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Using a full annual cycle model to evaluate long-term population viability of the conservation-reliant Kirtland's warbler after successful recovery

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Summary

1. Long-term management planning for conservation-reliant migratory songbirds is particularly challenging because habitat quality in different stages and geographic locations of the annual cycle can have direct and carry-over effects that influence the population dynamics. The Neotropical migratory songbird Kirtland's warbler *Setophaga kirtlandii* (Baird 1852) is listed as endangered under the U.S. Endangered Species Act and Near Threatened under the IUCN Red List. This conservation-reliant species is being considered for U.S. federal delisting because the species has surpassed the designated 1000 breeding pairs recovery threshold since 2001.

2. To help inform the delisting decision and long-term management efforts, we developed a population simulation model for the Kirtland's warbler that incorporated both breeding and wintering grounds habitat dynamics, and projected population viability based on current environmental conditions and potential future management scenarios. Future management scenarios included the continuation of current management conditions, reduced productivity and carrying capacity due to the changes in habitat suitability from the creation of experimental jack pine *Pinus banksiana* (Lamb.) plantations, and reduced productivity from alteration of the brown-headed cowbird *Molothrus ater* (Boddaert 1783) removal programme.

3. Linking wintering grounds precipitation to productivity improved the accuracy of the model for replicating past observed population dynamics. Our future simulations indicate that the Kirtland's warbler population is stable under two potential future management scenarios: (i) continuation of current management practices and (ii) spatially restricting cowbird removal to the core breeding area, assuming that cowbirds reduce productivity in the remaining patches by ≤41%. The additional future management scenarios we assessed resulted in population declines.

4. *Synthesis and applications*. Our study indicates that the Kirtland's warbler population is stable under current management conditions and that the jack pine plantation and cowbird removal programmes continue to be necessary for the long-term persistence of the species. This study represents one of the first attempts to incorporate full annual cycle dynamics into a population viability analysis for a migratory bird, and our results indicate that incorporating wintering grounds dynamics improved the model performance.

Key-words: Bahamas, bird, brown-headed cowbird *Molothrus ater*, full annual cycle, jack pine, Michigan, migratory, *Setophaga kirtlandii*, simulation model

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Introduction

Recovery of threatened and endangered animals often requires substantial management efforts to create and maintain environmental conditions suitable for population growth and subsequent stability (Soulé & Terborgh 1999; Felix *et al.* 2004). While carrying capacity is limited by quantity and quality of habitat, actual population size and stability is influenced by spatial and temporal interactions among abiotic and biotic factors (e.g. Akçakaya & Atwood 1997). These interactions are particularly complex for migratory birds, where environmental conditions experienced across the annual cycle can impact the population dynamics directly and through carry-over effects (e.g. Rockwell, Bocetti & Marra 2012).

Absent a full understanding of spatial and temporal dynamics, and a lack of large-scale experimental management actions, simulation models can be used to complement existing species information to improve our understanding of species–habitat relationships, investigate the drivers of population growth and assess the population viability under different environmental and management conditions (Akçakaya *et al.* 2004). In this study, we used simulation modelling to improve our understanding of population dynamics and investigate the impacts of potential future population management scenarios on Kirtland's warbler *Setophaga kirtlandii* (Baird 1852), a Neotropical migratory bird species listed as endangered under the U.S. Endangered Species Act and Near Threatened under the IUCN Red List (BirdLife International 2012).

Kirtland's warblers breed almost exclusively in the northern Lower Peninsula of Michigan (USA) and winter almost exclusively in the Bahamian archipelago (Haney, Lee & Walsh-McGehee 1998). Although conservation actions through intensive habitat management and brown-headed cowbird *Molothrus ater* (Boddaert 1783; hereafter cowbird) removal resulted in successful recovery (see Appendix S1, Supporting Information), continued persistence will likely require continued active management to maintain the population stability [i.e. the species is conservation-reliant (Scott *et al.* 2005)]. However, costs associated with continuing habitat management and cowbird control without federal funding if Kirtland's warbler is delisted are a major challenge for long-term management (Bocetti, Goble & Scott 2012). Thus, an evaluation of how management changes could impact population viability is needed.

We conducted a spatially explicit population viability analysis (PVA) for the Kirtland's warbler using a full annual cycle approach that included habitat quantity and quality on the breeding grounds and habitat quality on the wintering grounds (using precipitation as a proxy). We did not consider habitat quantity on the wintering grounds because Kirtland's Warbler density appears to be principally associated with food availability, which varies spatially and temporally due to the changes in precipitation (Wunderle *et al.* 2014). Our objectives were to assess the long-term population viability under current management conditions compared to potential future management conditions, while accounting for the influence of environmental variability. Potential future management scenarios included the modifications to habitat creation (i.e. jack pine *Pinus banksiana* [Lamb.] plantations) and adult cowbird removal efforts through trapping.

Managers are considering creating experimental jack pine plantations for up to 25% of future created habitat (Michigan Department of Natural Resources, U.S. Fish and Wildlife Service & U.S. Forest Service, unpublished report). The goal of experimental plantations is to test approaches for reducing planting costs and increasing timber value (e.g. reduced tree density and changes in habitat configuration), thus making the plantation programme more cost-effective. Because current planting prescriptions are designed to maximize the habitat quality, proposed modifications will likely negatively impact both the density of males and pairing success, thus affecting carrying capacity and productivity (Probst & Hayes 1987; Bocetti 1994). Reduced intensity of cowbird removal is a potential future management scenario due to the high annual cost for the programme (i.e. ca. $100 000; C. Mensing, U.S. Fish and Wildlife Service, pers. comm.). Brood parasitism by cowbirds reduces Kirtland's warbler fledgling production (Mayfield 1960, 1961; Walkinshaw 1983), and thus, reduced cowbird removal efforts would likely negatively impact Kirtland's warbler productivity.

We designed simulations to project the influence of each of these management scenarios on population trends, and thus to inform managers of possible outcomes of these management actions prior to initiation. In addition, the availability of long-term and range-wide monitoring data for Kirtland's warbler allowed us to test the importance of incorporating wintering grounds habitat dynamics in the population dynamics model. This study represents one of the first attempts to incorporate the full annual cycle dynamics into a PVA model for a migratory songbird (Hostetler, Sillett & Marra 2015), and thus provides insights that are relevant to future modelling studies for a wide range of migratory species.

Materials and methods

STUDY AREA

Our study area consisted of designated essential breeding habitat on federal and state lands in the Lower Peninsula (LP) of Michigan, USA (Byelich *et al.* 1985), and federal lands managed for Kirtland's warbler in the Upper Peninsula (UP) of Michigan (Fig. 1). Additional currently occupied breeding areas [i.e. Wisconsin (Anich *et al.* 2011), Ontario (Richard 2008), state lands in the Michigan UP, private lands] were not included because these lands are not managed specifically for Kirtland's warbler and long-term habitat availability is unpredictable. Thus, our estimated available breeding habitat was slightly conservative with

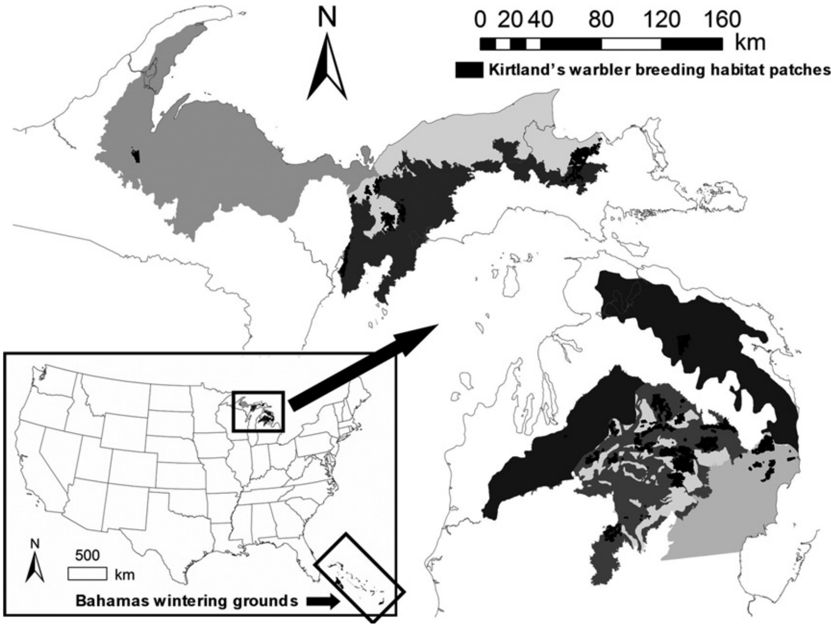

Fig. 1. Patches of Kirtland's warbler (*Setophaga kirtlandii*) breeding habitat used for assessing the long-term population viability given current environmental and potential future management conditions. The eight habitat regions (grey shades) in the northern Lower Peninsula (LP) and Upper Peninsula (UP) of Michigan, USA, contained different estimated growth rates for jack pine (*Pinus banksiana*; see Appendix S3 in supporting information).

respect to range-wide breeding patch occupancy, but realistic given expected long-term habitat availability.

MODELLING APPROACH

We developed a model structure that allowed us to link population demographics with spatially and temporally dynamic breeding habitat suitability, and temporally dynamic wintering grounds habitat quality (see Appendix S2 and Fig. S1), using the PVA program RAMAS GIS 5.0 (Akçakaya *et al.* 2004). The program uses a stage-based Lefkovitch matrix to project population dynamics (Caswell 2001). The matrix can be made spatially dynamic by linking stage values to equations derived from spatial layers and can be made temporally dynamic by using a time series of spatial layers.

Habitat Suitability

To estimate the changes in breeding habitat suitability, we identified suitable jack pine stands between 1979 and 2013 (LP) and 1999 and 2013 (UP) using federal and state habitat management programme records that included stand year-of-origin and jack pine habitat regeneration type (i.e. clear-cut and natural regeneration, plantation, wildfire). Although the UP now supports over 30 males annually (S. Sjogren, U.S. Forest Service, unpublished data), only 63 males were documented in the UP between 1978 and 1998 combined (Probst *et al.* 2003), and thus, we did not consider this area to be influential breeding habitat at the population level until 1999. The habitat regeneration types represent a gradient of tree densities, with natural regeneration stands typically having low tree densities (<2200 trees ha^{-1}) and plantation/wildfire stands typically having high tree densities (2500 to >7500 trees ha^{-1}; Probst & Weinrich 1993). Previous studies found that these habitat quality differences influenced the density and pairing success of Kirtland's warblers (Probst 1986; Probst & Hayes 1987; Bocetti 1994).

Previous studies using stand history data defined Kirtland's warbler habitat suitability based on stand age (Donner, Ribic & Probst 2009, 2010). However, jack pine growth rates are known to differ latitudinally and longitudinally due to the variations in temperature, precipitation and soil types (e.g. Kashian, Barnes & Walker 2003). Thus, we translated known stand ages across the study area to estimated stand heights to more accurately capture patch-specific habitat suitability over time (see Figs S2–S4). We created habitat suitability models based on a combination of habitat management regeneration categories and jack pine stand height. For each year, habitat was classified into the following suitability categories: unsuitable (0 – trees too short or too tall), low suitability (1 – short and tall natural regeneration), moderate suitability (2 – short and tall plantation or wildfire; mid-height natural regeneration) and high suitability (3 – mid-height plantation or wildfire; see Appendix S3).

To estimate the temporal changes in wintering grounds habitat suitability, we used precipitation as a proxy for habitat quality. Previous research found that total March precipitation recorded at the Nassau National Oceanic and Atmospheric Administration (NOAA) weather station in the Bahamas was correlated with the subsequent fledgling production on the breeding grounds and annual survivorship of Kirtland's warblers (Rockwell, Bocetti & Marra 2012; Rockwell 2013). Further, Wunderle *et al.* (2014) found that precipitation on the wintering grounds was correlated with food abundance and body condition of Kirtland's warblers, indicating that wintering grounds precipitation is a good proxy for temporal variation in wintering grounds habitat quality, and through carry-over effects (i.e. effects on body condition and/or timing of arrival on the breeding grounds), productivity the following spring (Rockwell, Bocetti & Marra 2012). We obtained the total March precipitation values for 1979–2013 at the Nassau NOAA station and used these values to create additional habitat layers, allowing us to link the non-spatial wintering grounds data to our stage matrix.

Populations, Dispersal and Carrying Capacity

Based on the minimum stand size occupied historically (Probst 1988; Donner, Ribic & Probst 2010), we used 32-ha (566 m × 566 m) cells in which we classified the breeding habitat suitability annually. We used a 15-cell search area to group suitable cells into large habitat patches that defined populations in the model. The number, size and location of patches changed over time as the distribution of suitable habitat changed, but they generally conformed to the locations of Kirtland's Warbler Management Areas. Occupancy of suitable habitat patches in a given year was based on abundance the previous year, a dispersal function and patch carrying capacity.

In the model, dispersal occurs among patches rather than cells. To estimate dispersal among patches, we used a negative exponential function, with the background annual dispersal rate and mean dispersal distance estimated using interyear capture–recapture data for male Kirtland's warblers between 1986 and 2001 ($n = 534$ observations; D. Donner and C. Bocetti, unpublished data). Walkinshaw (1983) found that first-year breeding male Kirtland's warblers did not typically disperse far from their natal sites (mean = 3·3 km, range = 0–21 km, $n = 8$), and thus, we used a single dispersal function for all age classes. The estimated annual dispersal rate between patches was 0·0356, and the mean dispersal distance for birds that moved between patches was 113 km.

