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Research Paper

Kirtland's Warbler breeding productivity and habitat use in red pine-dominated habitat in Wisconsin, USA

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ABSTRACT. During the breeding season, Kirtland's Warblers (*Setophaga kirtlandii*) are strongly associated with young jack pine (*Pinus banksiana*) forests in northern Lower Michigan, USA. Since 2007, the species has been breeding in unusual habitat, red pine (*Pinus resinosa*) dominated plantations, in central Wisconsin, USA. Kirtland's Warbler productivity and habitat use in red pine is not well understood, and the central Wisconsin population is at a range edge, a situation often associated with lower productivity. To compare range-edge and range-core populations, we estimated reproductive success and characterized habitat use of Kirtland's Warblers in central Wisconsin red pine-dominated plantations during 2015–2017 using logistic regression models. We also monitored nests and fledgling success, and estimated nest survival using logistic exposure models. Trees were closer together and herbaceous vegetation was taller and denser within territories than at randomly located points outside of territories. Females selected nest sites with deeper dead ground vegetation and live vegetation that was taller and denser than was available at randomly located points within male territories. Nest success was not strongly influenced by within-patch habitat factors. Nest daily survival rate was 0.97 (95% CI = 0.94–0.98). The average number of young fledged per nest was between 2.5 and 2.8. Nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) was 22.7%. Overall, reproductive success in the peripheral central Wisconsin breeding population of Kirtland's Warblers that used red pine-dominated plantations was similar to that of Kirtland's Warblers breeding in typical jack pine habitat in the range core. Young red pine-dominated habitat appears to approximate young jack pine in habitat quality for Kirtland's Warblers, and this may provide managers some flexibility in habitat maintenance for this conservation-reliant species.

Productivité de nidification de la Paruline de Kirtland et utilisation de l'habitat dans un milieu dominé par le pin rouge dans le Wisconsin, É.-U.

RÉSUMÉ. Pendant la saison de nidification, les Parulines de Kirtland (*Setophaga kirtlandii*) sont fortement associées aux jeunes forêts de pins gris (*Pinus banksiana*) dans le nord du Michigan inférieur, aux États-Unis. Depuis 2007, l'espèce niche dans un milieu inhabituel, des plantations dominées par le pin rouge (*Pinus resinosa*) dans le centre du Wisconsin, aux États-Unis. La productivité et l'utilisation de l'habitat de la Paruline de Kirtland dans les forêts de pins rouges ne sont pas bien comprises, et la population du centre du Wisconsin se trouve à la limite de l'aire de répartition, une situation souvent associée à une productivité plus faible. Pour comparer les populations en bordure d'aire de répartition et celles au cœur de l'aire, nous avons calculé le succès de nidification et caractérisé l'utilisation de l'habitat des Parulines de Kirtland dans les plantations dominées par le pin rouge du centre du Wisconsin, en 2015-2017, au moyen de modèles de régression logistique. Nous avons également suivi les nids et le succès des jeunes à l'envol, et chiffré la survie des nids à l'aide de modèles d'exposition logistique. Les arbres étaient plus rapprochés et la végétation herbacée plus haute et plus dense à l'intérieur des territoires qu'à des endroits situés au hasard en dehors des territoires. Les femelles ont choisi des sites de nidification où la végétation morte était plus épaisse et où la végétation vivante était plus haute et plus dense qu'à des endroits situés au hasard dans les territoires des mâles. Le succès de nidification n'a pas été fortement influencé par les caractéristiques d'habitat à l'intérieur du territoire. Le taux de survie quotidien des nids était de 0,97 (IC 95 % = 0,94-0,98). Le nombre moyen de jeunes à l'envol par nid se situait entre 2,5 et 2,8. Le parasitisme des nids par les Vachers à tête brune (*Molothrus ater*) était de 22,7 %. Dans l'ensemble, le succès de reproduction de la population en périphérie du centre du Wisconsin de Parulines de Kirtland qui utilisaient des plantations dominées par le pin rouge était similaire à celui des Parulines de Kirtland nichant dans l'habitat typique de pins gris au cœur de l'aire de répartition. Les milieux dominés par les jeunes pins rouges semblent se rapprocher des milieux de jeunes pins gris en termes de qualité d'habitat pour les Parulines de Kirtland; au vu de ce résultat, les gestionnaires ont peut-être une certaine flexibilité dans le maintien de l'habitat pour cette espèce qui dépend de la conservation.

Key Words: conservation-reliant; endangered species; habitat specialist; habitat use; Kirtland's Warbler; nesting success; *Setophaga kirtlandii*

INTRODUCTION

A species' range center is hypothesized to provide optimal habitat conditions (Brown 1984), while at range edges habitat may be less suitable (Lesica and Allendorf 1995), population dynamics more variable and populations less viable (Hoffmann and Blows 1994, Linder et al. 2000). In nature, peripheral populations may have lower reproductive success (Wright et al. 2007, Hollander et al. 2011, Golawski et al. 2016), greater reproductive success (Pidgeon et al. 2001, Hargrove and Rotenberry 2011), or reproductive success that does not differ from core populations (Barrientos et al. 2009). Differences in competitive ability, plasticity, adaptation, or exogenous factors related to local habitat patches, may be associated with demographic rates more strongly than proximity to the core range or large scale macroecological patterns in traits, e.g., latitudinal trends in clutch size, or number of breeding attempts (Ruskin et al. 2017). As populations exceed carrying capacity, birds may occupy habitat of lower suitability (Fretwell and Lucas 1969, Fretwell 1972, Hartman 1996, Wright et al. 2007) or similar quality habitat that was previously unoccupied (Hartman 1996). Often it is young or socially subordinate males that first occupy habitat (Van Horne 1983, Holmes et al. 1996, Weinberg and Roth 1998, Braillet et al. 2002).

The Kirtland's Warbler (*Setophaga kirtlandii*) historically nested in young (~5–20 years old) dense jack pine (*Pinus banksiana*) forests in sandy glacial outwash areas in Lower Michigan, USA (Bocetti et al. 2020). Prior to Euro-American settlement, nesting habitat was maintained by stand-replacing wildfire (Donner et al. 2008) with approximately a 60-year return interval (Cleland et al. 2004). Natural regeneration of breeding habitat virtually ended after Euro-American settlement because of wildfire suppression and conversion to residential and agricultural uses, resulting in a severe decline in Kirtland's Warbler population size over time (Mayfield 1972, 1983, Probst and Weinrich 1993, Bocetti 1994). The species was included on the endangered species list in 1966 (Federal Register 1967). The primary management strategy was establishment of jack pine plantations of high stem density, with small openings, mimicking naturally regenerated habitat (Kepler et al. 1996). Together with control of Brown-headed Cowbirds (*Molothrus ater*; Shake and Mattsson 1975, Kelly and DeCapita 1982, Cooper et al. 2019), this resulted in population recovery and the species was removed from the Federal List of Endangered and Threatened Wildlife (Federal Register 2019).

