobkin, D.S., Holmes, J.A., Wilcox, B.A., 1988. Traditional nest-site use by white-throated swifts. *Condor* 88, 252–253.
- Donner, D.M., Probst, J.R., Ribic, C.A., 2008. Influence of habitat amount, arrangement, and use on population trend estimates of male Kirtland's Warblers. *Landscape Ecol.* 23, 467–480.
- Donner, D.M., Ribic, C.A., Probst, J.R., 2009. Male Kirtland's Warblers' patch-level response to landscape structure during periods of varying population size and habitat amounts. *Forest Ecol. Manage.* 258, 1093–1101.
- Doran, P.J., Holmes, R.T., 2005. Habitat occupancy patterns of a forest dwelling songbird: causes and consequences. *Can. J. Zool.* 83, 1297–1305.
- Ellner, S.P., Fussmann, G., 2003. Effects of successional dynamics on metapopulation persistence. *Ecology* 84, 882–889.
- Etienne, R.S., ter Braak, C.J.F., Vos, C.C. 2004. Application of stochastic patch occupancy models to real metapopulations. In: *Ecology, Genetics, and Evolution of Metapopulations*, pp. 105–132.
- Forstmeier, W., 2002. Benefits of early arrival at breeding grounds vary between males. *J. Anim. Ecol.* 71, 1–9.
- Fortin, M.-J., Dale, M.R.T., 2005. Spatial Analysis, A Guide for Ecologists. Cambridge University Press, New York.
- Fretwell, S.D., Lucas, H.L., 1970. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheor.* 19, 16–36.
- Gaston, K.J., Blackburn, T.M., 2002. Large-scale dynamics in colonization and extinction for breeding birds in Britain. *J. Anim. Ecol.* 71, 390–399.
- Groom, J.D., Grubb Jr., T.C., 2006. Patch colonization dynamics in Carolina chickadees (*Parus carolinensis*) in a fragmented landscape: a manipulative study. *Auk* 123, 1149–1160.
- Hanski, I., 1999. *Metapopulation Ecology*. Oxford University Press, New York.
- Hastings, A., 2003. Metapopulation persistence with age-dependent disturbance or succession. *Science* 301, 1525–1526.
- Hodgson, J.A., Moilanen, A., Bourn, M.A.D., Bulman, C.R., Thomas, C.D., 2009. Managing successional species: modeling the dependence of heath fritillary populations on the spatial distribution of woodland management. *Biol. Conserv.* 142, 2743–2751.
- Johnson, M.P., 2000. The influence of patch demographics on metapopulations, with particular reference to successional landscapes. *Oikos* 88, 67–74.
- Johst, K., Brandl, R., Eber, S., 2002. Metapopulation persistence in dynamic landscape: the role of dispersal distance. *Oikos* 98, 263–270.
- Kashian, D.M., Barnes, B.V., 2000. Landscape influence on the spatial and temporal distribution of the Kirtland's Warbler at the Bald Hill burn, northern Lower Michigan, USA. *Can. J. Forest Res.* 30, 1895–1904.
- Kashian, D.M., Barnes, B., Walker, W.S., 2003. Landscape ecosystems of northern Lower Michigan and the occurrence and management of the Kirtland's Warbler. *Forest Sci.* 49, 140–159.
- Kepler, C.B., Irvine, G.W., DeCapita, M.E., Weinrich, J., 1996. The conservation management of Kirtland's Warbler *Dendroica kirtlandii*. *Bird Conserv. Int.* 6, 11–22.
- Keymer, J.E., Marquet, P.A., Velasco-Hernandez, J.X., Levin, S.A., 2000. Extinction thresholds and metapopulation persistence in dynamic landscapes. *Am. Nat.* 156, 478–494.
- Levins, R., 1969. Some demographic and genetic consequences of environmental heterogeneity of biological control. *Bull. Entomol. Soc. Am.* 15, 237–240.
- Marra, P.P., Hobson, K.A., Holmes, R.T., 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282, 1884–1886.
- Matthiopoulos, J., Harwood, J., Thomas, L., 2005. Metapopulation consequences of site fidelity for colonially breeding mammals and birds. *J. Anim. Ecol.* 74, 716–727.
- Matthysen, E., Currie, D., 1996. Habitat fragmentation reduces disperser success in juvenile nuthatches *Sitta europaea*: evidence from patterns of territory establishment. *Ecography* 19, 67–72.

- Matthysen, E., Andriansen, F., Dhondt, A.A., 1995. Dispersal distances of nuthatches, *Sitta europaea*, in a highly fragmented forest habitat. *Oikos* 72, 375–381.
- Morris, D.W., 2003. Toward an ecological synthesis: a case for habitat selection. *Oecologia* 136, 1–13.