Habitat quality influences Kirtland's warbler density (Probst 1986). High suitability habitat in the LP currently supports ca. 0·12 males ha^{-1} (Bocetti, Donner & Mayfield 2014), and we assumed that this density was representative of carrying capacity. The assumption that the LP is currently at carrying capacity is supported by census data that found population growth in the LP stabilized in 2007 (Bocetti, Goble & Scott 2012), and colonization of peripheral habitat increased thereafter (Probst *et al.* 2003; Richard 2008; Anich *et al.* 2011). To estimate carrying capacity in moderate and low suitability habitat, we calculated the mean number of males per hectare observed in each model suitability class in the LP between 2007 and 2013, and used the proportional differences to define the carrying capacity gradient. This analysis indicated that moderate suitability habitat could support 0·05 males ha^{-1} and low suitability habitat could support 0·04 males ha^{-1} (see Fig. S5).

Density Dependence and Stochasticity

We assumed ceiling-type density dependence, which allows populations to grow exponentially until they reach carrying capacity (Akçakaya 2005). This density-dependent structure is typically used for territorial songbirds (e.g. Alldredge *et al.* 2004; Bonnot, Thompson & Millspaugh 2011), as density is largely self-regulated. Because our patches were large and estimated annual dispersal between patches was low, we did not incorporate stochasticity into our dispersal estimate. We incorporated demographic stochasticity in annual survivorship by selecting annual survival rates from a normal distribution based on the mean and standard deviation from five annual survivorship estimates for Kirtland's warbler (see Table S3). Because annual productivity was estimated based on spatially and temporally dynamic habitat suitability, we did not incorporate stochasticity for this parameter in the model.

Matrix Models

Nearly all of the empirical data available for model parameterization were based on male observations, and thus, we used a single-sex model based on male empirical data for this study. To estimate the productivity based on males, we assumed that sex ratios of young were 1 : 1, and that each male in the model had only one mate (Alldredge *et al.* 2004). Breeding habitat suitability influenced the productivity indirectly by influencing carrying capacity and directly by influencing pairing success (Probst 1986; Probst & Hayes 1987; Bocetti, Donner & Mayfield 2014). Some polygyny occurs in high suitability habitat (Radabaugh 1972; Bocetti 1994; Rockwell 2013), and we accounted for this in our pairing success gradient (see Appendix S4). We did not consider the probability of nest success based on habitat quality because nest parasitism rates are currently <1% (Rockwell 2013), and the probability of nest loss does not appear to differ based on habitat quality or stand age (Bocetti 1994).

We constructed a stage-based matrix model using a pre-breeding census:

$$\begin{bmatrix} m \times s_0 & m \times s_0 \\ s_1 & s_{2+} \end{bmatrix},$$

where m represents maternity (i.e. the number of fledglings produced per individual) and s represents stage-specific survivorship values for hatch-year (s_0) and after hatch-year (s_1, s_{2+}) individuals, respectively. To estimate maternity, we used the mean of 23 fledgling production estimates for Kirtland's warbler derived from the literature (mean = 3·58, SD = 0·75; see Table S1). Thus, the estimated mean number of fledglings in our single-sex model was 1·79. After accounting for pairing success differences based on habitat quality (i.e. 0·85–0·97; Probst 1986; Rockwell 2013), the number of male fledglings produced per male was 1·52 and 1·74 in low/moderate suitability and high suitability habitat, respectively (see Fig. S6). We used an estimated hatch-year survivorship of 0·415 (see Appendix S5 and Table S2).

Candidate Models

We developed four variations in the population model to determine whether incorporating temporal variation in wintering grounds habitat quality improved the model performance (all models incorporated the effects of breeding grounds habitat on productivity and carrying capacity). The productivity–survivorship variations included (i) a *breeding grounds-only* model, which used the mean productivity estimate and an annual survivorship distribution (i.e. no wintering grounds component; see Table S3); (ii) a *wintering grounds–survivorship* model, which incorporated a predictive wintering grounds precipitation–annual survivorship relationship; (iii) a *wintering grounds–productivity* model, which incorporated a predictive wintering grounds precipitation–productivity relationship; and (iv) a *wintering grounds–survivorship and productivity* model, which incorporated predictive relationships that linked annual survivorship and productivity to wintering grounds precipitation (Fig. 2).

The models that incorporated wintering grounds effects on survival and productivity used empirically based wintering grounds precipitation–annual survival/productivity regressions (Rockwell, Bocetti & Marra 2012; Rockwell 2013; see Fig. S7). Detailed information and data for these regressions are provided in Appendices S4 and S5. We bounded maximum annual survival by the highest empirical estimate (i.e. 0·75; Probst 1986), and maximum fledgling production by the highest empirical estimate (i.e. 2·19 male fledglings per male; Shake & Mattsson 1975).

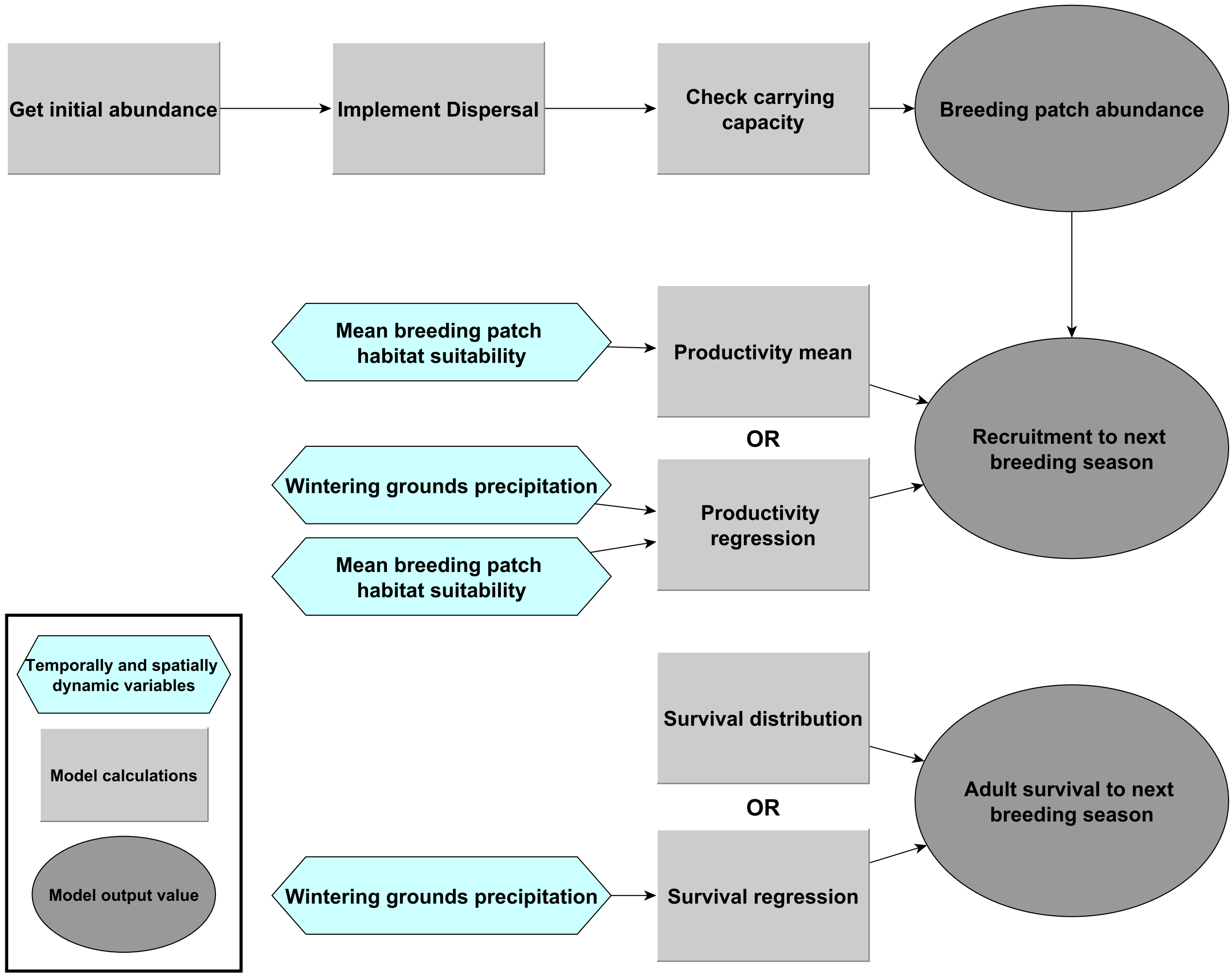

Fig. 2. Diagram showing the general model structure and model variations tested for the development of a population dynamics model for the Kirtland's warbler (*Setophaga kirtlandii*). [Colour figure can be viewed at wileyonlinelibrary.com].

MODEL EVALUATION

Habitat suitability

Since we defined habitat suitability differently than previous studies, we quantified the amount of suitable habitat over time to determine whether our definition resulted in temporal changes that were similar to previous work. In addition, we intersected male Kirtland's warbler census data collected between 1979 and 2013 with our habitat suitability layers to determine the percentage of observed individuals that were located within model-designated suitable habitat.

Candidate models

To determine which candidate model most accurately simulated Kirtland's warbler population dynamics, we ran long-term historical (1979–2013) and recent historical (2004–2013) simulations and compared model output to breeding male census results (U.S. Fish and Wildlife Service 2015). The long-term historical simulations gauged the ability of the different model variations to simulate the large observed population growth over the last three decades. The recent historical simulations were used to determine the most accurate model for future projections based on current habitat conditions. We set initial abundance to closely match the observed abundance and performed 1000 simulations for each model. To determine which simulation model output most closely matched the observed population data, we calculated the squared deviation between model output and observed data at each time step, and used the sum of the squared deviations (SSD) to rank the accuracy of the models. We used the model that most closely replicated the observed population dynamics (i.e. lowest SSD) for additional simulations.

FUTURE PROJECTIONS

We used our simulation model to project Kirtland's warbler population dynamics based on five potential future management scenarios: (i) current suitable habitat and current cowbird removal; (ii) reduced suitable habitat and current cowbird removal; (iii) current suitable habitat and reduced cowbird removal; (iv) current suitable habitat and no cowbird removal; and (v) reduced suitable habitat and reduced cowbird removal.

Evaluation of population viability with current management conditions

To project the population viability, we used a single breeding habitat year representative of recent breeding habitat availability (i.e. 2010). Thus, we assumed that average habitat suitability in our large habitat patches will remain constant over time as breeding habitat is created and expires. To estimate wintering grounds precipitation each year, we randomly selected values from a uniform distribution representing the lower 90th percentile of total March precipitation recorded at the Nassau NOAA weather station from 1994 to 2013 (0·65–6·19 cm). We removed the upper 10% of observation years for the distribution because they represented low-frequency extreme precipitation years (e.g. 21·02 cm recorded in 2001). We also note that March precipitation at this weather station was unreported for 43% of days between 1994 and 2013, and we made the assumption that no rainfall occurred on those days. We used the breeding and wintering grounds habitat suitability layers to project population dynamics for 50 years, with the simulation replicated 1000 times. To account for the possible effects of randomized precipitation selection order on the projected population trend, we conducted five independent simulations and computed the mean, minimum and maximum annual abundance for each simulation.

Evaluation of population viability with management condition changes

To estimate the impacts of reduced habitat suitability due to experimental jack pine plantations, we randomly selected 25% of the habitat cells and reduced habitat suitability by one suitability class. We simulated two possible reduced cowbird removal scenarios: (i) trapping was implemented in the core breeding area, but not in the surrounding (i.e. satellite) habitat patches in the northern LP (Fig. 3) and (ii) all trapping was eliminated. To simulate cowbird parasitism impacts, we reduced the productivity in the non-trapped habitat patches. Observations of fledgling production before and after implementing the cowbird removal programme indicate that cowbird parasitism reduced the productivity of Kirtland's warblers by 41–73% (Mayfield 1960; Shake & Mattsson 1975). We used the lower and middle values from this historical range (i.e. 41% and 57%) to model reduction in productivity due to cowbird parasitism.

We projected population dynamics with the management condition changes using the same randomized precipitation values as the current management projection, allowing a direct comparison of output among the simulations. To estimate the long-term population growth, we computed the annual growth rates from each simulation ($\lambda = N_{t+1}/N_t$). For each scenario, we calculated the geometric mean and 95% confidence interval for λ (based on a *t*-distribution; Stevens 2009).