Kirtland's Warblers expanded into Michigan's Upper Peninsula in 1994 (Probst et al. 2003, Donner et al. 2008), and into Ontario, Canada and Wisconsin in 2007 (Trick et al. 2008, Donner et al. 2009, Richard 2014). Annually increasing population size coupled with a stable amount of breeding habitat in Lower Michigan likely fueled this expansion (Probst et al. 2003, Donner et al. 2008, 2009). Unlike Kirtland's Warblers in Lower Michigan, which breed in young, dense jack pine habitat, Kirtland's Warblers in Renfrew County, Ontario and Adams County, Wisconsin, breed in red pine (*Pinus resinosa*) plantations that include lesser components of naturally regenerated jack pine and oak (*Quercus* spp.; Trick et al. 2008, Anich et al. 2011, Richard 2014). Although Kirtland's Warblers were previously observed breeding in red pine plantations occasionally (Mayfield 1960, Orr 1975, Probst 1986), it is unclear whether red pine plantations support viable populations of the species or are marginal habitat supporting low demographic rates. Data on nesting success and habitat use are

needed to determine the long-term viability of populations using red pine plantations.

Habitat selection is a hierarchical process influencing fitness of individuals (Hutto 1985, Chalfoun and Martin 2007, Luepold et al. 2015) at increasingly fine resolution (Battin and Lawler 2006, Guttery et al. 2017), from the geographic range to the habitat patch, territory, and the nest site (Johnson 1980). Habitat use is an outcome of selection (Jones 2001). At the habitat patch scale, Kirtland's Warbler habitat use may be a product of selection for tree species composition (Mayfield 1953, Walkinshaw 1983, Probst 1988), landscape context, tree density, and ground vegetation composition. Kirtland's Warblers in Adams County, Wisconsin may have selected red pine-dominated plantations because of their structural similarity to jack pine, and low availability of suitably aged jack pine habitat. Proximity to nearby occupied patches and the presence of conspecifics likely influenced selection at the patch level (Mayfield 1953, 1960, Bocetti 1994, Donner et al. 2009, Anich and Ward 2017).

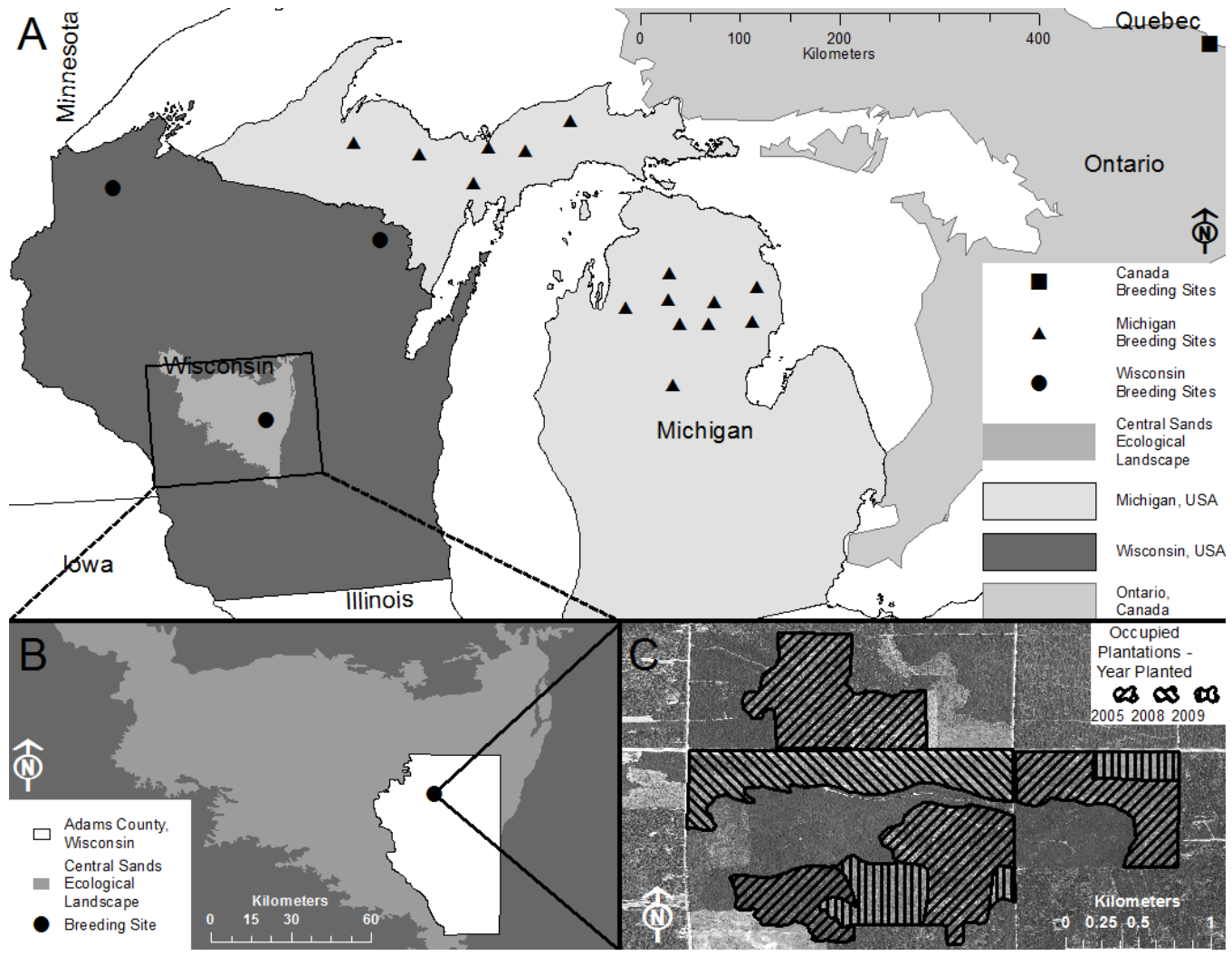
At the territory scale, habitat use is influenced by factors including habitat structure (Luepold et al. 2015), adult predation risk (Lima 2009), food availability (Chalfoun and Martin 2007), presence and breeding success of conspecifics (Danchin et al. 1998, Lima 2009, Anich and Ward 2017), territory quality (own or conspecifics; Danchin et al. 1998, Hoover 2003), and previous breeding success (Hoover 2003, Howlett and Stutchbury 2003, Lima 2009). Kirtland's Warblers forage more often in jack pine trees than on the ground, in deciduous trees, snags, or woody debris (Fussman 1997). Males establish breeding territories (Mayfield 1960, Walkinshaw 1983), and males select areas with relatively high pine density, often in the vicinity of conspecifics (Anich and Ward 2017).

Nest site selection occurs at yet a finer scale. Females should select nest sites that increase fitness (Lima 2009), and nest site selection is impacted by many factors, including thermal conditions (Nelson and Martin 1999, Hoekman et al. 2002, Davis 2005, Warren and Anderson 2005, Fisher and Davis 2010), visibility or openness (Götmark et al. 1995), nest depredation risk (Davis 2005, Luepold et al. 2015), brood parasitism risk (Forsman and Martin 2009), and post-fledging habitat needs (Fisher and Davis 2011). Understanding factors that influence nest success is important for understanding avian population dynamics (Hoekman et al. 2002).

Recently established Kirtland's Warbler populations provided an opportunity to determine how habitat use and reproductive success differ in the range core versus the range periphery. Further, because young jack pine habitat has been considered a requirement for breeding, understanding reproductive success and habitat use in red pine plantations may provide insights into the species' niche flexibility that can guide management.