- Muller, K.L., Stamps, J.A., Krishnan, V.V., Willits, N.H., 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). *Am. Nat.* 150, 650–661.
- Ovaskainen, O., Hanski, I., 2004. Metapopulation dynamics in highly fragmented landscapes. In: Hanski, I., Gaggiotti, O.E., (Eds.), *Ecology, Genetics, and Evolution of Metapopulations*, pp. 73–103.
- Pellet, J., Fleishman, E., Dobkin, D.S., Gander, A., Murphy, D.D., 2007. An empirical evaluation of the area and isolation paradigm of metapopulation dynamics. *Biol. Conserv.* 136, 483–495.
- Petrucha, M.E., Carlson, E., 2007. The 2007 Kirtland's Warbler census. *Michigan Birds and Natural History*, vol. 15. Michigan Audubon Soc. pp. 1–6.
- Pickett, S.T.A., White, P.S., 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, San Diego, California. 472 p.
- Probst, J.R., 1986. A review of factors limiting the Kirtland's Warbler on its breeding grounds. *Am. Midl. Nat.* 116, 87–100.
- Probst, J.R., 1988. Kirtland's Warbler breeding biology and habitat management. In: Hoekstra, J.W., Capp, J. (Eds.), *Integrating Forest Management for Wildlife and Fish*. USDA General Technical Report NC-122. US North Central Research Station, St. Paul, Minnesota, pp. 28–35.
- Probst, J.R., DonnerWright, D.M., 2003. Fire and shade effects on ground cover structure in Kirtland's Warbler habitat. *Am. Midl. Nat.* 149, 320–334.
- Probst, J.R., Weinrich, J., 1993. Relating Kirtland's Warbler population to changing landscape composition and structure. *Landscape Ecol.* 8, 257–271.
- Probst, J.R., Donner, D.M., Bocetti, C.I., Sjogren, S., 2003. Population increase in Kirtland's Warbler and summer range expansion to Wisconsin and Michigan's Upper Peninsula, USA. *Oryx* 37, 365–373.
- Probst, J.R., Donner, D.M., Worland, M., Weinrich, J., Huber, P., Ennis, K.R., 2005. Comparing census methods for the endangered Kirtland's Warbler. *J. Field Ornithol.* 76, 50–60.
- Pulliam, H.R., Danielson, B.J., 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *Am. Nat.* 132, S50–S66.
- Ryel, L.A., 1981. The fourth decennial census of Kirtland's Warbler, 1981. *Jack-Pine Warbler* 59, 93–95.
- Scott, T.A., Wehtje, W., Wehtje, M., 2001. The need for strategic planning in passive restoration of wildlife populations. *Restor. Ecol.* 9, 262–271.
- Scott, M.S., Heglund, P.J., Morrison, M.L., Haufler, J.B., Raphael, M.G., Wall, W.A., Samson, F.B., 2002. *Predicting Species Occurrences: Issues of Accuracy and Scale*. Island Press, Washington, DC.
- Sirami, C., Brotons, L., Martin, J., 2008. Spatial extent of bird species response to landscape changes: colonization/extinction dynamics at the community-level in two contrasting habitats. *Ecography* 31, 509–518.
- Smith, A.T., Peacock, M.M., 1990. Conspecific attraction and the determination of metapopulation colonization rates. *Conserv. Biol.* 4, 320–323.
- Thompson III, F.R., DeGraaf, R.M., 2001. Conservation approaches for woody, early successional communities in the eastern United States. *Wildlife Soc. Bull.* 29, 483–494.
- Tryjanowski, P., Sparks, T.H., 2001. Is the detection of the first arrival date of migrating birds influenced by population size? A case study of the red-back shrike *Lanius collurio*. *Int. J. Biometeorol.* 45, 217–219.
- Villard, M., Merriam, G., Maurer, B.A., 1995. Dynamics in subdivided populations of neotropical migratory birds in a fragmented temperate forest. *Ecology* 76, 27–40.
- Walker, W.S., Barnes, B.V., Kashian, D.M., 2003. Landscape ecosystems of the Mack Lake Burn, northern Lower Michigan, and the occurrence of the Kirtland's Warbler. *Forest Sci.* 49, 119–139.
- Walkinshaw, L.H., 1983. *Kirtland's Warbler: The Natural History of An Endangered Species*. Cranbrook Institute of Science, Michigan.
- Wilcox, C., Cairns, B.J., Possingham, H.P., 2006. The role of habitat disturbance and recovery in metapopulation persistence. *Ecology* 87, 855–863.
- Wood, S., 2006. *Generalized Additive Models: An Introduction with R*. Chapman and Hall/CRC, Florida.