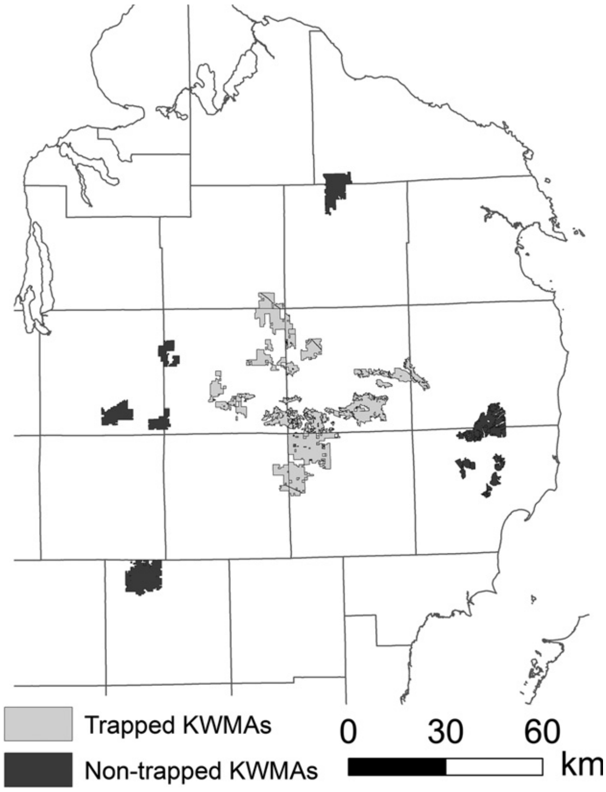

Fig. 3. Potential scenario for future management of brown-headed cowbirds (*Molothrus ater*) in Kirtland's Warbler Management Areas (KWMAs). KWMAs were specified as trapped or non-trapped to assess the impacts of spatially restricted removal on Kirtland's warbler (*Setophaga kirtlandii*) abundance. In this scenario, we assumed that trapping would continue in the core breeding area, but not in the surrounding KWMAs in the northern Lower Peninsula (LP) of Michigan, USA.

Results

MODEL EVALUATION

Based on our habitat suitability model, the total amount of suitable breeding habitat ranged from 9792 ha in 1979 to 26 272 ha in 2001 (Fig. 4a). Total carrying capacity in the model increased from a low of 668 males in 1981 to a high of 1878 males in 2001, with a mean carrying capacity of 1644 males between 2004 and 2013 (range = 1513–1776). This temporal pattern of suitable habitat was similar to previously reported suitable habitat estimates, including a large increase in the mid-late 1980s and mid-late 1990s and a slight decrease after 2001. Of the 29 767 males observed during the Kirtland's warbler male censuses between 1979 and 2013, 26 122 (i.e. 87·8%) were located in a patch designated as a suitable breeding habitat in the model during the observation year.

All of the four productivity–survivorship models were able to simulate the long-term historical (1979–2013) Kirtland's warbler population growth (Fig. 4b). Projected growth rates were higher than the observed growth rate in the early mid-1980s, but were similar to the observed rate thereafter. The recent historical simulation (2004–2013) indicated that the *wintering grounds–productivity* model most accurately reflected recently observed population dynamics (SSD = $1{\cdot}0 \times 10^5$), followed by the *breeding grounds-only* model (SSD = $1{\cdot}2 \times 10^5$). The *wintering grounds–survivorship* (SSD = $6{\cdot}1 \times 10^5$) and *wintering grounds–survivorship and productivity* (SSD = $1{\cdot}1 \times 10^6$) models underprojected recent population levels (Fig. 5). Thus, the *wintering grounds–productivity* model was used for future projections.

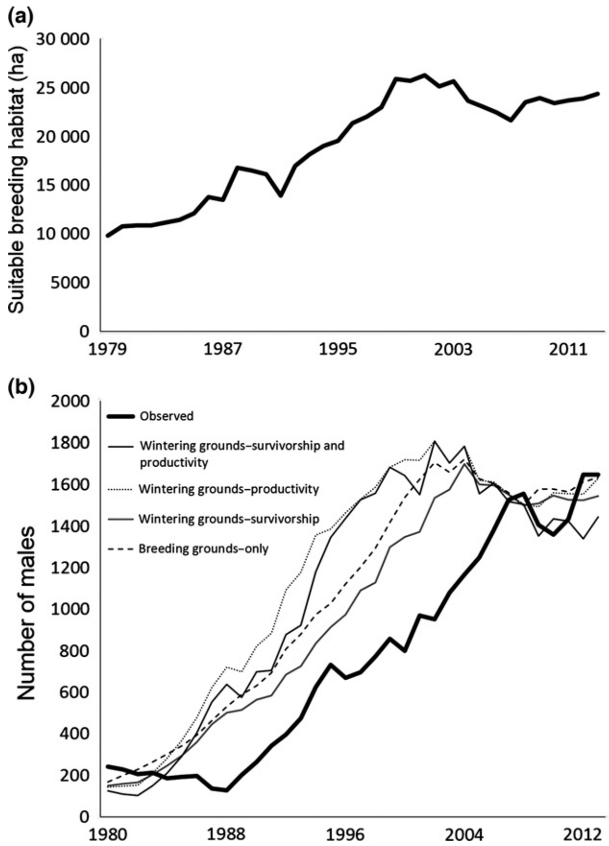

Fig. 4. Comparison of four productivity–survivorship models for simulating Kirtland's warbler (*Setophaga kirtlandii*) population dynamics from 1979 to 2013: (i) a *breeding grounds-only* model using a mean productivity estimate and an annual survivorship distribution; (ii) a *wintering grounds–survivorship* model using a predictive annual survivorship relationship and a mean productivity estimate; (iii) a *wintering grounds–productivity* model using a predictive productivity relationship and an annual survivorship distribution; and (iv) a *wintering grounds–survivorship and productivity* model using predictive relationships for both annual survivorship and productivity. Panel a shows the estimated amount of suitable breeding habitat from 1979 to 2013. Panel b shows the observed and simulated abundance of male Kirtland's warblers.

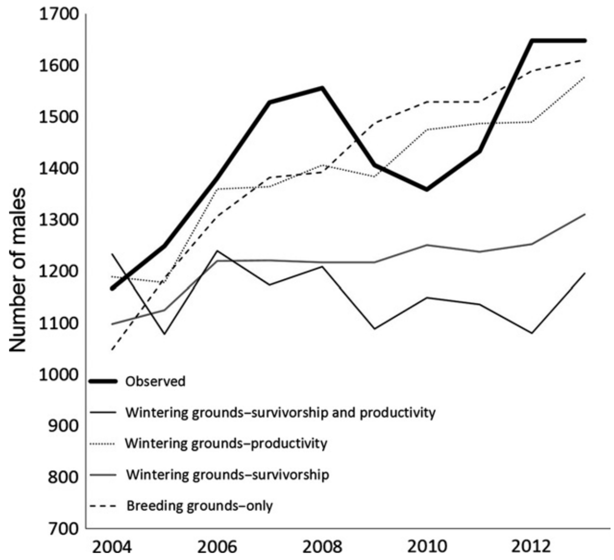

Fig. 5. Comparison of four productivity–survivorship models for simulating Kirtland's warbler (*Setophaga kirtlandii*) population dynamics from 2004 to 2013: (i) a *breeding grounds-only* model using a mean productivity estimate and an annual survivorship distribution; (ii) a *wintering grounds–survivorship* model using a predictive annual survivorship relationship and a mean productivity estimate; (iii) a *wintering grounds–productivity* model using a predictive productivity relationship and an annual survivorship distribution; and (iv) a *wintering grounds–survivorship and productivity* model using predictive relationships for both annual survivorship and productivity.

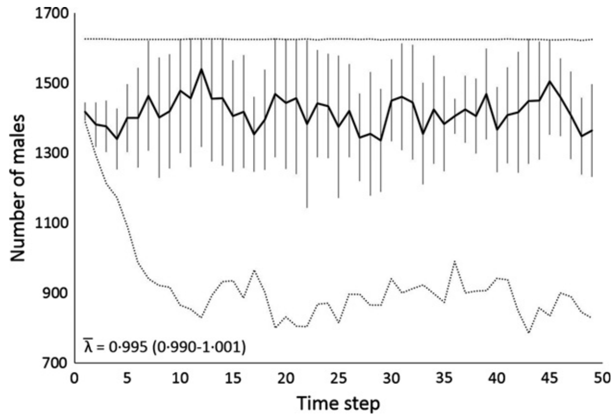

Fig. 6. Projections of future Kirtland's warbler (*Setophaga kirtlandii*) population dynamics based on current management conditions. The dark solid line shows the mean number of males per year from five independent simulations, with 1000 iterations per simulation. The grey lines show the standard deviation each year among the five simulations. The dotted lines show the maximum and minimum number of males each year across all simulations.

FUTURE PROJECTIONS

Under current management conditions, abundance of males fluctuated between 1280 and 1623 (grand mean = 1378), with a minimum simulated value of 785 and a maximum simulated value of 1626 (representing model carrying capacity). The population was stable over the 50-year simulation period ($\bar{\lambda}$ = 0·995 [0·990–1·001]; Fig. 6). For the experimental jack pine plantation management scenario, abundance of males fluctuated between 1002 and 1362 (grand mean = 1104), with a minimum simulated value of 619 and a maximum simulated value of 1365 (representing model carrying capacity with the reduced habitat suitability). The population declined slowly over the 50-year simulation period ($\bar{\lambda}$ = 0·994 [0·988–0·999]; Fig. 7).

For the scenario where cowbird removal was restricted to the core breeding area and productivity was reduced by 57% in satellite patches, abundance of males fluctuated between 1085 and 1623 (grand mean = 1256), with a minimum simulated value of 387. The population declined slowly over the 50-year simulation period ($\bar{\lambda}$ = 0·992

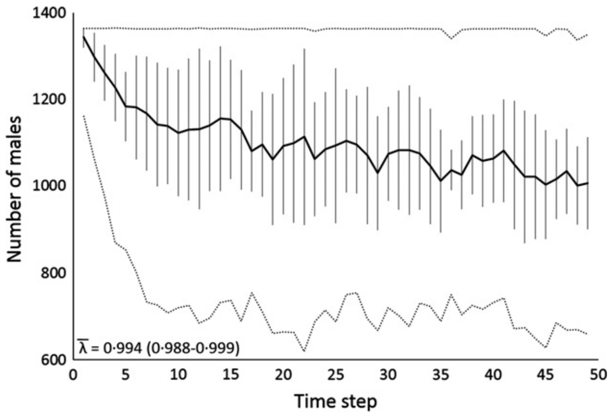

Fig. 7. Projected impacts of a 25% reduction in habitat suitability due to the implementation of experimental jack pine (*Pinus banksiana*) plantations on Kirtland's warbler (*Setophaga kirtlandii*) population dynamics. The dark solid lines show the mean number of males per year from five independent simulations, with 1000 iterations per simulation. The grey lines show the standard deviation for each year among the five simulations. The dotted lines show the maximum and minimum number of males each year across all simulations.

[0·985–0·999]; Fig. 8a). For the scenario where cowbird removal was restricted to the core breeding area and productivity was reduced by 41% in satellite patches, abundance of males fluctuated between 1226 and 1623 (grand mean = 1341), with a minimum simulated value of 569. The population was stable over the 50-year simulation period ($\bar{\lambda}$ = 0·994 [0·988–1·001]; Fig. 8b).

For the scenario where cowbirds were not removed from either the core breeding area or satellite breeding patches and productivity was reduced by 57%, abundance of males declined rapidly ($\bar{\lambda}$ = 0·900 [0·893–0·906]), with a year 50 mean of nine individuals (Fig. 8c). Extinction occurred in 3·5–13·5% of replicates among the five simulation runs. For the scenario where cowbirds were not removed from either the core breeding area or satellite breeding patches and productivity was reduced by 41%, abundance of males also declined rapidly ($\bar{\lambda}$ = 0·953 [0·946–0·961]), with a year 50 mean of 160 individuals (Fig. 8d). However, extinction did not occur within 50 years.