Our overarching goal was to characterize Kirtland's Warbler breeding productivity and habitat use in red pine plantations at a set of nested scales. We quantified nest success and identified habitat features associated with territories and nest sites. We expected Kirtland's Warbler nest success would increase with nest concealment and decrease as the breeding season advanced because of increased efficiency by predators (Grant et al. 2005, Grant and Shaffer 2012). We expected that males would select

Fig. 1. Map of the study area in Adams County, Wisconsin in the Central Sands Ecological Landscape where Kirtland's Warblers (*Setophaga kirtlandii*) have been documented breeding. (A) Our study area in relation to other known Kirtland's Warbler breeding areas in northern Wisconsin and Michigan USA, and Ontario, Canada. (B) The location of the study area in Adams County, Wisconsin. (C) Eight of the 10 red pine-dominated plantations occupied by Kirtland's Warblers during the breeding seasons of 2015–2017, overlaid on a grayscale aerial photo. Two red pine dominated plantations occupied by Kirtland's Warblers in Adams County during the study were ~8.4 km and ~15.4 km northeast of the 8 adjacent plantations and are not shown in this figure.



territories with dense low vegetation, and abundant blueberries because such vegetation provides potential nest sites and foraging opportunities, and blueberries may be important food late in the breeding season (Fussman 1997, Deloria 2000, Deloria-Sheffield et al. 2001). Finally, we expected red pine plantations used by Kirtland's Warblers to be structurally similar to jack pine habitat they use in the range core.

METHODS

Study area

Our study area was in Adams County, Wisconsin (Fig. 1). This landscape is a glacial outwash plain with well drained, sandy soil and a continental climate (Wisconsin Department of Natural

Resources 2015). Vegetation includes jack pine, scrub oak, barrens, and jack and red pine plantations, forested and non-forested wetland, grassland, and agriculture (Wisconsin Department of Natural Resources 2015).

Our study area was ~418 km west of the core Michigan Kirtland's Warbler breeding area and consisted of red pine plantations in which jack pine was a naturally regenerating component. Kirtland's Warbler breeding attempts were documented in Adams County beginning in 2007 by nest monitors employed through Wisconsin Department of Natural Resources (WDNR; Trick et al. 2008, 2009, Grveles 2009, Anich et al. 2011). During our study the plantations were under a conservation easement with the WDNR (Michigan Department of Natural Resources et al. 2015). Little management had occurred in the plantations. Kirtland's

Warblers occupied 10 red pine plantations between 2015 and 2017 that were planted between 2005 and 2009 and were 2.7 ha to 46.9 ha (mean = 24.8 ha), with a combined area of 248.1 ha. Eight of the 10 plantations were clustered together, separated by roads (~6–27 m wide) or 75–480 m of non-suitably aged red pine plantations (Fig. 1). Two additional occupied plantations were ~8.4 and ~15.4 km northeast of the cluster of eight. The occupied plantations were embedded within a matrix of red and jack pine plantations of various ages, with minor components of natural forest, wetland, agriculture, pastures, and private residences. Brown-headed Cowbirds were trapped near occupied plantations from approximately 10 April to 10 July each year and humanely euthanized, by U.S. Department of Agriculture Animal and Plant Health Inspection Service personnel.

Data collection

Most males were individually identifiable by colored plastic leg bands (Refsnider et al. 2009, Trick et al. 2009, Anich et al. 2011). Male age was determined at the time of banding (Pyle 1997, Probst et al. 2007), and individual return histories were known from yearly resightings (Fig. A1.1).

Nest and territory monitoring

Beginning in mid-May (2015–2017), we observed singing males, recorded the locations of singing perches using handheld GPS units (95% typical use GPS accuracy < 10 m), and noted behaviors indicating they were paired. We recorded an average of 2.4 singing locations per individual approximately every four days, starting when males were first observed and ending upon completion of nesting, for an average of 17 singing locations per male (min = 3, max = 37, SD = 7.75). We considered singing locations to represent males' territories. We classified males as paired if they were associating with a female, singing with food, singing muffled songs, or if we observed copulation.

Nest monitoring was conducted under guidelines of WDNR, U. S. Fish and Wildlife Service (USFWS), and the Kirtland's Warbler Recovery Team. Because of the species' endangered status at the time, the guidelines required that nests be observed from a distance (Olah 2019). Once a male was classified as paired, we attempted to locate the nest. After locating the nest, we put flagging tape ~10 m away. We observed nests from the flag, approximately every two days, observing only long enough to determine whether nests were active or until 30 minutes elapsed. In the rare event that adults seemed agitated by our presence, we left and observed from farther away on the next visit. If we found nests accidentally, we noted nest contents at that time. If nests were found by observing male behaviors only and not approached, we inferred nest stage based on adult behaviors. We inferred that a nest contained eggs if we infrequently saw the male approach the nest with food and rarely observed the female off the nest (Bocetti et al. 2020). We inferred eggs had hatched if both adults were frequently visiting the nest with food (Bocetti et al. 2020). We inferred hatch date based on the shift from infrequent to frequent adult activity at the nest and estimated an expected fledge date (hatch day + average nestling stage length [9.4 days]; Bocetti et al. 2020). If after two 30-minute observations on sequential days, we did not observe activity near the nest during the nestling stage we assumed the nest had failed and approached to look for evidence of the cause of failure. We approached nests after they became inactive to look for unhatched eggs or evidence of

depredation. To estimate nest success and contents for nests that were not approached while active, we used information such as adults feeding fledglings or the presence of unhatched eggs. We considered nests successful if at least one Kirtland's Warbler fledged. Nest failure was assigned to one of four potential causes: depredation (clear evidence of a predator at a nest), abandonment (cold eggs, dead nestlings, no observed adult activity in two days), parasitism (nests contained only cowbird eggs or nestlings), or unknown. If we approached a nest and observed it had been parasitized, we removed the Brown-headed Cowbird nestlings, per guidelines.

We defined productivity as the number of Kirtland's Warbler young that fledged from nests. Because of restrictions placed on nest approaches, we did not know the number of nestlings in a subset of nests, for which we determined the possible minimum and maximum number fledged. For example, if we did not approach a nest prior to chicks fledging but we observed three fledglings with the adults and found one unhatched egg in the nest we concluded that a minimum of three young fledged (three fledglings observed) and a maximum of four young fledged (usual clutch size is five, but one egg remained unhatched thus five could not have fledged). Thus, we estimated high and low averages of young fledged per year, assuming that the true number fell within this range.

Vegetation at nest sites vs available sites within territories

We collected vegetation data in 2015–2017, 3–14 days after a nest attempt ended, at nests and at an equal number of points located in a random direction and distance of between 1–55 m (mean = 26.2 m, min = 3.3 m, max = 55 m) from the nest (hereafter, random points). All nests were within the associated male's territory boundaries (as defined by a minimum convex polygon; see territory vegetation measurements section, below), and all but two random points fell within the territory boundary. We characterized live trees and shrubs within 10 m of sampling points using point-centered-quarter (PCQ) methodology (Cottam and Curtis 1956, Warde and Petranka 1981). In each quadrant we recorded the height and distance to the nearest shrub, the nearest tree 1–3 m tall, and the nearest tree > 3 m tall. For trees, we measured the height from the ground of the lowest live branch (Buech 1980). Using our PCQ method, nests and random points within 20 m of each other could include trees or shrubs that were sampled twice, but post-hoc we found that only 3 of 210 trees and 2 of 105 shrubs were sampled twice. Our protocol reflected our expectation that trees of the two height classes may provide different resources, such that shorter trees may have lower live branches offering greater nest concealment (per Mayfield 1960) and taller trees may offer more attractive song perches.

