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# Spatially structured brown-headed cowbird control measures and their effects on Kirtland's warbler long-term population sustainability

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## ABSTRACT

**Context.** Brown-headed cowbirds (*Molothrus ater*), through brood parasitism, can exert extrinsic population growth pressures on North American songbirds. Cowbird removal programs may reduce parasitism rates on host species but can be expensive and difficult to implement throughout a host species' breeding range. **Aim.** We estimated cowbird abundance and nest parasitism rates within Kirtland's warbler (*Setophaga kirtlandii*) primary breeding range in Michigan, USA, and determined the maximum sustainable parasitism rate for Kirtland's warblers under several spatially structured cowbird removal designs. **Methods.** We conducted point counts to estimate cowbird abundance and monitored nests to quantify nest parasitism rates during 2019–2021. We used the modelling software STELLA to determine the maximum sustainable parasitism rate for Kirtland's warblers under different spatially structured cowbird removal scenarios (complete, core-only, and no removal). **Key results.** Cowbird abundance and parasitism rates remained low following cowbird trap closures in 2018. In the simulation study, complete removal was the most robust scenario with no replications having <1000 Kirtland's warbler males. The core-only removal scenario had a substantially higher sustainable parasitism rate in the peripheral breeding area than the no removal scenario. Assumed hatch-year dispersal distance had the greatest impact on the maximum sustainable parasitism rate in the core-only scenario. **Conclusions.** Low cowbird abundance and nest parasitism following suspension of cowbird removal efforts showed resuming the removal program may not be required in the short-term. If cowbird abundance increases, however, adaptive cowbird removal programs can be used to sustain Kirtland's warbler populations long-term. **Implications.** Our results indicate that incorporating spatial structure of host species' habitat into designing cowbird removal programs may minimise costs of cowbird management while sustaining populations of Kirtland's warbler and possibly other host species that are affected by brood parasitism.

**Keywords:** adaptive management, brood parasitism, brown-headed cowbird, conservation reliance, cowbird removal, Kirtland's warbler, *Setophaga kirtlandii*, simulation model.

## Introduction

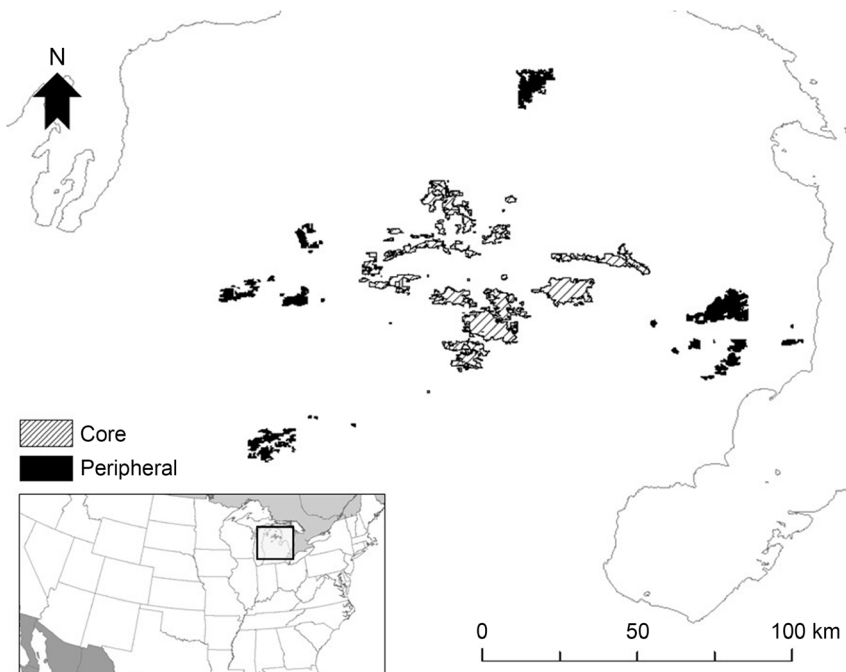
Extrinsic population growth factors can strongly regulate a species' ability to persist over space and time. Species that are unable to respond to these extrinsic limitations, through behavioural adaptations or other means, are at a greater risk of local extirpation or extinction. For some songbird species in North America, brood parasitism by the brown-headed cowbird (*Molothrus ater*) is an extrinsic factor that reduces productivity (Brittingham and Temple 1983; Robinson *et al.* 1995; Benson *et al.* 2010). Because of their large home-range (Thompson 1994), cowbirds can have a disproportionately large impact on the reproductive output of host species over large spatial scales