For the scenario where habitat suitability was reduced, cowbird removal was restricted to the core breeding area, and parasitism was 57%, abundance of males fluctuated between 803 and 1362 (grand mean = 986), with a minimum simulated value of 305. The population declined over the 50-year simulation period ($\bar{\lambda}$ = 0·989

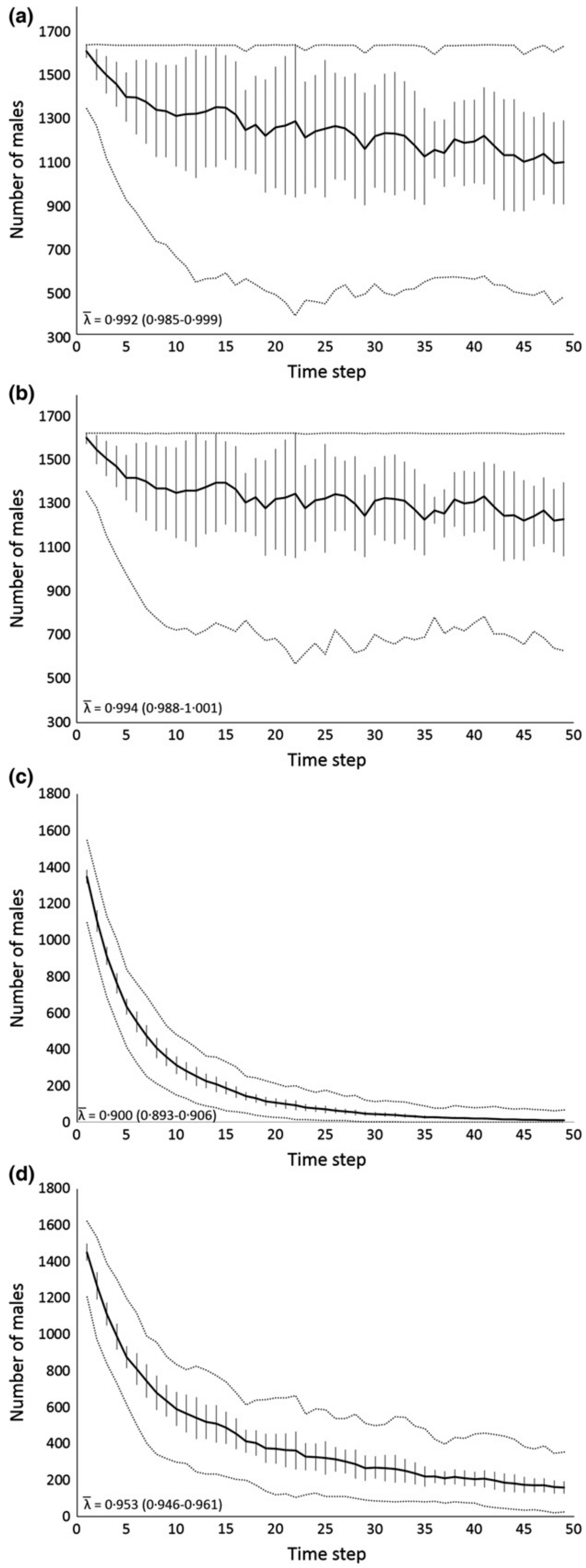

Fig. 8. Projected impacts of reduced brown-headed cowbird (*Molothrus ater*) removal on Kirtland's warbler (*Setophaga kirtlandii*) population dynamics. The dark solid lines show the mean number of males per year from five independent simulations, with 1000 iterations per simulation. The grey lines show the standard deviation for each year among the five simulations. The dotted lines show the maximum and minimum number of males each year across all simulations. Panels a and b show the results of reducing cowbird trapping to only the core breeding area, with 57% and 41% reduced productivity in patches without cowbird trapping, respectively. Panels c and d show the results of eliminating cowbird trapping from the management programme, with 57% and 41% reduced productivity in all patches, respectively.

[0·982–0·996]; Fig. 9a). For the scenario where habitat suitability was reduced, cowbird removal was restricted to the core breeding area and parasitism was 41%, abundance of males fluctuated between 931 and 1362 (grand mean = 1061), with a minimum simulated value of 451. The population declined over the 50-year simulation period ($\bar{\lambda}$ = 0·992 [0·985–0·999]; Fig. 9b).

Discussion

Our study indicates that the Kirtland's warbler population is stable under current management conditions and that the two primary management actions, maintenance of a large quantity of breeding habitat and cowbird removal, are both important for the long-term stability of the species. However, a spatial design that restricted trapping to the core breeding area was effective for preventing a rapid decline, and could be a viable management option as long as cowbird parasitism reduces the productivity by ≤41% in non-trapped patches. We found that linking wintering grounds precipitation to annual survivorship improved the model performance compared to not having that linkage. Overall, our results indicate that habitat quality on the wintering grounds influences population dynamics, congruent with the increasing literature documenting carry-over effects among stages of the annual cycle for long-distance migratory birds (e.g. Balbontin *et al.* 2009).

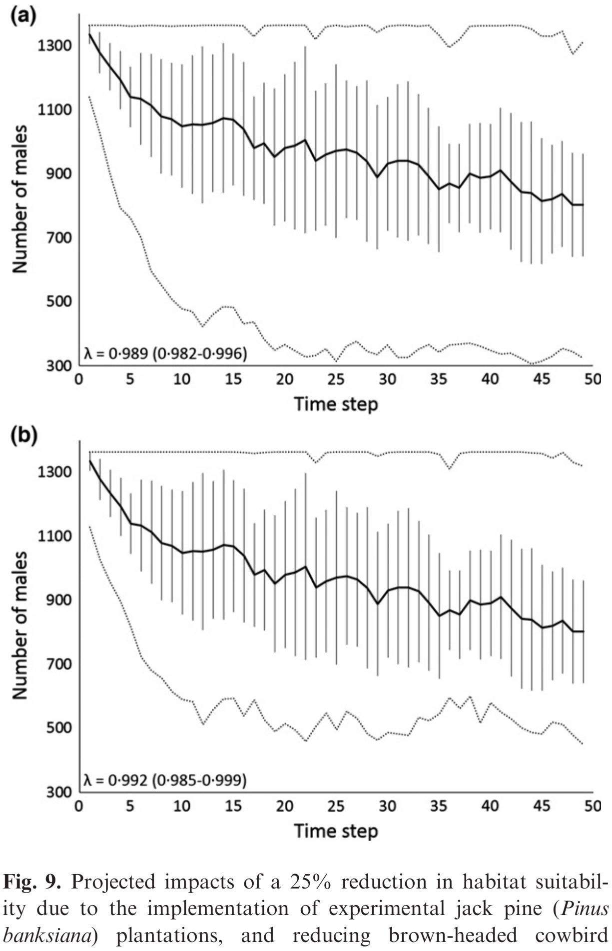

Fig. 9. Projected impacts of a 25% reduction in habitat suitability due to the implementation of experimental jack pine (*Pinus banksiana*) plantations, and reducing brown-headed cowbird (*Molothrus ater*) removal to only the core breeding area, on Kirtland's warbler (*Setophaga kirtlandii*) population dynamics. The dark solid lines show the mean number of males per year from five independent simulations, with 1000 iterations per simulation. The grey lines show the standard deviation for each year among the five simulations. The dotted lines show the maximum and minimum number of males each year across all simulations. Panels a and b show the results with 57% and 41% reduced productivity in patches without cowbird trapping, respectively.

While we had data to incorporate a number of important biological processes in our model, there are still a number of relationships that could be refined to improve model realism. First, hatch-year survivorship in our model was set as a constant. Environmental conditions likely influence first-year survivorship (Rockwell 2013; Wunderle *et al.* 2014), but predictive relationships have not been developed. Secondly, the current wintering grounds precipitation relationships only predict the differences in productivity and survivorship across a range of dryer-than-average years. Given the apparent importance of this relationship for productivity, it would be valuable to conduct additional research that spans a greater range of precipitation. Likewise, refinement of the relationship between wintering grounds precipitation and annual survivorship may enhance the predictor's performance in the simulation model. Despite these limitations, our model projection matched up well with the observed historical population trend, indicating that we captured the main processes driving Kirtland's warbler abundance. We hypothesize that the overpredicted abundance in the early mid-1980s was due to the real population taking longer to gain breeding pairs in newly suitable wildfire-generated habitat than the model population, as the total population during this period consisted of only ca. 200 males (Donner, Probst & Ribic 2008).

For this study, we assumed that cowbird parasitism rates would be similar to historic rates. However, there are substantially more Kirtland's warblers on the landscape now, and Breeding Bird Survey data indicate a 2·1–3·3% decline in brown-headed cowbirds in Michigan since 1966 (Sauer *et al.* 2014), both of which could affect parasitism rates under current conditions. We used estimates based on historical parasitism rates due to the absence of recent estimates, but acknowledge that these estimates could be high (although we did not use the highest historical estimate). We also assumed that environmental conditions would not change in future. Although this assumption is probably valid for at least the next decade, current climate change projections indicate that habitat suitability could decrease on the breeding and wintering grounds (e.g. Neelin *et al.* 2006; Iverson, Prasad & Matthews 2008; Duveneck *et al.* 2014). Thus, investigating climate change impacts on Kirtland's warbler will be our next step in helping to inform proactive management of the species over the next century.

This study represents one of the first attempts to integrate the full annual cycle dynamics into a migratory bird PVA (Hostetler, Sillett & Marra 2015). We chose to develop this model using the program RAMAS GIS due to its wide use and flexibility (e.g. Akçakaya *et al.* 2004). We found that by treating the wintering grounds data as a breeding grounds habitat layer, we were able to link non-spatial, but temporally dynamic, wintering grounds habitat quality to population demographics. This modelling strategy could be easily implemented for other species where statistical relationships have been developed that link non-breeding habitat conditions and population demographics. In addition, full annual cycle models such as this one could be enhanced by incorporating spatially explicit wintering grounds data. Given the importance of incorporating full annual cycle dynamics in population models, we encourage the further development of population models to explicitly incorporate these dynamics.

In conclusion, our study indicates that both the jack pine plantation and cowbird removal programme continue to be necessary for the long-term persistence of Kirtland's warbler. Given the comparatively large population size today compared to the 1980s, the timing is appropriate for improving our understanding of population sensitivity to manipulation of one or both programmes. However, we recommend that proposed modifications to current management be approached in an experimental framework that allows for science-based decision-making.

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Data accessibility

Model equations and values: Appendix S1, Appendix S2, Appendix S3.

Spatial ASCII layers and RAMAS GIS Code: Dryad Digital Repository http://dx.doi.org/10.5061/dryad.kk85k (Brown *et al.* 2016).

References

Akçakaya, H.R. (2005) *RAMAS GIS: Linking Spatial Data with Population Viability Analysis, User Manual for Version 5*. Applied Biomathematics, New York.

Akçakaya, H.R. & Atwood, J.L. (1997) A habitat based metapopulation model of the California gnatcatcher. *Conservation Biology*, **11**, 422–434.

Akçakaya, H.R., Burgman, M.A., Kindvall, O., Wood, C.C., Sjögren-Gulve, P., Hatfield, J.S. & McCarthy, M.A. (2004) *Species Conservation and Management: Case Studies*. Oxford University Press, New York.

Alldredge, M.W., Hatfield, J.S., Diamond, D.D. & True, C.D. (2004) Golden-cheeked warbler (*Dendroica chrysoparia*) in Texas. *Species Conservation and Management: Case Studies* (eds H.R. Akçakaya, M.A. Burgman, O. Kindvall, C.C. Wood, P. Sjögren-Gulve, J.S. Hatfield & M.A. McCarthy), pp. 371–383. Oxford University Press, New York.

Anich, N.M., Trick, J.A., Grveles, K.M. & Goyette, J.L. (2011) Characteristics of a red pine plantation occupied by Kirtland's warblers in Wisconsin. *The Wilson Journal of Ornithology*, **123**, 199–205.

Balbontin, J., Møller, A.P., Hermosell, I.G., Marzal, A., Reviriego, M. & de Lope, F. (2009) Individual responses in spring arrival date to ecological conditions during winter and migration in a migratory bird. *Journal of Animal Ecology*, **78**, 981–989.

BirdLife International (2012) *Dendroica kirtlandii*. The IUCN Red List of Threatened Species2012. e.T22721722A39850126. http://dx.doi.org/10.2305/IUCN.UK.2012-1.RLTS.T22721722A39850126.en.

Bocetti, C.I. (1994) *Density, demography, and mating success of Kirtland's warblers in managed and natural habitats*. PhD thesis, The Ohio State University, Columbus, OH.

Bocetti, C.I., Donner, D.M. & Mayfield, H.F. (2014) Kirtland's warbler (*Setophaga kirtlandii*). *The Birds of North America Online* (ed. A. Poole). Cornell Lab of Ornithology, New York. http://bna.birds.cornell.edu/bna/species/019/.

Bocetti, C.I., Goble, D.D. &, Scott, J.M. (2012) Using conservation management agreements to secure postrecovery perpetuation of conservation-reliant species: the Kirtland's warbler as a case study. *BioScience*, **62**, 874–879.

Bonnot, T.W., Thompson III, F.R. & Millspaugh, J.J. (2011) Extension of landscape-based population viability models to ecoregional scales for conservation planning. *Biological Conservation*, **144**, 2041–2053.

Brown, D.J., Ribic, C.A., Donner, D.M., Nelson, M.D., Bocetti, C.I. & Deloria-Sheffield, C.M. (2016) Data from: Using a full annual cycle model to evaluate long-term population viability of the conservation-reliant Kirtland's warbler after successful recovery. *Dryad Digital Repository*, http://dx.doi.org/10.5061/dryad.kk85k.

Byelich, J., Irvine, G.W., Johnson, N.I., Mayfield, J., DeCapita, M.E., Radtke, R.E., Jones, W.R. & Mahalak, W.J. (1985) *Updated Kirtland's Warbler Recovery Plan*. U.S. Fish and Wildlife Service, Twin Cities, MN.

Caswell, H. (2001) *Matrix Population Models: Construction, Analysis, and Interpretation*, Second edn. Sinauer Associates Inc, Sunderland, MA.

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 Ecology*, **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 Ecology and Management*, **258**, 1093–1101.

Donner, D.M., Probst, J.R. & Ribic, C.A. (2010) Patch dynamics and the timing of colonization-abandonment events by male Kirtland's warblers in an early succession habitat. *Biological Conservation*, **143**, 1159–1167.

Duveneck, M.J., Scheller, R.M., White, M.A., Handler, S.D. & Ravenscroft, C. (2014) Climate change effects on northern Great Lake (USA) forests: a case for preserving diversity. *Ecosphere*, **5**, Article 23.

Felix, A.B., Campa, H., Millenbah, K.F., Winterstein, S.R. & Moritz, W.E. (2004) Development of landscape-scale habitat-potential models for forest wildlife planning and management. *Wildlife Society Bulletin*, **32**, 795–806.