We estimated percent ground cover (bare ground, moss, lichen, litter, woody debris, grass, sedge (*Carex* spp.), blueberry shrubs, shrubs, trees) in 1x1 m plots centered on the nest or random point in three categories (0%, < 50%, > 50%) to maximize detection of differences. We measured vegetation-height density (Robel et al. 1970) at two heights (1 m, 0.25 m) that were one and four meters from each point, in each cardinal direction. For each combination of height and distance, we averaged the four measures, resulting in four estimates of vegetation-height density. We measured dead herbaceous vegetation at three spots centered on the nest or for

random points, at the angles of an equilateral triangle with sides of 10 cm (outer diameter of Kirtland's Warbler nests) and averaged these values. We estimated nest concealment from above by placing a cardboard disc 5.8 cm in diameter (interior nest diameter) in the nest. We estimated the percent of the disc obscured by vegetation from eye level (~1.5 m) from four equidistant locations, each 0.5 m from the nest, and averaged the estimates. We did not estimate concealment from above at random points.

Delineating territories and characterizing territory vegetation

We recorded singing locations of males on 56 territories (min = 3, max = 37, mean = 17 locations per territory, SD = 7.75) between 2015 and 2017. We used asymptote tests (Laver and Kelly 2008) to determine whether the number of singing locations was sufficient for calculating territory boundaries. Specifically, for each individual we first randomly selected n singing locations and from them created 90% minimum convex polygons, repeating 100 times for each 1 unit increase in number of singing locations from $n = 4$ to $n =$ maximum number of singing locations, in the "adehabitatHR" package in R (Calenge 2006). Then we created 95% confidence intervals around the mean of the 100 bootstrapped estimates of territory size at each number of singing locations (Fig. A2.1). If the 90% minimum convex polygon based on all singing locations was within the 95% confidence interval, we considered the territory well defined. We had too few singing locations to do this for five territories. Using this assessment, 46 were well defined (13 from 2015, 16 from 2016, 17 from 2017).

To assess habitat within and outside of territories we collected vegetation data in 2016 and 2017. Of the 38 territories delineated in 2016 and 2017, six were not well defined using the above criteria so we excluded those data. From the remaining 33, we randomly selected three of each male's singing locations at which to compare vegetation with vegetation collected at random points located outside of all territory 90% minimum convex polygons; no random points fell within any territory boundaries as defined. This occurred after nesting ended to avoid disturbing nests. Vegetation sampling began in early July and ended in early August. We averaged data for each male so that the unit of analysis was the territory (hereafter, territory points), and averaged data collected at random points outside of territories. We characterized live trees and shrubs at sampling points using the PCQ methodology. We estimated tree density and height by species across territory points and across random points.

We categorized percent vegetation cover in four 1 m² plots located 3 m from a sampling point in each cardinal direction, using similar cover categories and the same percent categories used for nest site vegetation sampling. We used a majority rule to consolidate information from the 12 plots: if more than half had the same percent cover class for a ground cover category then we assigned the majority percent cover value, and if the plots were evenly split between percent cover values, we assigned the middle cover value (< 50%). Vegetation-height density was also measured as is described for nest site vegetation sampling.

Occupied patch characteristics

We defined a patch as an area of contiguous pine plantation of uniform age. We calculated tree densities and frequencies within

each occupied patch by combining tree data collected at Kirtland's Warbler locations and random points within the same patch. We calculated tree density in patches using PCQ methodology. We defined trees as those ≥ 2.5 cm in diameter at 50 cm height, and shrubs as woody plants ≥ 50 cm tall with multiple stems at or above 10 cm above ground. We estimated relative frequency, relative density, and average tree height, overall and by tree species.

Analysis

Nest survival and productivity

We calculated daily survival rates using logistic exposure (Shaffer 2004). We modeled daily survival for all years combined, and separately for 2016 and 2017 but not for 2015 because only one nest failed that year. All analyses were conducted in R version 3.6.2 (R Core Team 2019). We created generalized linear (binomial) models with the following link function:

$$g(\theta) = \log_e \left(\frac{\theta \frac{1}{t}}{1 - \theta \frac{1}{t}} \right) \quad (1)$$

The link function included exposure, where t = the number of days between successive observations. We excluded known re-nesting attempts ($n = 4$) from survival models because we could not account for male identity in models because our small dataset necessitated limiting model size. We used unstandardized variables in models so that we could make interpretable predictions in the units of the variables (Greenland et al. 1986, Luskin 1991, Grace and Bollen 2005, Menard 2011). We created a global generalized linear model using the R package MASS (Venables and Ripley 2002) and ranked all possible subsets of variable combinations by AICc using the package MuMIn (Bartoń 2018). We excluded collinear variables (Spearman's rank order correlation ≥ 0.7), here and in all subsequent analyses. In the global logistic exposure model, we included these predictors: concealment from above, vegetation-height density 1.25, and season day (the number of days after the first nest was found each season). We considered models with AICc differences ≤ 2 (Δ AICc) from the minimum AICc model to be in the confidence set (Burnham and Anderson 2004). To compare models, we calculated Akaike weights (w_i) and evidence ratios (Burnham and Anderson 2004). Variable importance was calculated over the confidence set and the entire model set (Burnham and Anderson 2004). As a measure of model fit, we calculated generalized R² values (Nakagawa and Schielzeth 2013) with the MuMIn package (Bartoń 2018), and area under the receiver operator curve (AUC) using the modEva package (Barbosa et al. 2016). Within individual models in the confidence set we considered variables to be significant if $P \leq 0.1$, following Arnold (2010). We assumed that variables with higher variable importance values and that were significant in individual models would be most useful in distinguishing between nest success and failure. To generate period survival estimates from the null model, we raised the estimated daily survival rate to the power of the period length (14 days for incubation through hatching, 24 days for incubation through fledging), such that the predictor function was:

$$s(x) = \frac{e^{\beta_0}}{1 + e^{\beta_0}} \quad (2)$$

We calculated percent of nests parasitized annually. We used a binomial logistic regression model to assess whether proximity to cowbird traps influenced the likelihood of nest parasitism.

Nest sites vs non-nest sites within territories

We compared vegetation at 38 nests and 35 random locations, using generalized linear models with logit-link functions,

$$(\text{logit } \pi_i = \beta_0 + \beta_1 x_1 + \dots + \beta_k x_k) \quad (3)$$

following the modeling procedure described for nest survival, above, combining data from 2016 and 2017. The response variable had a binary outcome of “nest” or “random location.” The global model included the following predictor variables, none of which were strongly correlated: vegetation-height density 1.25, vegetation-height density 4.1, depth of dead vegetation on the ground, blueberry cover, pine branch cover, and distance to nearest trees. We chose global model variables based on our expectation that nests would be better concealed from predators, brood parasites, or the elements where vegetation cover and density were greater, and trees were closer together than random points.

As described for our nest survival models, we considered models ≤ 2 AICc from the minimum AICc model to be in the confidence set (Burnham and Anderson 2004), and used Akaike weights, evidence ratios, variable importance values, R^2 values, and AUC to compare models. We examined the effect of individual predictor variables on the probability of a point being a nest or not, while holding other model variables constant (Shaffer and Thompson 2007).