(Hahn and Hatfield 1995; Howell et al. 2007; Hovick and Miller 2013). In the upper Midwest, forest fragmentation and conversion of forests to agriculture led to greater prevalence of brown-headed cowbirds (Rothstein and Robinson 1994; Cox et al. 2012). To mitigate decreasing forest species' populations that were due, in part, to brood parasitism (Robinson et al. 1993), agencies began implementing large-scale cowbird removal programs to reduce brood parasitism and increase reproductive output for endangered forest songbirds (e.g. black-capped vireo [*Vireo atricapilla*], Kirtland's warbler [*Setophaga kirtlandii*], least Bell's vireo [*Vireo bellii pusillus*], southwestern willow flycatcher [*Empidonax traillii extimus*]; Peer et al. 2020). However, due to variability in the spatial scale of brood parasitism and the spatial structure of host species populations (Hochachka et al. 1999), removal programs are often expensive and difficult to spatially design (Eckrich et al. 1999; Rothstein and Peer 2005).

Many threatened and endangered species in the United States, and likely globally, remain conservation-reliant because they require intensive management actions such as control of other species (e.g. brown-headed cowbirds), active habitat management, and artificial recruitment to maintain their populations (Scott et al. 2010). Conservation reliance presents serious regulatory, financial, and logistical challenges for habitat and population managers (Scott et al. 2010; Bocetti et al. 2012; Rodewald 2016). To reduce conservation reliance and increase cost-effectiveness, managers have to regularly evaluate both the necessity and the effectiveness of specific management actions (Cooper et al. 2019).

The Kirtland's warbler is a Nearctic-Neotropical migratory songbird that breeds in large stands of young (5–20 years old)

jack pine (*Pinus banksiana*) primarily in the northern Lower Peninsula of Michigan, USA and winters primarily in The Bahamas (Radabaugh 1974; Probst 1986; Cooper et al. 2017, 2019). In 1967, the Kirtland's warbler was listed as federally endangered due to extreme breeding habitat limitation and high susceptibility to brood parasitism by the brown-headed cowbird (Kepler et al. 1996). As part of the recovery plan, 23 Kirtland Warbler Management Areas (KWMA) were designated to provide essential breeding habitat for Kirtland's warblers across federal and state lands (Fig. 1; Byelich et al. 1985). These KWMA were distributed across 13 counties in northern Lower Peninsula of Michigan resulting in a 'core' group of management areas centrally located and several 'peripheral' management areas surrounding core areas across the landscape (Fig. 1; Byelich et al. 1985). In 1972, the United States Fish and Wildlife Service (USFWS) began trapping and removing cowbirds within the KWMA to increase reproductive success and stabilise the declining population (Kelly and DeCapita 1982). Cowbird decoy traps were placed at ~1.6 km<sup>2</sup> intervals within Kirtland's warbler nesting areas (Shake and Mattsson 1975) and tending these traps required employees to travel ~200 km daily from mid-April through June each year (Kepler et al. 1996). The resulting program success led to reduced parasitism rates from ~75% to ~6% and tripled reproductive success of Kirtland's warbler (Walkingshaw 1983). Continuation of the cowbird removal program resulted in a further decline of parasitism rates to <1% in the 2000s (Cooper et al. 2019). However, the Kirtland's warbler population did not subsequently increase until the amount of suitable breeding habitat increased (Donner et al. 2008).



**Fig. 1.** Map of core (hatched) and peripheral (black) Kirtland's warbler (*Setophaga kirtlandii*) management areas (KWMA) in the northern Lower Peninsula of Michigan, USA.

The combined efforts of removing cowbirds and creating nesting habitat over the past 50 years has resulted in the recovery of the Kirtland's warbler from ~200 breeding males in 1971 to >2200 breeding males in 2021 (Bocetti *et al.* 2012; U.S. Fish and Wildlife Service (USFWS) 2019; C. Mensing pers. comm.). The Kirtland's warbler was delisted from the U.S. Endangered Species Act (ESA) in November 2019 (U.S. Fish and Wildlife Service (USFWS) 2019). However, the Kirtland's warbler is a conservation-reliant species, dependent on human intervention (habitat creation and potentially cowbird control) for long-term persistence (Bocetti *et al.* 2012; Rohlf *et al.* 2014). Delisting eliminated all ESA funding for cowbird control, and responsibility for the cowbird control program has shifted to the Michigan Department of Natural Resources (MDNR).