Haney, J.C., Lee, D.S. & Walsh-McGehee, M. (1998) A quantitative analysis of winter distribution and habitats of Kirtland's warblers in the Bahamas. *Condor*, **100**, 201–217.

Hostetler, J.A., Sillett, T.S. & Marra, P.P. (2015) Full-annual-cycle population models for migratory birds. *The Auk*, **132**, 433–449.

Iverson, L., Prasad, A. & Matthews, S. (2008) Modeling potential climate change impacts on the trees of the northeastern United States. *Mitigation and Adaptation Strategies for Global Change*, **13**, 487–516.

Kashian, D.M., Barnes, B.V. & Walker, W.S. (2003) Landscape ecosystems of northern Lower Michigan and the occurrence and management of the Kirtland's warbler. *Forest Science*, **49**, 140–159.

Mayfield, H. (1960) *The Kirtland's Warbler*. Cranbrook Institute of Science, Bloomfield Hills, MI.

Mayfield, H.F. (1961) Vestiges of proprietary interest in nests by the brown-headed cowbird parasitizing the Kirtland's warbler. *The Auk*, **78**, 162–166.

Neelin, J.D., Munnich, M., Su, H., Meyerson, J.E. & Holloway, C.E. (2006) Tropical drying trends in global warming models and observations. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 6110–6115.

Probst, J.R. (1986) A review of factors limiting the Kirtland's warbler on its breeding grounds. *American Midland Naturalist*, **116**, 87–100.

Probst, J.R. (1988) Kirtland's warbler breeding biology and habitat management. *Integrating Forest Management for Wildlife and Fish* (eds T.W. Hoekstra & J. Capp), pp. 28–35. U.S. Forest Service General Technical Report NC-122, St. Paul, MN.

Probst, J.R. & Hayes, J.P. (1987) Pairing success of Kirtland's warblers in marginal vs. suitable habitat. *The Auk*, **104**, 234–241.

Probst, J.R. & Weinrich, J. (1993) Relating Kirtland's warbler population to changing landscape composition and structure. *Landscape Ecology*, **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.

Radabaugh, B.E. (1972) Polygamy in the Kirtland's warbler. *Jack-Pine Warbler*, **50**, 48–52.

Richard, T. (2008) Confirmed occurrence and nesting of the Kirtland's warbler at CFB Petawawa, Ontario: a first for Canada. *Ontario Birds*, **26**, 2–15.

Rockwell, S.M. (2013) *Carry-over effects from the non-breeding season influence spring arrival dates, reproductive success, and survival in an endangered migratory bird, the Kirtland's warbler* (Setophaga kirtlandii). PhD thesis, University of Maryland, College Park, MD.

Rockwell, S.M., Bocetti, C.I. & Marra, P.P. (2012) Carry-over effects of winter climate on spring arrival date and reproductive success in an endangered migratory bird, Kirtland's warbler (*Setophaga kirtlandii*). *The Auk*, **129**, 744–752.

Sauer, J.R., Hines, J.E., Fallon, J.E., Pardieck, K.L., Ziolkowski, Jr D.J. & Link, W.A. (2014) *The North American Breeding Bird Survey, Results and Analysis 1966–2013*. Version 01.30.2015. U.S. Geological Survey, Patuxent Wildlife Research Center, Maryland. http://www.mbr-pwrc.usgs.gov/bbs/.

Scott, J.M., Goble, D.D., Wiens, J.A., Wilcove, D.S., Bean, M. & Male, T. (2005) Recovery of imperiled species under the Endangered Species Act: the need for a new approach. *Frontiers in Ecology and the Environment*, **3**, 383–389.

Shake, W.F. & Mattsson, J.P. (1975) Three years of cowbird control: an effort to save the Kirtland's warbler. *Jack-Pine Warbler*, **53**, 48–53.

Soulé, M.E. & Terborgh, J. (1999) Conserving nature at regional and continental scales – a scientific program for North America. *BioScience*, **49**, 809–817.

Stevens, M.H.H. (2009) *A Primer of Ecology with R*. Springer, New York.

U.S. Fish and Wildlife Service (2015) Kirtland's Warbler census results. http://www.fws.gov/midwest/endangered/birds/Kirtland/Kwpop.html.

Walkinshaw, L.H. (1983) *Kirtland's Warbler: The Natural History of an Endangered Species*. Cranbrook Institute of Science, Bloomfield Hills, MI.

Wunderle Jr, J.M. , Lebow, P.K., White, J.D., Currie, D. & Ewert, D.N. (2014) Sex and age differences in site fidelity, food resource tracking, and body condition of wintering Kirtland's warblers (*Setophaga kirtlandii*) in the Bahamas. *Ornithological Monographs*, **80**, 1–62.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Breeding habitat and population management.

Appendix S2. Model development.

Appendix S3. Breeding season – habitat availability, suitability, and occupancy.

Appendix S4. Breeding season – recruitment.

Appendix S5. Annual survival.

Fig. S1. Conceptual population dynamics model for Kirtland's warbler (*Setophaga kirtlandii*).

Fig. S2. Jack pine (*Pinus banksiana*) growth curves.

Fig. S3. Jack pine (*Pinus banksiana*) growth curve regions.

Fig. S4. Relationships between jack pine (*Pinus banksiana*) stand age and Kirtland's warbler (*Setophaga kirtlandii*) density.

Fig. S5. Breeding habitat suitability-carrying capacity relationship.

Fig. S6. Breeding habitat suitability-annual productivity relationship.

Fig. S7. Wintering grounds precipitation-annual survivorship relationship.

Table S1. Fledgling production estimates.

Table S2. Hatch-year annual survivorship estimates.

Table S3. After hatch-year annual survivorship estimates.

Supporting Information: Using a full annual cycle model to evaluating long-term population viability of the conservation-reliant Kirtland's warbler after successful recovery

Appendix S1: Breeding habitat and population management

Kirtland's warblers (*Setophaga kirtlandii*) breed almost exclusively in the northern Lower Peninsula (LP) of Michigan (USA) and winter almost exclusively in the Bahamian archipelago, particularly the northern and central islands (Haney, Lee & Walsh-McGehee 1998; Jones, Akresh & King 2013). This species is a habitat specialist on its breeding grounds, restricted to large stands of young, dense jack pine (*Pinus banksiana*) in glacial outwash plains containing well-drained sandy soils (Probst 1988; Probst *et al.* 2003). Ecologically, young jack pine trees provide low hanging branches that Kirtland's warblers use for concealment of their ground nests, and well-drained sandy soils reduce the probability that nests will become inundated with water during heavy rainfall events (Mayfield 1960; Probst 1988). Males establish breeding territories in jack pine-dominated patches that are typically larger than 32 ha, with tree densities greater than 2000 stems per ha, and trees ca. 5−23 years old (Walkinshaw 1983; Probst 1988; Probst & Weinrich 1993).

Kirtland's warbler breeding habitat quality is positively associated with jack pine stem density and associated canopy cover (Probst 1986; Bocetti 1994; Nelson & Buech 1996). Dense jack pine stands were historically generated naturally through large wildfires with ca. 60 year return intervals (Mayfield 1993; Cleland *et al.* 2004), but due to broad-scale fire suppression, an extensive network of jack pine plantations is currently used to maintain large amounts of suitable habitat on the landscape (Probst & Weinrich 1993; Donner, Ribic & Probst 2009). In addition, nest parasitism by the brown-headed cowbird (*Molothrus ater*; hereafter cowbird) was found to dramatically reduce Kirtland's warbler fledgling production (Mayfield 1960, 1961; Walkinshaw 1983). In response, a cowbird removal program has been implemented continuously since 1972, which substantially increased fledgling production and likely stabilized the population in the early 1980s until a large-scale habitat management program could be implemented (Kelly & DeCapita 1982; Probst 1986). In addition, the Mack Lake wildfire of 1980 (Simard *et al.* 1983) resulted in a substantial increase in suitable habitat during the late 1980s and early 1990s, providing an unforeseen recovery bridge until management activities became fully operational. These management actions (and stochastic wildfires) resulted in Kirtland's warblers recovering from ca. 200 males in 1971 to over 2000 males since 2012 (Mayfield 1972; Bocetti, Donner & Mayfield 2014). The population surpassed the minimum 1000 males required for delisting consideration in 2001 (Bocetti, Goble & Scott 2012).

Appendix S2: Model development

To identify key factors influencing dynamics in the Kirtland's warbler population, we first developed a conceptual model based on existing literature and expert knowledge (Fig. S1). This conceptual model included three process modules for simulating population dynamics: 1) a *breeding season – habitat availability, suitability, and occupancy* module for estimating annual distribution and suitability of breeding habitat, and occupancy of habitat patches (which house 'populations'); 2) a *breeding season – recruitment* module for estimating annual fledgling production in each population; and 3) an *annual survivorship* module for estimating the number of individuals that survive until the following breeding season.

Based on the conceptual model, we developed a population dynamics model to simulate annual changes in distribution and abundance of Kirtland's warblers, using the program RAMAS

GIS (Version 5.0). We linked spatially and temporally dynamic breeding habitat suitability layers to population demographics using habitat suitability functions. We also tested the ability of previously developed empirical relationships between wintering grounds precipitation and recruitment/survival (Rockwell, Bocetti & Marra 2012, Rockwell 2013) to capture long-term population dynamics by comparing model output to historical abundance data, with and without those relationships included. Below, we provide detailed methods and data that supplement the key model features presented in the manuscript.

Appendix S3: Breeding season − habitat availability, suitability, and occupancy

We created habitat suitability models based on a combination of habitat management-regeneration categories (natural regeneration or plantation/wildfire) and jack pine (*Pinus banksiana*) stand height, with management-regeneration categories being a proxy for stem density (Probst 1988). We considered jack pine stands that were subjected to low intensity prescribed burns to represent either natural regeneration or plantation/wildfire stem densities based on stand records that indicated whether or not seedling trees were subsequently planted in the stand. To translate known stand ages to estimated stand heights in the study area (northern LP and Upper Peninsula [UP] of Michigan, USA), we initially divided the study area into nine subsections using the U.S. Forest Service's Ecological Subregions, Sections, and Subsections classification system (Cleland *et al.* 2004), and compiled jack pine age-height estimates from Forest Inventory and Analysis (FIA) site tree data. We obtained 1 202 age-height estimates for the study area after removing six outliers from the data set. Jack pine ages in the FIA data set represented age at breast height (1.4 m), rather than total age of the tree. To provide total age estimates for the growth curves, we added four years to each age at breast height based on the jack pine growth literature (Longpré, Bergeron & Paré 1994; Béland & Bergeron 1996).

We grouped the six UP subsections into three growth curve regions: north-central UP (212Ra); south-central UP (212Rb, 212Rc); and west-central UP (212Sc, 212Sn, 212Sq) due to low FIA data sample sizes in the UP. We subdivided the core breeding area subsection in the LP (i.e., 212Hg) into three growth curve regions based on Kashian, Barnes & Walker (2003). Specifically, we used separate growth curves for the Grayling and Standish subdistricts (Albert 1995), with the Grayling subdistrict containing separate growth curves for outwash plains and ice contact areas (Kashian, Barnes & Walker 2003), which were spatially delineated using Farrand (1982). We used FIA data for the remaining two LP subsections. For each growth curve region based on FIA data, we computed a least squares line of best fit for the age-height estimates, with the intercept fixed at 0 (Fig. S2). For the three growth curve regions within subsection 212Hg, we used growth rates reported in Kashian, Barnes & Walker (2003), with the outwash plains growth rate estimate representing the mean of the six estimates reported in the study. For the final eight growth regions used in this study, estimated annual growth ranged from 0·2368 m to 0·3019 m (Fig. S3).

In previous studies, age of jack pine stands was used to define suitable time frames for Kirtland's warbler occupancy, with most previous research conducted in the core breeding area (i.e., Grayling Subdistrict). Probst & Weinrich (1993) stated that Kirtland's warblers use wildfire patches that are 5−23 years old, with highest densities in patches 10−17 years old. Bocetti (1994) found that years of use for plantations and wildfire patches were similar. Donner, Ribic & Probst (2010) reported that mean patch age at colonization was 9·0 (plantation) and 8·5 (wildfire), with larger patches colonized earlier. Donner, Ribic & Probst (2010) found that patches were abandoned at a mean age of 14·5 years (SD = 3·7; range 5−24 years).

Since most previous work on age suitability was conducted when abundance was much lower than it is currently, we created new age suitability definitions based on an analysis of Grayling Subdistrict plantation habitat use between 1990 and 2013. We found the mean age of colonization was 7 years, and the mean age of last use was 14 years, with 18 years being the maximum observed use of plantation stands included in the analysis (three birds were found in 18 year old stands). Further, we found that density of Kirtland's warbler use peaked at around age 10, and duration of use was similar between smaller (<80 ha) and larger (>80 ha) plantation patches for 212Hg as a whole (Fig. S4). Using these results, we bounded stand age at colonization and abandonment to define periods of low and high stand height suitability. We also set a maximum suitable height at 5 m (Probst & Weinrich 1993). These age values translated to unsuitable heights <1·2 m and >5·0 m; high suitability heights 1·7−3·3m, and low suitability heights 1·2−1·7 m and 3·3−5·0 m. Combining classes of habitat management regeneration and stand height suitability resulted in four habitat suitability classes: unsuitable (0 – trees too short or too tall), low suitability (1 – short and tall natural regeneration), moderate suitability (2 – short and tall plantation or wildfire; mid-height natural regeneration), and high suitability (3 – mid-height plantation or wildfire).