Territory vegetation vs available vegetation

We compared vegetation at 32 territory points and 26 random points (outside of territories) using generalized linear models with logit-link functions (Eqn. 3) using the modeling procedure described above. The response variable had a binary outcome of “territory” or “non-territory.” The global model included the following variables, none of which were strongly correlated: vegetation-height density 1.1, vegetation-height density 1.25, vegetation-height density 4.1, vegetation-height density 4.25, blueberry shrub cover, pine branch cover, bare ground cover, shrub distance, and tree distance. Our choice of variables was based on the expectation that territories would include dense, low vegetative cover, and abundant blueberries, a potentially important food source. Although we initially expected shrub cover to be an important factor differentiating territories from non-territories, we excluded it because all but one point had 0% shrub cover.

As described above, we considered models ≤ 2 AICc from the minimum AICc model to be in the confidence set and we assessed territory models in the same way as nest survival and nest site models. We examined the effect of individual predictor variables on the probability of a point being a territory point or not, while holding other model variables constant (Shaffer and Thompson 2007).

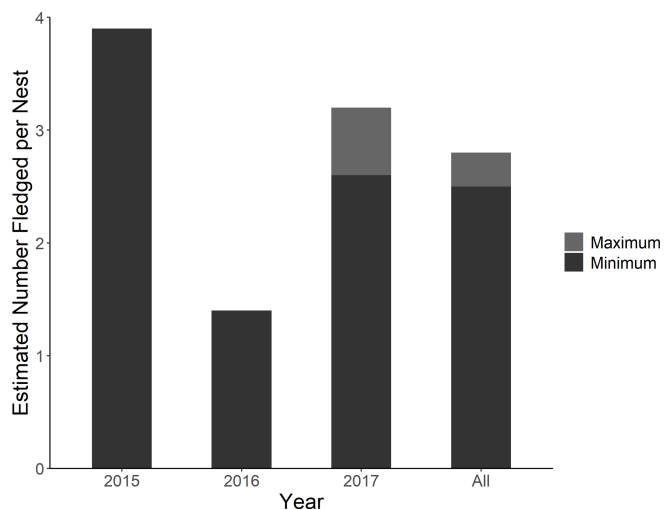
We assessed whether males used specific tree species in two ways using chi-square tests. First, we compared the number of territory and random points in which the nearest tree was red pine, jack pine, or oak. Second, we compared the relative frequency of tree species present on all territory points with the relative frequency of tree species at all random points.

RESULTS

Nests, nest survival, and productivity

We found the first nest on 2 June in 2015 and 2016, and 5 June in 2017. The last fledging date was 24 July in 2015, 12 July in 2016, and 27 July in 2017. In 2015, 51 young fledged from 12 nests; in 2016, 22–23 young fledged from 7 nests; and in 2017, 39–48 young fledged from 11 nests (Fig. 2). Six nests were never approached while active: 4 in 2015, and 2 in 2016. We considered the 4 nests in 2015 to be successful based on adult behaviors indicating the presence of fledglings. Both nests that were not approached in 2016 became inactive during the nestling stage, and subsequent inspection revealed they had failed.

Fig. 2. Kirtland’s Warbler (*Setophaga kirtlandii*) nest productivity 2015–2017 in Adams County, Wisconsin. Because of uncertainty about exact number of fledglings in some nests, we present high and low estimates of productivity for 2017. The column “all” combines data from all three-years.



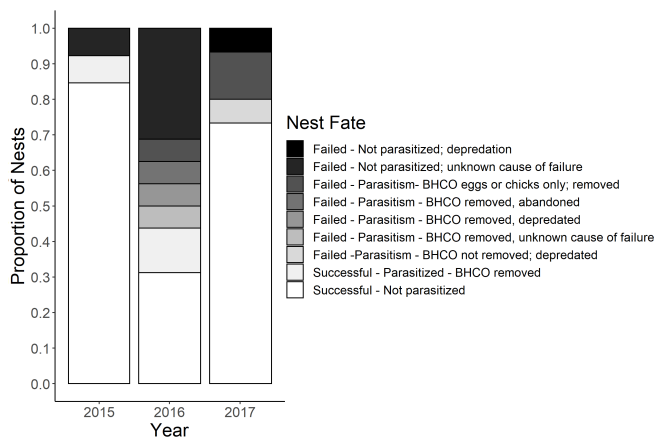
In 2015, only one of the 13 nests failed (Fig. 3) and we did not model nest survival for that year. In 2016, 7 of the 16 nests were successful; failure was attributed to depredation and abandonment. Of the 2016 nests, four were parasitized by Brown-headed Cowbirds. The cowbird chicks ($n = 4$, one per nest) were removed. The relationship between cowbird removal and ultimate nest failure cause was not clear. In 2017, failures (4 nests) were attributed to depredation and brood parasitism (Fig. 3).

In nest survival models, concealment from above had the highest variable importance in 2016 and in the combined year model (VI = 0.28 and 0.48 respectively; Table 1), however the nature of this relationship varied and was not significant at $\alpha = 0.1$ in any model. In the 2017 model set, season day had the greatest variable importance value (VI = 0.52; Table 1), exhibiting a slight negative

Table 1. Variable importance values (the sum of AICc weights of all models containing a variable) for explanatory variables used in modeling Kirtland’s Warbler (*Setophaga kirtlandii*) habitat use and nest survival in Adams County, Wisconsin. Variable importance values were calculated across the full set of models and the models ≤ 2 AICc from the minimum AICc model (Cand. Set). Not all variables were included in the global models. VHD indicates the different measures of vegetation-height density. VHD 1.1 = vegetation height density measured from 1 m horizontal distance and eye 1 m above ground. VHD 1.25 = vegetation height density measured from 1 m horizontal distance and eye 0.25 m above ground. VHD 4.1 = vegetation height density measured from 4 m horizontal distance and eye 1 m above ground. VHD 4.25 = vegetation height density measured from 4 m horizontal distance and eye 0.25 m above ground. For nest site models tree branch cover included cover of all tree branches within 0.5 m of the ground, and for territory models tree branch cover included only pine branches within 0.5 m of the ground.

Variable	Territory		Nest Site		Nest Survival					
	Full Set	Cand. Set	Full Set	Cand. Set	2016		2017		All Years	
					Full Set	Cand. Set	Full Set	Cand. Set	Full Set	Cand. Set
Concealment					0.28	0.16	0.36	0.26	0.48	0.35
Cover - Blueberry	0.24	0	0.27	0						
Cover - Tree Branches	0.24	0	0.87	0.48						
Dead Veg Depth			1	0.48						
Season Day					0.26	0	0.52	0.48	0.35	0.26
Shrub Distance	0.27	0.05								
Tree Distance	0.9	0.23	0.24	0						
VHD 1.1	0.7	0.23								
VHD 1.25	0.8	0.23	0.96	0.48	0.27	0	0.33	0.16	0.27	0
VHD 4.1	0.24	0	0.24	0.15						
VHD 4.25	0.38	0.06								

Fig. 3. Nest fates and associated causes of failure for 44 Kirtland’s Warbler (*Setophaga kirtlandii*) nests in Adams County, Wisconsin 2015–2017. Where cause of failure is “Parasitism - BHCO removed” Brown-headed Cowbird (*Molothrus ater*) nestlings were removed from nests.



relationship with survival that was not significant at $\alpha = 0.1$. We predicted daily survival rates and period survival rate estimates (through hatching and through fledging) for 2016, 2017, and the combined-year data. We used the null models because they were within the confidence set in each case (Table 2). The estimated daily survival rate was 0.95 (95% CI = 0.90, 0.98) in 2016, 0.93 (95% CI = 0.84, 0.98) in 2017, and 0.97 (95% CI = 0.94, 0.98) across all years. Our period survival estimates through hatching were 0.48 (95% CI = 0.21, 0.71) in 2016, 0.39 (95% CI = 0.09,

0.70) in 2017, and 0.62 (95% CI = 0.43, 0.76) across all three years. Our period survival estimates through fledging were 0.28 (95% CI = 0.07, 0.55) in 2016, 0.20 (95% CI = 0.02, 0.55) in 2017, and 0.43 (95% CI = 0.23, 0.62) for all three years.