The relatively high cost of cowbird control (~US\$110 000/year) led the USFWS, MDNR, and Kirtland's Warbler Conservation Team ([www.kwconservation.org](http://www.kwconservation.org)) to consider alternative cowbird control strategies to reduce costs while ensuring Kirtland's warbler populations remain stable. Using an adaptive management experiment, Cooper *et al.* (2019) found that gradually reducing and eventually suspending cowbird control across all of the Kirtland's warbler primary breeding range did not lead to an increase in cowbird parasitism, presumably because the brown-headed cowbird population had decreased in Kirtland's warbler breeding areas, the Great Lakes Region, and nationally since trapping began in Michigan in 1972. Based on this information, the cowbird trapping program was suspended while initiating a cowbird monitoring program to ensure that managers would be able to respond quickly to increases in cowbird abundance and Kirtland's warbler nest parasitism. However, without a clear understanding of what the maximum sustainable parasitism rate for the Kirtland's warbler population is or how these rates are related to cowbird abundance, appropriate triggers for reinstatement of the cowbird control program cannot be developed. Kirtland's warbler populations can increase and remain stable under post-trapping levels of parasitism (~1%), and previous population modelling suggested that a return to near pre-trapping levels of parasitism (41–57%) across the northern Lower Peninsula would likely result in the population falling below 200 males (Brown *et al.* 2017). Thus, further information on the long-term suitability of adaptive cowbird control measures throughout the Kirtland's warbler primary breeding range with varying levels of parasitism on the landscape is necessary to determine when and how cowbird control strategies could be re-initiated to ensure long-term Kirtland's warbler persistence.

The objectives of our study were to: (1) confirm cowbird abundance and parasitism of Kirtland's warbler nests remains low after suspension of cowbird trapping in 2018, (2) determine the maximum sustainable parasitism rate for the Kirtland's warbler population, and (3) evaluate the effectiveness of an alternative spatial arrangement of

cowbird traps should trapping be necessary in the future. The spatial structure of the Kirtland's warbler population provides a unique opportunity to test various spatially explicit cowbird control strategies and evaluate the effects on the Kirtland's warbler population. We tested various dispersal rates among spatially concentrated core and peripheral management areas on maximum sustainable parasitism rates. Incorporating dispersal into the population simulation model builds on previous models for the Kirtland's warbler that have focused on incorporating full annual cycle dynamics (Brown *et al.* 2017) and environmental variability (Brown *et al.* 2019) in an effort to mimic real-world processes and produce a model that can inform management decision making.

## Methods

### Study area

Our study area included lands within the KWMA (Fig. 1). These management areas were established based on specific criteria, including on relatively level Grayling sands or closely associated soil types and having jack pine or capable of supporting jack pine, historically occupied by Kirtland's warbler, ≥130 ha in size within close proximity (3 km) to five or more areas, and be in public ownership. (Byelich *et al.* 1985; Kepler *et al.* 1996). This region is the primary breeding habitat for the species and contains >95% of all breeding individuals (U.S. Fish and Wildlife Service (USFWS) 2012).

### Cowbird abundance and nest parasitism

For detailed methods regarding nest searching and point counts, see Cooper *et al.* (2019). Briefly, from 2019 to 2021, we found and monitored Kirtland's warbler nests at 6–9 Kirtland's warbler breeding sites in the northern Lower Peninsula of Michigan. We found 143 nests in 2019, 30 in 2020 (reduced season due to Covid-19), and 153 in 2021. We estimated cowbird abundance at 220 point count locations during 2019–2020 with sampling occurring every 2 weeks and at 228 point count locations during 2021 with sampling occurring every 10 days in May and June. Regardless of year, points were distributed widely across the northern Lower Peninsula breeding areas, including both planted and naturally regenerated habitat of all ages suitable for breeding. Each point count lasted 13.5 min (four 3-min observation periods with 30 s pauses in between), and we used cowbird playback during the final 3 min to increase cowbird detectability (Rothstein *et al.* 2000). We determined the sex of each individual detected using visual and audio cues when possible. We incorporated distance sampling, time-removal, and repeated counts into our sampling design following Hostetter *et al.* (2019) to account for imperfect detection. However, consistent with Cooper *et al.* (2019), we detected so few cowbirds that analysis was not possible,

and therefore we only report the number and locations of cowbirds that were detected. We only report data from the final periods of sampling (16 June–30 June 2019–2020; 21–30 June 2021) because this matches most closely with when cowbird point counts were carried out in the previous study (15 June–15 July).