To estimate carrying capacity based on breeding habitat suitability, we used the current carrying capacity estimate for high suitability habitat (0·12 males/ha), and estimated the carrying capacity in moderate and low suitability habitat. Specifically, we calculated the mean number of males/ha observed in each model suitability class in the LP between 2007 and 2013, and used the proportional differences to define the carrying capacity gradient (Fig. S5).

Appendix S4: Breeding season – recruitment

For a non-spatial model, the matrix value for productivity represents maternity (i.e., number of fledglings produced per individual) x hatch-year survivorship (Akçakaya 2005). For a spatial model that incorporates breeding habitat suitability effects on productivity, the baseline value from the matrix is linked to a spatial layer to derive a relative productivity value. To account for non-spatial wintering grounds effects, one can link the baseline value to a regression equation that includes annual data from both a breeding grounds habitat layer and a wintering grounds habitat layer. In our study, the wintering grounds habitat layer was simply the breeding grounds habitat layer, but with each cell containing the wintering grounds precipitation value for March of that year. By setting the baseline matrix value to 1, we were able to obtain patch-level annual productivity estimates directly from the regression (i.e., 1 x regression output).

To estimate maternity in the *breeding grounds-only* model, we used the mean of 23 fledgling production estimates for Kirtland's warbler derived from the literature (Table S1). These estimates represent productivity after implementation of the cowbird removal program. For the UP, maternity estimates are currently lacking and cowbird removal does not occur. For this study, we assumed productivity was the same as the LP given the lack of maternity estimates and presumed minimal cowbird parasitism. We assumed a 1:1 sex ratio, and thus the estimated mean number of male fledglings produced per male was 1·79. We incorporated effects of habitat quality on productivity by accounting for pairing success differences between low and high suitability habitat (Probst 1986; Probst & Hayes 1987). We used 0·85 for habitat suitability values ≤ 2 based on the estimate of Probst (1986). We used 0·97 for habitat suitability value = 3 based on Rockwell (2013). The Rockwell (2013) estimate accounted for both non-paired individuals (8%), and individuals with two mates (5%). Multiplying our baseline maternity estimate (i.e., 1·79) by these pairing success estimates resulted in estimated maternity values of 1·52 and 1·74 for birds occupying low/moderate suitability and high suitability habitat, respectively.

To estimate annual productivity for the Lefkovitch matrix, we multiplied the maternity values by estimated hatch-year survivorship (i.e., 0·415). This value represents the average of the male and female hatch-year survivorship estimates reported in Bocetti, Donner & Mayfield (2014; Table S2). We note that we tested two additional hatch-year survivorship estimates based on the literature (i.e., 0·35 and 0·46), and found that we these values projections were much too low and much too high, respectively, relative to the observed abundance trend. Estimated productivity based on breeding grounds habitat suitability ranged from 0·6308 (breeding grounds habitat suitability $\leq$ 2) to 0·7221 (breeding grounds habitat suitability = 3). We used a linear regression to predict productivity based on average patch habitat suitability values (Figure S6).

For the models that incorporated wintering grounds effects (i.e., the *wintering grounds-productivity* and *wintering grounds-survivorship and productivity* models), our predictive productivity equation used estimates from an empirical study that linked March precipitation measured at the National Oceanic and Atmospheric Administration (NOAA) station in Nassau to subsequent fledgling production on the breeding grounds during the same calendar year (Rockwell, Bocetti & Marra 2012). We discovered a 1 cm precipitation discrepancy between the current NOAA records and those used by Rockwell, Bocetti & Marra (2012) for one of the years (i.e., 2007). Thus, we used a slightly different predictive equation for this study.

To allow both breeding grounds habitat suitability and wintering grounds precipitation to predict productivity, our equation included two predictive components. The first component estimated the baseline productivity based on breeding grounds habitat suitability. To obtain this estimate, we first transformed the wintering grounds precipitation-maternity equation to a wintering grounds-productivity equation by multiplying maternity by hatch year survivorship. The intercept of this equation (i.e., 0·4612) represented the baseline number of new males produced per male each year. We then multiplied the intercept by the pairing success estimates for low/moderate suitability (0·85) and high suitability (0·97) breeding habitat. This resulted in baseline productivity values of 0·3920 and 0·4474 for birds occupying low/moderate suitability and high suitability habitat, respectively. As with the *breeding-grounds only* model, we used a regression equation to estimate baseline productivity values from average patch habitat suitability: Baseline productivity = 0·2813 + (0·0553 x [Habitat Suitability]).

For the second component of the equation, we used the slope of the wintering grounds precipitation-productivity equation to estimate the number of new males produced above the baseline per cm of precipitation: Additional productivity = 0·0697 x [precipitation (cm)]. Combining the influence of breeding and wintering grounds habitat suitability on annual productivity: Productivity = (0·2813 + (0·0553 x [Habitat Suitability])) + (0·0697 x [precipitation (cm)]). Because there is no upper bound to this equation, we bounded maximum fledgling production by the largest empirical estimate (i.e., 4·39 fledglings per male; Shake & Mattsson 1975): Maximum productivity = (4·39/2) x 0·415 = 0·9109.

Appendix S5: Annual survival

The *breeding grounds-only* model used the mean and standard deviation from five annual survivorship estimates for Kirtland's warbler derived from the literature (mean = 0·67, SD = 0·07; Table S3). The *wintering grounds-survivorship* and *wintering grounds-survivorship and* *productivity* models used an empirically-based wintering grounds precipitation-annual survival regression (Rockwell 2013; Figure S7). We bounded maximum annual survival by the largest empirical estimate (i.e., 0·75; Probst 1986).

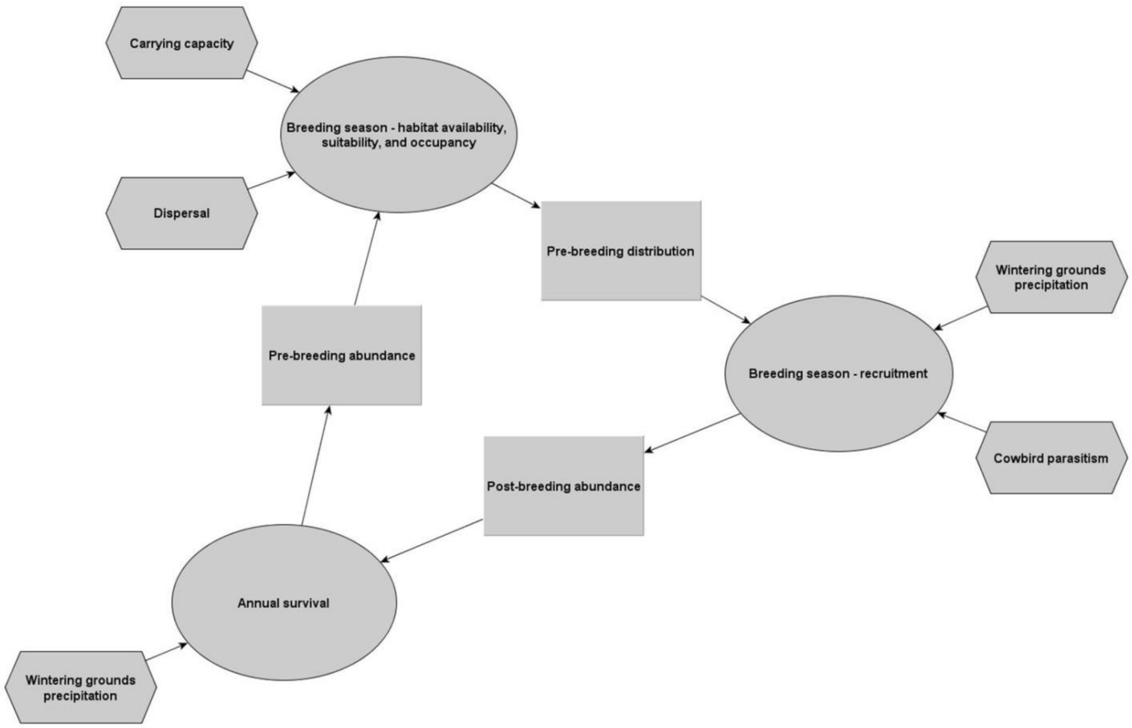

Fig. S1. Conceptual population dynamics model for investigating population viability of the Kirtland's warbler (*Setophaga kirtlandii*) under future environmental and management conditions. Ovals represent modules where information is processed, hexagons represent dynamic input factors that influence process module output, and rectangles represent information output.

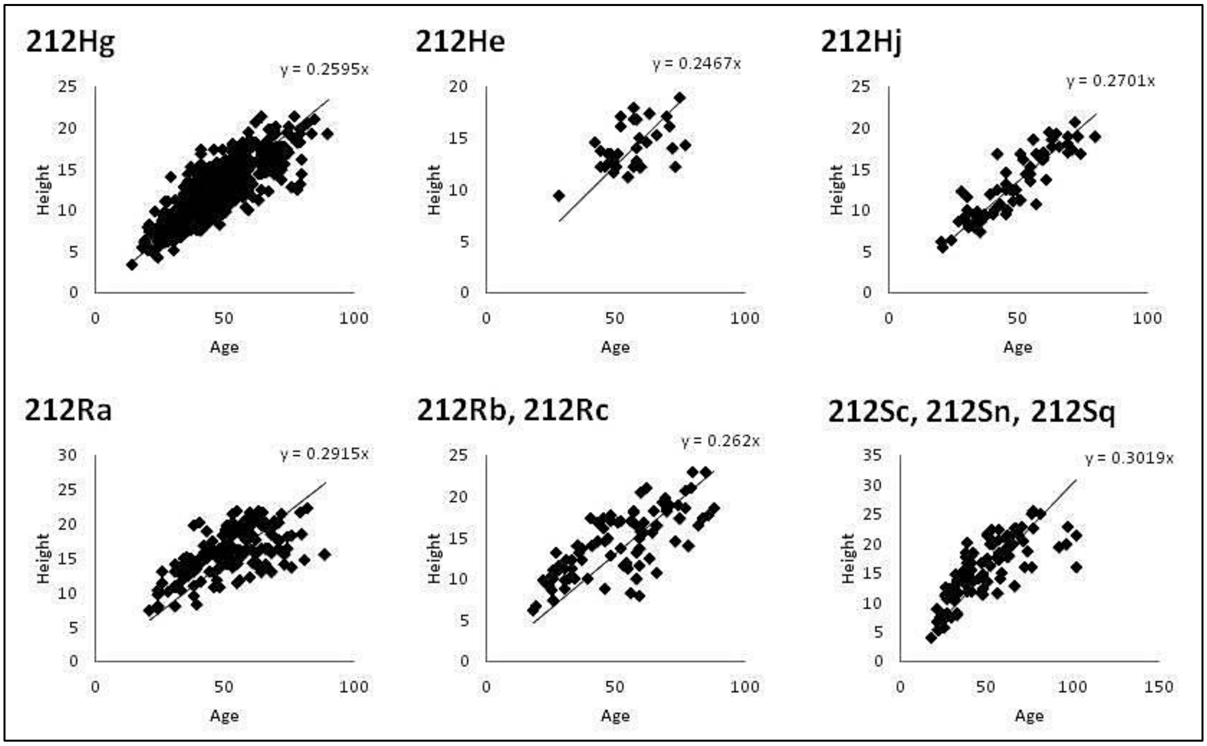

Fig. S2. Jack pine (*Pinus taeda*) growth curves for 6 ecological subsections/groups in Michigan based on FIA plot data.