The average number of young produced per nest was between 2.55 and 2.77 (all years combined; Fig. 2). In 2015, one nest was parasitized by Brown-headed Cowbirds, the cowbird nestling was removed, and Kirtland’s Warbler young fledged. In 2016, cowbirds parasitized six nests, the cowbird nestlings were removed, and Kirtland’s Warbler young fledged from two of the nests. In 2017, two nests contained only cowbird eggs or nestlings, which were removed. An additional nest in 2017 containing Kirtland’s Warbler and cowbird eggs was depredated.

The brood parasitism rate was 22.7% (2015 = 7.7%, 2016 = 37.5%, 2017 = 20%). Nests were on average within 1.28 km of a cowbird trap (min = 0.20 km, max = 7.19 km, SD = 1.6 km). Parasitized nests were on average 0.45 km further from cowbird traps than unparasitized nests, however distance to nearest trap was not significant in binomial regression ($P = 0.38$). Brood parasitism rates in Michigan ranged from 0% to 1.6% between 2015 and 2018, even with reduced cowbird management (Cooper et al. 2019).

Nest site vegetation

Red pine was the nearest tree to 63% of nests ($n = 27$), *Quercus* spp. was closest to 21% of nests ($n = 9$), jack pine was closest to 9% of nests ($n = 4$), and other tree species were closest to 7% of nests ($n = 3$). Nests were in live grasses (31%, $n = 13$), blueberry (19%, $n = 8$), red pine duff (17%, $n = 7$), low live red pine branches (10%, $n = 4$), live sedge (10%, $n = 4$), dead sedge (7%, $n = 3$), other dead vegetation (5%, $n = 2$), and dead grass (2%, $n = 1$). Dead herbaceous vegetation depth around the perimeter of nests varied

Table 2. Kirtland’s Warbler (*Setophaga kirtlandii*) nest survival in Adams County, Wisconsin modeled for 2016, 2017, and combined across all years (2015–2017). We could not model survival in 2015 because of only one known failure. We show only the confidence set models (< 2 AICc from minimum AICc model) ranked by differences in Akaike’s information criterion corrected for small sample sizes (ΔAICc). Column k indicates number of model parameters, w_i indicates Akaike weight, AUC is the area under the receiver operator curve, and R^2 is Nagelkerke’s pseudo R^2 . Evidence ratios (Ev. Ratio) are the ratio of w_l/w_i where model l has the lowest AICc and i indexes the rest of the models in the set. Variables marked with an asterisk (*) were considered to be significant at $\alpha = 0.1$.

	k	$\Delta\text{AICc}^\dagger$	w_i	Evidence Ratio	AUC	R^2
2016						
Null	0	0	0.39		0.65	0
Concealment	1	1.8	0.16	0	0.66	0.01
Vegetation-height Density 1.25	1	2	0.14	0	0.65	0
2017						
Season Day	1	0	0.22		0.85	0.14
Null	0	0.24	0.19	1.1	0.7	0
Concealment	1	0.61	0.16	1.4	0.7	0.1
Vegetation-height Density 1.25 + Season Day*	2	0.65	0.16	1.4	0.82	0.22
Concealment + Season Day	2	1.51	0.1	2.1	0.82	0.18
Combined Years (2015-2017)						
Null	0	0	0.26		0.69	0
Concealment	1	0.33	0.22	1	0.72	0.03
Concealment + Season Day	2	1.29	0.14	1.6	0.73	0.04
Season Day	1	1.51	0.12	1.8	0.71	0.01

[†]Minimum AICc values: 2016 = 45.07, 2017 = 25.81, All Years = 86.55

from 5 cm to 15.73 cm (5–10 cm deep at 40% of nests, 10–13 cm deep at 48% of nests, and 14–15.73 cm deep at 12% of nests).

Nest sites had greater dead herbaceous vegetation depth, vegetation-height density 1.25, and tree cover relative to random points within territories. In the confidence set of nest site models (Table 3), dead herbaceous vegetation depth, vegetation-height density 1.25, and tree branch cover had equal variable importance values (VI values = 0.48; Table 1). Across all nest site models, dead herbaceous vegetation depth had greatest variable importance value (VI value = 1.0), followed by vegetation-height density 1.25 (VI value = 0.96), and tree branch cover (VI value = 0.87; Table 1). As vegetation-height density 1.25 increased from 0 cm to 20 cm, the probability of nest placement increased from 0.03 to 1.0. As dead herbaceous vegetation depth increased from 0 cm to 15.73 cm the probability of nest placement increased from < 0.001 to 1.0. The predicted probability of nest placement increased from 0.23 when tree branch cover was 0%, to 0.97 when tree branch cover was < 50%, to 1.0 when tree branch cover was > 50%.

Male ages and territory characteristics

Of males observed in Adams County from 2008 to 2019, 58% (min = 25%, max = 80%) were after second-year males (hatched at least two years previous), 30% (min = 13%, max = 47%) were second-year males (hatched the previous year), and 12% (min = 0%, max = 38%) were of unknown age (Fig. A1.1).

Average density of trees within territories (1577 trees ha⁻¹) was greater than outside of territories in the same patch (1094 trees ha⁻¹; Fig. 4). Red pine occurred at greatest density both in territories (1292 trees ha⁻¹, $n = 331$) and outside of territories (885 trees ha⁻¹, $n = 284$), followed by jack pine (territories = 265 trees

ha⁻¹, $n = 68$; outside of territories = 203 trees ha⁻¹, $n = 65$; Fig. 4). The relative frequencies of red pine and jack pine were similar in and outside of territories (territories: red pine = 66%, jack pine = 32%; outside of territories: red pine = 67%, jack pine = 32%; Fig. 4).

Fig. 4. Relative densities (A) and relative frequencies (B) of red pine (*Pinus resinosa*), jack pine (*Pinus banksiana*), and oak (*Quercus* spp.) across random locations and territory locations within red pine-dominated habitat patches occupied by Kirtland’s Warblers (*Setophaga kirtlandii*) in Adams County, Wisconsin. Data were collected in 2016 and 2017.