### Cowbird control model scenarios

We used simulation modelling of the Kirtland's warbler population to estimate the maximum reduction in productivity that the population could sustain without declining within 50 years under different cowbird removal scenarios and Kirtland's warbler dispersal and parasitism rates. These scenarios included (1) complete cowbird removal with a constant parasitism rate based on recent field estimates, which served as the baseline model, (2) no cowbird removal with four different dispersal scenarios, and (3) core-only cowbird removal with four different dispersal scenarios (Table 1). For the no cowbird removal and core-only cowbird removal models, we estimated potential Kirtland's warbler dispersal rates by after-hatch-year (AHY) and

**Table 1.** Estimated threshold brown-headed cowbird (*Molothrus ater*) maximum sustainable parasitism rate for maintaining a stable Kirtland's Warbler (*Setophaga kirtlandii*) population in the Lower Peninsula of Michigan, USA, under different levels of cowbird control and dispersal assumptions.

Model scenarios	Lower CI	Mean $\lambda$	Upper CI	$N < 1000$ (%)
Full cowbird removal	–	–	–	0
No cowbird removal				
Mean HY, mean AHY	15	15	15	1.8
Mean HY, minimum AHY	13	14	14	7.3
Minimum HY, mean AHY	17	18	18	2.3
Minimum HY, minimum AHY	15	16	16	4.7
Core-only cowbird removal				
Mean HY, mean AHY	59	66	70	0.7
Mean HY, minimum AHY	57	62	65	1.1
Minimum HY, mean AHY	83	92	94	0.2
Minimum HY, minimum AHY	83	90	92	2.5

All models include a core and peripheral sub-population. The full cowbird removal model includes a parasitism rate of 0.54% in both sub-populations. The core-only models assume no cowbird removal in the peripheral sub-population, with four dispersal scenarios tested (minimum and mean distance moved for hatch-year [HY] and after-hatch-year [AHY] birds). Lower CI, Mean  $\lambda$ , and Upper CI represent the maximum parasitism rate (%) in the peripheral areas for core-only scenarios and in the core and peripheral areas for no removal scenarios that can occur before the lower bound of the 95% confidence interval, mean population growth rate ( $\lambda$ ), and upper bound of the 95% confidence interval decrease below 1, respectively. In addition, we report the proportion of simulations where the total population dropped below 1000 males under each scenario, based on the Mean  $\lambda$  parasitism threshold.