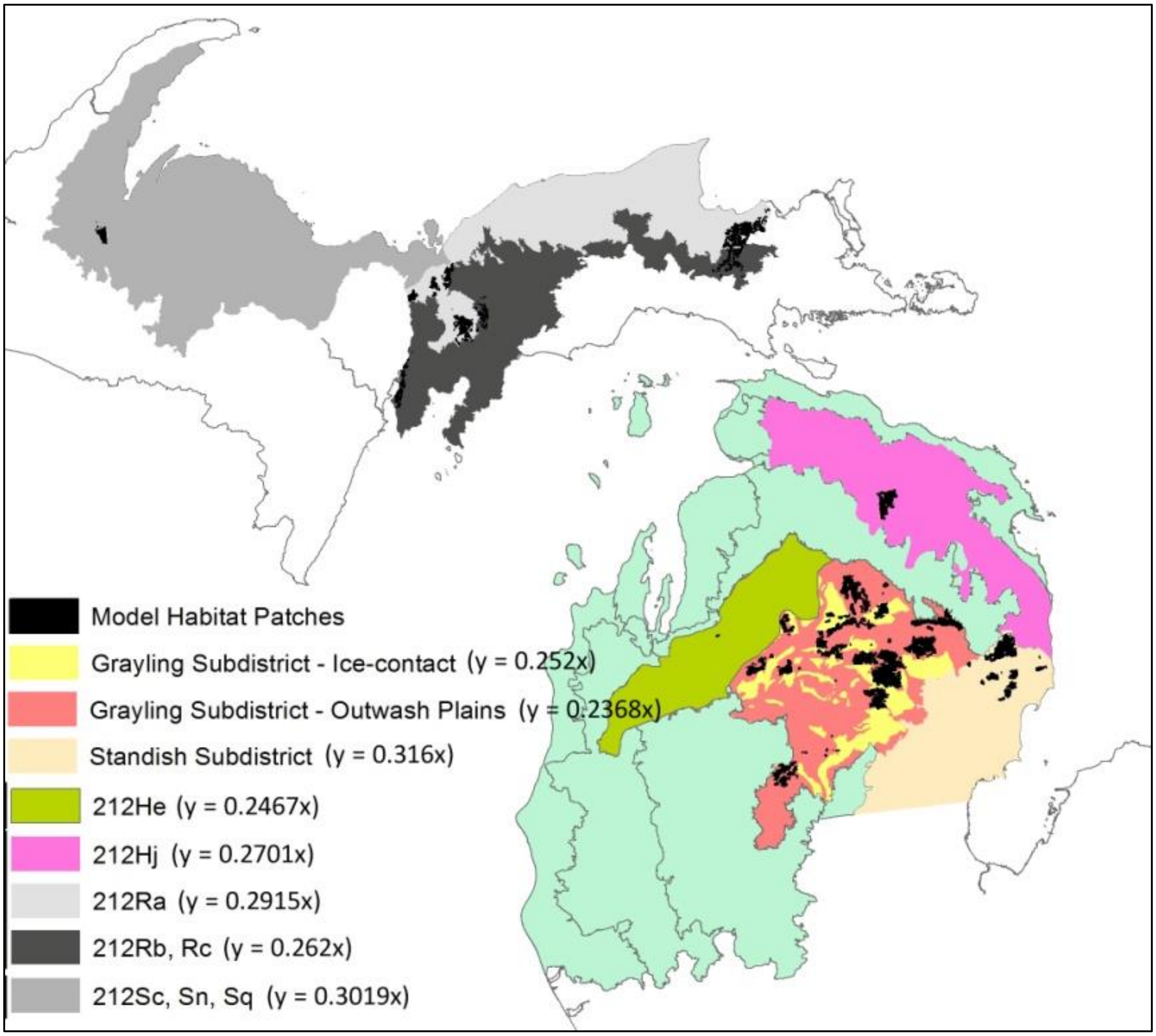

Fig. S3. Jack pine growth curve regions used to translate known stand ages to estimated stand heights. Growth rate models are shown next to each region name. The black patches represent Kirtland's warbler (*Setophaga kirtlandii*) breeding habitat.

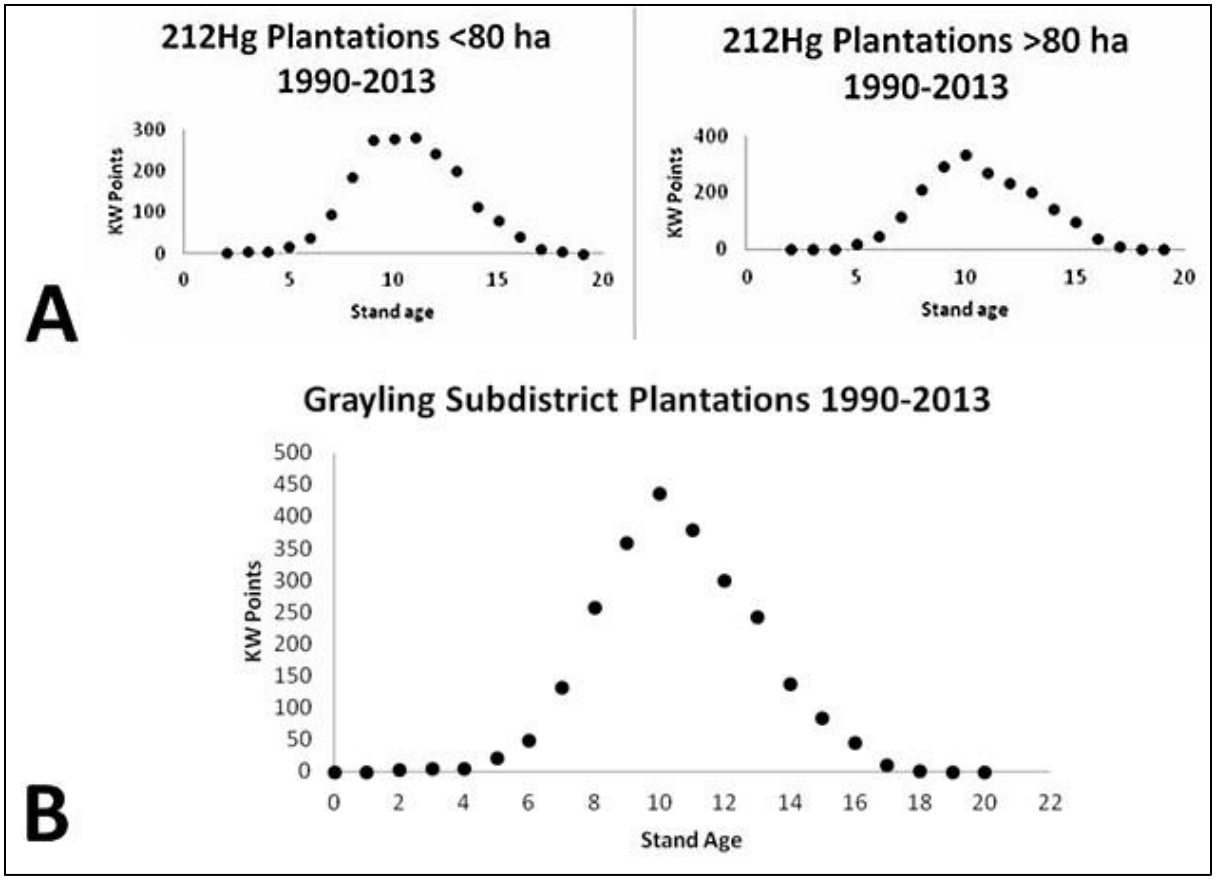

Fig. S4. Panel A shows the number of male Kirtland's Warblers (*Setophaga kirtlandii*) documented between 1990 and 2013 with respect to plantation stand age in ecological subsection 212Hg. Panel B shows the density of male Kirtland's Warblers between 1990 and 2013 with respect to plantation stand age in the Grayling Subdistrict. Only stands established and abandoned during this time frame were included in the analyses.

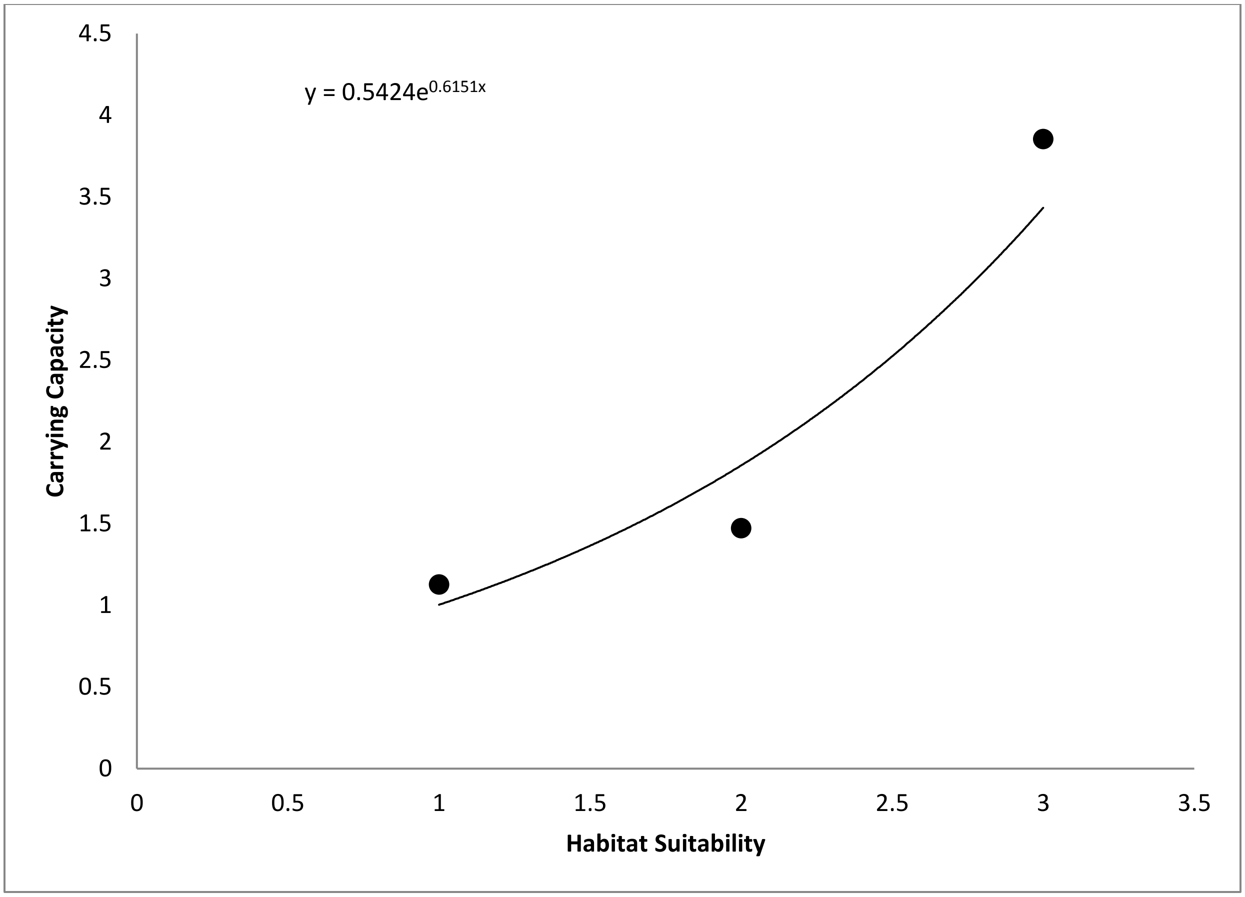

Fig. S5. Kirtland's warbler (*Setophaga kirtlandii*) breeding habitat suitability-carrying capacity equation. Carrying capacity is shown as number of males per 32 ha (the size of habitat cells).

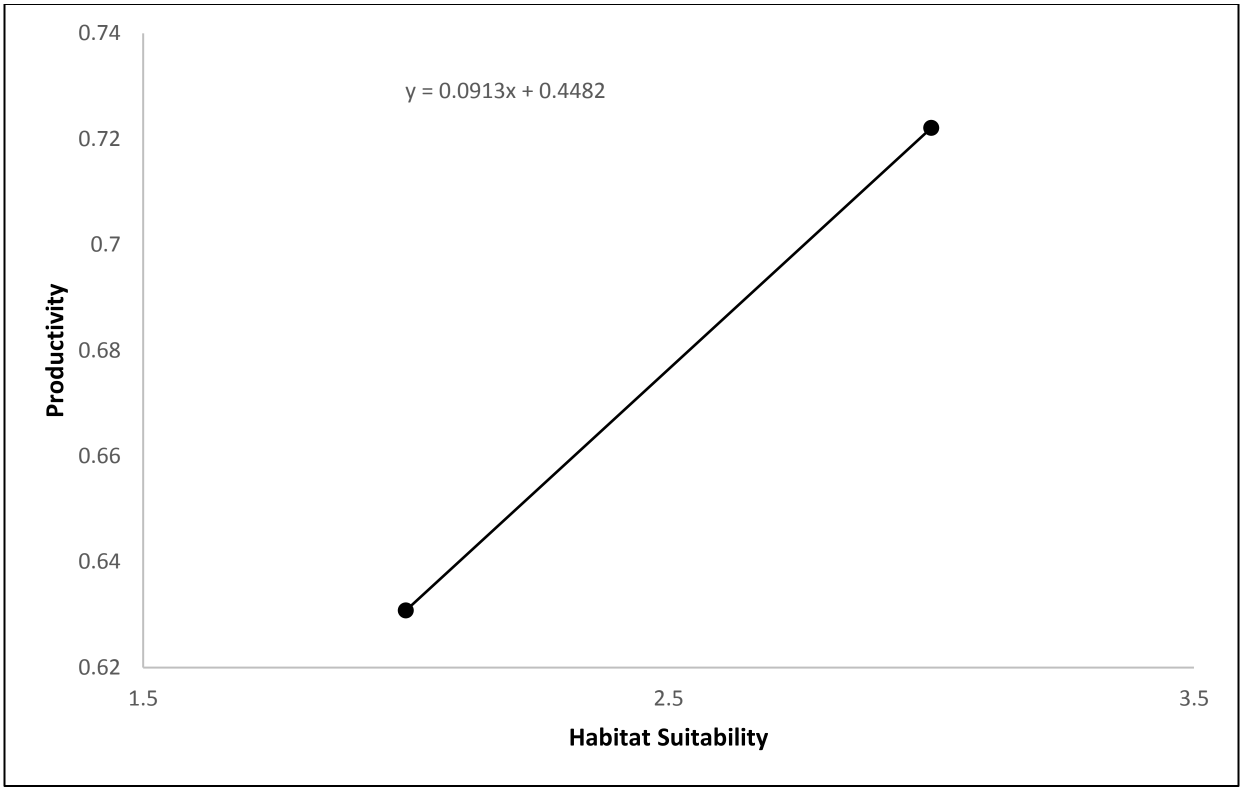

Figure S6. Regression equation used to estimate annual productivity for Kirtland's warblers (*Setophaga kirtlandii*) based on breeding grounds habitat suitability: Productivity = 0·4482 + (0·0913 x [Habitat Suitability]).