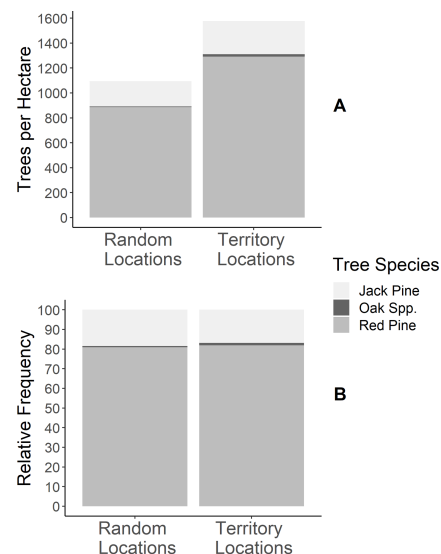


Table 3. Kirtland's Warbler (*Setophaga kirtlandii*) nest site habitat use in Adams County, Wisconsin, 2015–2017. We show only the confidence set models (< 2 AICc from minimum AICc model) ranked by differences in Akaike's information criterion corrected for small sample sizes (Δ AICc). Column k indicates number of model parameters, w_i indicates Akaike weight, AUC is the area under the receiver operator curve, and R^2 is the generalized R^2 (Nakagawa and Schielzeth 2013). Evidence ratios (Ev. Ratio) are the ratio of w_i/w_j where model i has the lowest AICc and j indexes the rest of the models in the set. Variables marked with an asterisk(*) were considered to be significant at $\alpha = 0.1$.

	k	Δ AICc [†]	w_i	Ev. Ratio	AUC	R^2
Vegetation-height Density 1.25* + Dead Vegetation Depth* + Tree Branch Cover <50%* + Tree Branch Cover > 50%	4	0	0.34		0.99	0.95
Vegetation-height Density 1.25* + Vegetation-height density 4.1 + Dead Vegetation Depth* + Tree Branch Cover < 50%* + Tree Branch Cover > 50%	5	1.68	0.15	2.3	0.99	0.95

[†]Minimum AICc value = 30.3

In predicting whether points were within or outside of territories, distance to the nearest tree (which characterizes tree density of the entire territory [AO, AP, *personal observation*]) discriminated most strongly (variable importance [VI] value = 0.92); the shorter the distance, the greater the probability a point was within a territory. Vegetation height density 1.25 (VI value = 0.80), and vegetation-height density 1.1 (VI = 0.70; Table 1) were also important discriminators (Table 4). The predicted probability of a point being within a territory increased from 0.38 to 1.0 when vegetation-height density 1.25 increased from 0 cm to 150 cm while other variables were held constant at their mean. The probability of a point being within a territory decreased from 0.83 to 0.04 when vegetation-height density 1.1 increased from 0 cm to 133 cm while other variables were held at their mean. The probability of a point being within a territory decreased from 0.89 to 0.05 when average distance to the nearest tree increased from 1.8 m to 5.4 m while other variables were held at their mean.

Between territory and random points, we found no difference in the proportion of points in which the nearest tree was red pine, jack pine, or oak (chi-square test, $\chi = 0.4$, $P = 0.8$). Red pine was the closest tree at 77–80% of points, jack pine was the closest tree at 19–21% of points, and oak was the closest tree at 1–2% of points.

Occupied patches

On average, occupied patches consisted of 70% red pine, 28% jack pine, and 2% oak. Average tree height in occupied patches was 4.1 m (SD = 1.1 m, $n = 2552$ trees) and was identical for red and jack pine, $n = 2138$ and 391 respectively), while the average height of oaks was 2.8 m (SD = 1.5, $n = 13$). Low live branch height of red pines was closer to the ground (mean = 8.7 cm, SD = 11.6, $n = 2138$) than jack pine (mean = 51.4 cm, SD = 46.0, $n = 391$). Mean tree density in occupied patches was 1937 trees ha⁻¹ (SD = 912 trees ha⁻¹, $n = 8$ patches).

DISCUSSION

In a population of Kirtland's Warblers breeding at the range periphery in red pine-dominated plantations, a relatively little used habitat type, nesting success was similar to that in long-occupied jack pine habitat used by the core population. Both nest survival (WI = 0.43, all years combined; MI = 0.32, Bocetti et al. 2020) and average number of young fledged per nest (Wisconsin, 2.5–2.8, 2015–2017; Michigan, 2.8–3.6; Shake and Mattsson

1975, Kelly and DeCapita 1982, Bocetti 1994, Rockwell et al. 2012) were comparable in the peripheral and core populations. This suggests that nesting success is not reduced in red pine-dominated plantations.

Although Kirtland's Warbler nests were closer to red pines than to other tree species, nests were placed directly in grass, blueberry, or red pine duff and rarely directly under low live tree branches. In Michigan, nests were typically placed in open areas of low vegetation within one meter of a pine thicket (Bocetti et al. 2020), with vegetation directly covering nests mainly composed of grasses, sedges, and blueberry (Mayfield 1960). Nest sites had deeper dead herbaceous vegetation, greater vegetation height-density, and greater cover of low tree branches within 0.5 m of the nest than non-nest points, suggesting that concealment of nests by vegetation, even if not touching the nest, is important. Perhaps this is because Kirtland's Warblers use surrounding vegetation to conceal their nest approaches (Mayfield 1960). Tall dense vegetation may offer nest concealment from predators or shelter from the elements (Martin and Roper 1988, Nelson and Martin 1999, Davis 2005, Warren and Anderson 2005, Fisher and Davis 2010). Dead vegetation is also likely a primary source of nest cover early in the season before full green up (Mayfield 1960, Davis 2005, Warren and Anderson 2005, Fisher and Davis 2010). Many Kirtland's Warbler nests are built before ground vegetation has fully emerged; thus females may select sites with high proportions of dead vegetation because of benefits (concealment, thermal etc.) those features may confer. We collected vegetation data after a nesting effort ended regardless of nest fate. This delayed measurement may have resulted in measuring conditions other than what the birds experienced at nest initiation, leading to spurious conclusions (McConnell et al. 2017), although we note that vegetative growth rates slowed considerably as the summer progressed, mitigating differences in time of use versus time of measurement.

We found that occupied red pine-dominated plantations in Adams County had similar proportions of pine (~90% pine; in MI up to 20% broadleaf; Smith 1979, Probst 1988) but lower densities of trees (1860 trees ha⁻¹) than jack pine plantations used by Kirtland's Warblers in Lower Michigan (2000–3345 jack pine ha⁻¹; Bocetti 1994, Houseman and Anderson 2002). Additionally, live red pine branches were nearer to the ground than live jack pine branches in our study site, which could explain why Kirtland's Warblers would occupy lower density red pine plantations.

Table 4. Male Kirtland’s Warbler (*Setophaga kirtlandii*) territory use in Adams County, Wisconsin, 2016–2017. We show only the confidence set models (< 2 AICc from minimum AICc model) ranked by differences in Akaike’s information criterion corrected for small sample sizes (ΔAICc). Column k indicates number of model parameters, w_i indicates Akaike weight, AUC is the area under the receiver operator curve, and R^2 is the generalized R^2 (Nakagawa and Schielzeth 2013). Evidence ratios (Ev. Ratio) are the ratio of w_i/w_j where model i has the lowest AICc and j indexes the rest of the models in the set. Variables marked with an asterisk(*) were considered to be significant at $\alpha = 0.1$.

	k	$\Delta\text{AICc}^\dagger$	w_i	Ev. Ratio	AUC	R^2
Vegetation-height density 1.25* + Vegetation-height density 1.1* + tree distance*	3	0	0.12		0.83	0.68
vegetation-height density 1.25* + vegetation-height density 1.1* + vegetation-height density 4.25 + tree distance*	4	1.56	0.06	2.18	0.83	0.65
vegetation-height density 1.25* + vegetation-height density 1.1* + shrub distance + tree distance*	4	1.73	0.05	2.38	0.83	0.68