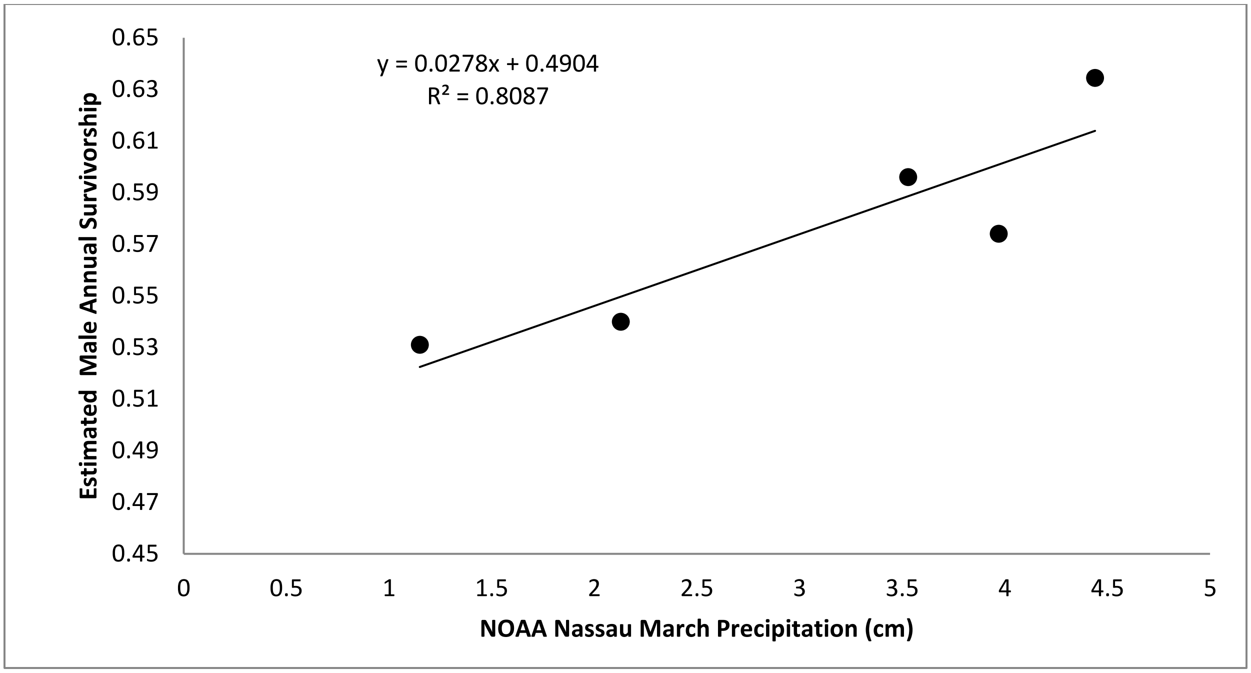

Figure S7. Regression equation used to estimate annual survival for Kirtland's warblers (*Setophaga kirtlandii*) based on wintering grounds precipitation: Survivorship = 0·49 + (0·0278 x [precipitation (cm)]).

Table S1. The 23 estimates of fledgling production used to derive mean fledgling production for simulation of Kirtland's warbler (*Setophaga kirtlandii*) population dynamics. Nest losses through parasitism or predation were accounted for in the estimates.

Source	Year(s)	Estimated fledglings / male (nest)
Mayfield (1960, p.204)	1950's	2·2 (1·48)
Orr (1975)	1974	3·72 (3·19)
Shake & Mattsson (1975)	1972	4·26 (2·84)
Shake & Mattsson (1975)	1973	4·18 (2·79)
Shake & Mattsson (1975)	1974	4·39 (2·93)
Ryel (1981)	1972	3·35 (2·72)
Ryel (1981)	1973	2·97 (2·71)
Ryel (1981)	1974	3·35 (2·87)
Ryel (1981)	1975	3·19 (2·76)
Ryel (1981)	1976	2·97 (2·70)
Ryel (1981)	1977	2·21 (2·06)
Kelly & DeCapita (1982)	1975	4·2 (2·8)
Kelly & DeCapita (1982)	1976	4·05 (2·7)
Kelly & DeCapita (1982)	1977	3·15 (2·1)
Kelly & DeCapita (1982)	1978	4·8 (3·2)
Kelly & DeCapita (1982)	1979	4·05 (2·7)
Kelly & DeCapita (1982)	1980	3·9 (2·6)
Kelly & DeCapita (1982)	1981	4·35 (2·9)
Walkinshaw (1983, p.164)	1972−1977	2·22 (1·48)
Rockwell *et al.* (2012)	2007−2009	3·3
Bocetti (unpublished)	1990	4·214
Bocetti (unpublished)	1991	4·2
Bocetti (unpublished)	1992	3·143
MEAN		**3·58**

Table S2. Annual survivorship estimates for hatch-year Kirtland's warblers (*Setophaga kirtlandii*). For this study, we used the mean of the Bocetti, Donner & Mayfield (2014) estimates (i.e., 0·415). During the model development stage we found that survivorship estimates of 0·35 and 0·46 resulted in abundance projections that were too low and high, respectively, relative to the observed abundance data.

Estimated survivorship	**Information about estimates**	**Source**
0·35	Best guess based on field data	Ryel (1979, 1981)
0·28	Values derived from those needed to maintain a static population	Probst (1986)
0·21	Values derived from those needed to maintain a static population (low estimate)	Probst & Hayes (1987)
0·26	Values derived from those needed to maintain a static population (high estimate)	Probst & Hayes (1987)
0·3	Field data	Bocetti (1994)
0·35	Citing Rockwell and Bocetti, unpublished data	Rockwell (2013)
0·46	Hatch-year male	Bocetti, Donner & Mayfield (2014)
0·37	Hatch-year female	Bocetti, Donner & Mayfield (2014)

Table S3. Annual survivorship estimates for after hatch-year male Kirtland's warblers (*Setophaga kirtlandii*). For this study, we used the mean (0·67) and standard deviation (0·07) of these estimates for our baseline survivorship distribution.

Estimated survivorship	Information about estimates	Source
0·74	Data based on adult males banded and found again in another year (1931-1966)	Berger & Radabaugh (1968)
0·65	Best guess based on field data	Ryel (1981)
0·75	Based on 60% return rate + estimated 15% missed floaters	Probst (1986); Probst & Hayes (1987)
0·57	Mean annual male survival estimated from capture-recapture data; SY and ASY estimates were averaged	Rockwell (2013)
0·65	Age-specific and sex-specific estimates of annual survivorship were determined by USGS scientists using mark-recapture techniques from 775 Kirtland's Warblers that were uniquely colour-marked from 1987 to 1992 at 5 major breeding areas.	Michigan Department of Natural Resources, U.S. Fish and Wildlife Service & U.S. Forest Service, unpublished report

References

Akçakaya, H.R. (2005) RAMAS GIS: *Linking Spatial Data with Population Viability Analysis, User Manual for Version 5*. Applied Biomathematics, New York.

Albert, D.A. (1995) *Regional Landscape Ecosystems of Michigan, Minnesota, and Wisconsin: A Working Map and Classification*. U.S. Forest Service General Technical Report NC-178, St. Paul, Minnesota.

Béland, M. & Bergeron, Y. (1996) Height growth of jack pine (*Pinus banksiana*) in relation to site types in boreal forests of Abitibi, Quebec. *Canadian Journal of Forest Research*, **26**, 2170−2179.

Berger, A.J. & Radabaugh, B.E. (1968) Returns of Kirtland’s warblers to the breeding grounds. *Bird-Banding*, **39**, 161−186.

Bocetti, C.I. (1994) Density, demography, and mating success of Kirtland's warblers in managed and natural habitats. PhD thesis, The Ohio State University, Columbus.

Bocetti, C.I., Goble, D.D. & J.M. Scott, J.M. (2012) Using conservation management agreements to secure postrecovery perpetuation of conservation-reliant species: the Kirtland's warbler as a case study. *Bioscience*, **62**, 874–879.

Bocetti, C.I., Donner, D.M. & Mayfield, H.F. (2014) Kirtland’s warbler (*Setophaga kirtlandii*). *The Birds of North America Online* (ed A. Poole). Cornell Lab of Ornithology, New York. http://bna.birds.cornell.edu/bna/species/019/.

Cleland, D.T., Crow, T.R., Saunders, S.C., Dickmann, D.I., Maclean, A.L., Jordan, J.K., Watson, R.L., Sloan, A.M. & Brosofske, K.D. (2004) Characterizing historical and modern fire regimes in Michigan (USA): a landscape ecosystem approach. *Landscape Ecology*, **19**, 311−325.

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 Ecology and Management*, **258**, 1093–1101.

Donner, D.M., Ribic, C.A. & Probst, J.R. (2010) Patch dynamics and the timing of colonization-abandonment events by male Kirtland's warblers in an early succession habitat. *Biological Conservation*, **143**, 1159−1167.

Farrand, W.H. (1982) *Quaternary Geology of Michigan*. Michigan Department of Natural Resources, Geological Survey Division. http://www.dnr.state.mi.us/spatialdatalibrary/metadata/quaternary_geology.htm.

Haney, J.C., Lee, D.S. & Walsh-McGehee, M. (1998) A quantitative analysis of winter distribution and habitats of Kirtland's warblers in the Bahamas. *Condor*, **100**, 201–217.

Jones, T.M., Akresh, M.E. & King, D.I. (2013) Recent sightings of Kirtland's warblers on San Salvador Island, the Bahamas. *Wilson Journal of Ornithology*, **125**, 637–642.

Kashian, D.M., Barnes, B.V. & Walker, W.S. (2003) Landscape ecosystems of northern Lower Michigan and the occurrence and management of the Kirtland's warbler. *Forest Science*, **49**, 140−159.

Kelly, S.T. & DeCapita, M.E. (1982) Cowbird control and its effect on Kirtland's warbler reproductive success. *Wilson Bulletin*, **94**, 363–365.

Longpré, M-H., Bergeron, Y. & Paré, D. (1994) Effect of companion species on the growth of jack pine (*Pinus banksiana*). *Canadian Journal of Forest Research*, **24**, 1846−1853.

Mayfield, H. (1960) *The Kirtland's Warbler*. Cranbrook Institute of Science, Michigan.

Mayfield, H.F. (1961) Vestiges of proprietary interest in nests by the brown-headed cowbird parasitizing the Kirtland's warbler. *Auk*, **78**, 162−166.

Mayfield, H.F. (1972) Third decennial census of Kirtland's warbler. *Auk*, **89**, 263–268.

Mayfield, H.F. (1993) Kirtland's warblers benefit from large forest tracts. *Wilson Bulletin*, **105**, 351–353.

Nelson, M.D. & Buech, R.R. (1996) A test of 3 models of Kirtland's warbler habitat suitability. *Wildlife Society Bulletin*, **24**, 89–97.

Orr, C.D. (1975) 1974 breeding success of the Kirtland's warbler. *Jack-Pine Warbler*, **53**, 59−68.

Probst, J.R. (1986) A review of the factors limiting the Kirtland's warbler on its breeding grounds. *American Midland Naturalist*, **116**, 87−100.

Probst, J.R. (1988) Kirtland's warbler breeding biology and habitat management. *Integrating Forest Management for Wildlife and Fish* (eds T.W. Hoekstra & J. Capp), pp. 28–35. U.S. Forest Service General Technical Report NC-122, Minnesota.

Probst, J.R. & Hayes, J.P. (1987) Pairing success of Kirtland's warblers in marginal vs. suitable habitat. *Auk*, **104**, 234−241.

Probst, J.R. & Weinrich, J. (1993) Relating Kirtland's warbler population to changing landscape composition and structure. *Landscape Ecology*, **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.

Rockwell, S.M. (2013) Carry-over effects from the non-breeding season influence spring arrival dates, reproductive success, and survival in an endangered migratory bird, the Kirtland's warbler (*Setophaga kirtlandii*). PhD thesis, University of Maryland.

Rockwell, S.M., Bocetti, C.I. & Marra, P.P. (2012) Carry-over effects of winter climate on spring arrival date and reproductive success in an endangered migratory bird, Kirtland's warbler (*Setophaga kirtlandii*). *Auk*, **129**, 744–752.

Ryel, L.A. (1979) On the population dynamics of Kirtland's warbler. *Jack-Pine Warbler*, **57**, 76–83.

Ryel, L.A. (1981) Population change in the Kirtland's warbler. *Jack-Pine Warbler*, **59**, 76–91.

Shake, W.F. & Mattsson, J.P. (1975) Three years of cowbird control: an effort to save the Kirtland's warbler. *Jack-Pine Warbler*, **53**, 48−53.

Simard, A.J., Haines, D.A., Blank, R.W., & Frost, J.S. (1983) *The Mack Lake Fire*. U.S. Forest Service General Technical Report NC-83, Minnesota.

Walkinshaw, L.H. (1983) *Kirtland's Warbler: The Natural History of an Endangered Species*. Cranbrook Institute of Science, Michigan.