[†] Minimum AICc value = 70.33

Within occupied patches, territories had slightly greater tree density than random locations (~480 trees ha⁻¹ greater). Relative frequencies of red and jack pine were not different between territories and random locations. If males were using jack pine in greater proportion than was present in occupied patches, territories should have a higher proportion of jack pine than locations outside of territories. Point level measures of distance to trees (our proxy of point-level tree density) indicates that trees within territories are closer together than trees outside of territories. On territories, vegetation-height density measured at 0.25 m height was greater than in areas outside of territories but within the same patch, suggesting that males establish territories in areas with greater low vegetation cover, possibly because it offers better foraging opportunities, more potential nest sites, or lower detection by predators. However, we also found that territories had lower vegetation-height density measured at 1 m height than outside of territories. It is less clear why this negative association exists with density of tall vegetation, but we speculate that dense tall grass may be more difficult for Kirtland’s Warblers to fly through. Although we expected blueberry cover to be an important habitat feature, we did not find that to be the case. Although blueberry cover may be important for foraging opportunities or nest concealment, it is possible that at scales larger than the nest site Kirtland’s Warblers may accept a wide range of ground cover compositions (Probst 1988, Probst and DonnerWright 2003). It is also possible that blueberry is unimportant on territories because fruiting does not occur until territories begin to break down as the nesting period ends.

The population of Kirtland’s Warblers in Adams County is likely still growing. All suitable territories in occupied plantations may not be filled, nor all suitable habitat patches occupied. The contrast in habitat attributes between territory and non-territory points may be subtle if non-territory points are also suitable but unoccupied (Fretwell and Lucas 1969, Fretwell 1972, Hartman 1996). Conspecific attraction also influences habitat occupancy in Kirtland’s Warblers (Mayfield 1960, Bocetti 1994, Anich and Ward 2017), and likely enhances suitability of occupied patches through (positive) Allee effects (Allee et al. 1949). If red pine-dominated habitat in Adams County was of marginal quality, we would expect most new males observed each year to be second year birds or birds that were subordinate. We did not find evidence of this. Most newly observed males were after-second-year birds, suggesting that red pine plantations are perceived to be of similar

quality to jack pine plantations in the core range. However, we cannot rule out the possibility that newly arrived after-second-year birds in Adams County were subordinate to territory holders in the core habitat, as metrics associated with dominance were not measured.

Demographic rates are often hypothesized to be greatest at a species’ geographic range center, coinciding with peak species abundance, and lowest at the range periphery. This pattern is found in multiple species (Wright et al. 2007, Hollander et al. 2011, Golawski et al. 2016). However, demographic rates are not always greater at the core of a species’ range. Local habitat quality may more strongly influence fecundity across geographic ranges than large scale environmental gradients (Pidgeon et al. 2001, Hargrove and Rotenberry 2011, Ruskin et al. 2017). Or there may be no differences in reproductive success between populations across a geographic range (Barrientos et al. 2009). Kirtland’s Warblers align with this latter group, in that nest survival rates and number of young fledged per nest in peripheral habitat and the core of the breeding range are similar.

In response to habitat creation and Brown-headed Cowbird control, the Kirtland’s Warbler population has recovered and is no longer listed as federally endangered (Federal Register 2019). A goal stated in the Kirtland’s Warbler Conservation Plan is to provide suitable breeding habitat in areas peripheral to the core range for 10% (100 pairs) of the Kirtland’s Warbler population (Michigan Department of Natural Resources et al. 2015). Kirtland’s Warblers will always remain conservation-reliant because wildfire suppression prevents natural habitat creation, and cowbird parasitism depresses their productivity. The challenge in the post-delisting period is to continue creating suitable breeding habitat and managing Brown-headed Cowbirds. Although Kirtland’s Warblers in the core range appear to be resilient to relaxed levels of cowbird control (Cooper et al. 2019), the small population in Adams County suffers from high levels of brood parasitism even with active cowbird management and a declining Brown-headed Cowbird population in Wisconsin (-2.67% over the period 2007–2017, North American Breeding Bird Survey, Patuxent Wildlife Research Center-Bird Population Studies, <https://www.mbr-pwrc.usgs.gov/>). The cowbird population trend is comparable to that in Michigan over this same 10-year period (-3.06%, *ibid*). Low parasitism rates in Michigan are attributed to low cowbird population size, associated with reforestation (Cooper et al. 2019); however, in Adams County

WI, agriculture is prevalent, which could account for the differences in nest parasitism rates in the two states.

Managers will likely need to minimize costs associated with creating Kirtland's Warbler habitat, and managers in Wisconsin will likely need to continue managing cowbirds. One option for increasing timber value is inter-planting red and jack pine trees in plantations, a strategy included in the most recent Kirtland's Warbler Conservation Plan (Michigan Department of Natural Resources et al. 2015).

Our findings, together with others from red pine-dominated plantations (Anich et al. 2011, Richard 2014), suggest that suitable Kirtland's Warbler breeding habitat can consist of various combinations of red pine and jack pine in a managed plantation. When the Kirtland's Warbler population was lowest, management focused on habitat known to sustain the population: young jack pines intermixed with grassy openings. Now that the species is no longer threatened with extinction, managers have more flexibility to plant a range of tree species composition proportions that Kirtland's Warblers will use as breeding habitat, which may facilitate lower costs of managing habitat for this conservation-reliant species.

Responses to this article can be read online at:
<https://www.ace-eco.org/issues/responses.php/2009>

Author Contributions:

All authors conceptualized the project, designed the research, and participated in writing and editing. AO collected and formally analyzed the data, and wrote the original draft. AP and CR participated in analysis of the data, reviewing and editing, and funding acquisition for the project. KG, DL, and SW assisted with project logistics.

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Appendix 1. Male Kirtland's Warbler ages 2008-2019

Fig. A1.1. Proportion of male Kirtland's warblers observed in Adams County each year (2008-2019), in 6 different age classes. Ages were estimated at the time of banding based on plumage and morphological characteristics or based on returns of locally produced individuals banded as nestlings (known-age birds). In a given year, any males that had never been observed in Adams County previously were considered to be 'New Males'. Many of these new males were captured and given uniquely identifiable combinations of color bands. Many new males were aged to after-second year (not hatched the previous year; ASY) or second year (hatched the previous year; SY). Some males had a mix of characteristics, making them only ageable to an after-hatch-year (an adult, not hatched the current year; AHY). Some males were never captured or banded, and remained of unknown age (New Male, age unknown). Many males returned to Adams County in multiple years. In the year they were captured they were classified as a new male, but in any successive year they returned they were classified as 'Male banded locally as adult, \geq ASY'. These males are all after-second year (ASY). In several years we had individuals banded as nestlings, that returned to their natal site for their first breeding season (Male locally hatched, SY). Total number of observed males in each year are noted above the bars.



Appendix 2. Territory size asymptote tests

Fig. A2. 1.

Bootstrapped territory size estimates (90% minimum convex polygon of n singing locations, randomly sampled 100 times) for individual male Kirtland's Warblers ($n=52$). Red lines are 95% confidence intervals, the black line is the mean territory size of the 90% minimum convex polygons based on n locations, and the blue dashed line is the 90% minimum convex polygon of the territory based on all an individual's locations. If the 90% minimum convex polygon based on all locations (blue dashed line) was within the confidence interval (red lines), we considered territories to be well defined.