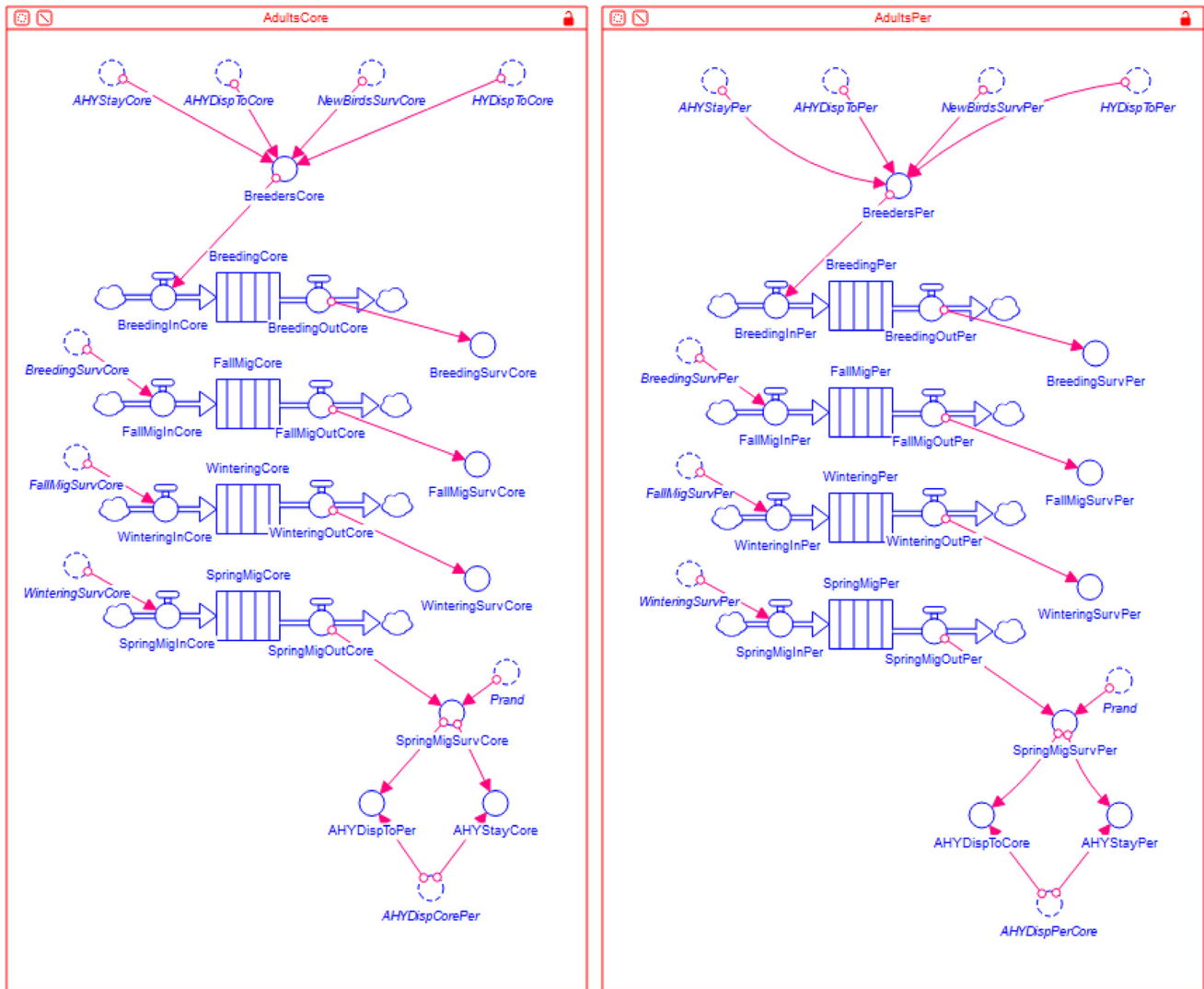
hatch-year (HY) males, testing all combinations of dispersal proportions based on mean and minimum distances between core and peripheral sub-populations (mean HY and mean AHY, mean HY and minimum AHY, minimum HY and mean AHY, minimum HY and minimum AHY; see Model Parameterisation section for further information). We used the mean HY and AHY dispersal rates for the baseline model. We estimated maximum sustainable parasitism rate to the nearest 1%.

For each model scenario, we projected the population for 50 years and completed 1000 replications. To estimate long-term population growth, we computed annual growth rates over the 50-year simulation based on total breeding bird abundance at each time step ( $\lambda = N_{t+1}/N_t$ ). Each simulation began with the population at carrying capacity. We then calculated the geometric mean and 95% confidence interval (CI) for  $\lambda$  (based on a *t*-distribution; Stevens 2009). Using the maximum sustainable parasitism rate, we computed the proportion of years where total abundance fell below 1000 males, which is the perpetual goal for minimum number of breeding pairs (U.S. Fish and Wildlife Service (USFWS) 2018).

### Model parameterisation

For the full cowbird removal scenario, we modified a previously developed base population simulation model for the Kirtland's warbler for a single population (Brown et al. 2019) to include two spatially structured sub-populations based on the geographic location of the KWMA (core and peripheral; Figs 2, 3) to incorporate the influence of cowbird parasitism on productivity. The model links population demographics with temporally dynamic environmental conditions on the breeding and wintering grounds, using the program STELLA Professional (ver. 1.9.1; isee systems, Lebanon, New Hampshire, USA). Environmental conditions on the breeding grounds influence productivity, and environmental conditions on the wintering grounds influence survival and productivity. Most of the data available for model parameterisation are based on male observations, and thus it is structured as a single-sex model based on male empirical data. The model was found to perform well for simulating Kirtland's warbler population dynamics based on deterministic model simulation results compared to observed abundances from the annual Kirtland's warbler breeding male census (Brown et al. 2019).

Here, we provide a concise overview of the model. For a more detailed description of the model specification, see Brown et al. (2017, 2019). Adult male (i.e. AHY) annual survival is modelled as a function of wintering grounds habitat quality, using estimates from an empirical study on Kirtland's warbler (Rockwell et al. 2017). Baseline AHY annual survival is 0.4544 and increases by 0.0395 with every 1 cm increase in wintering grounds precipitation. Annual AHY survival is bounded by the highest empirical estimate (0.75; Probst 1986). Mean hatch-year (HY) survival



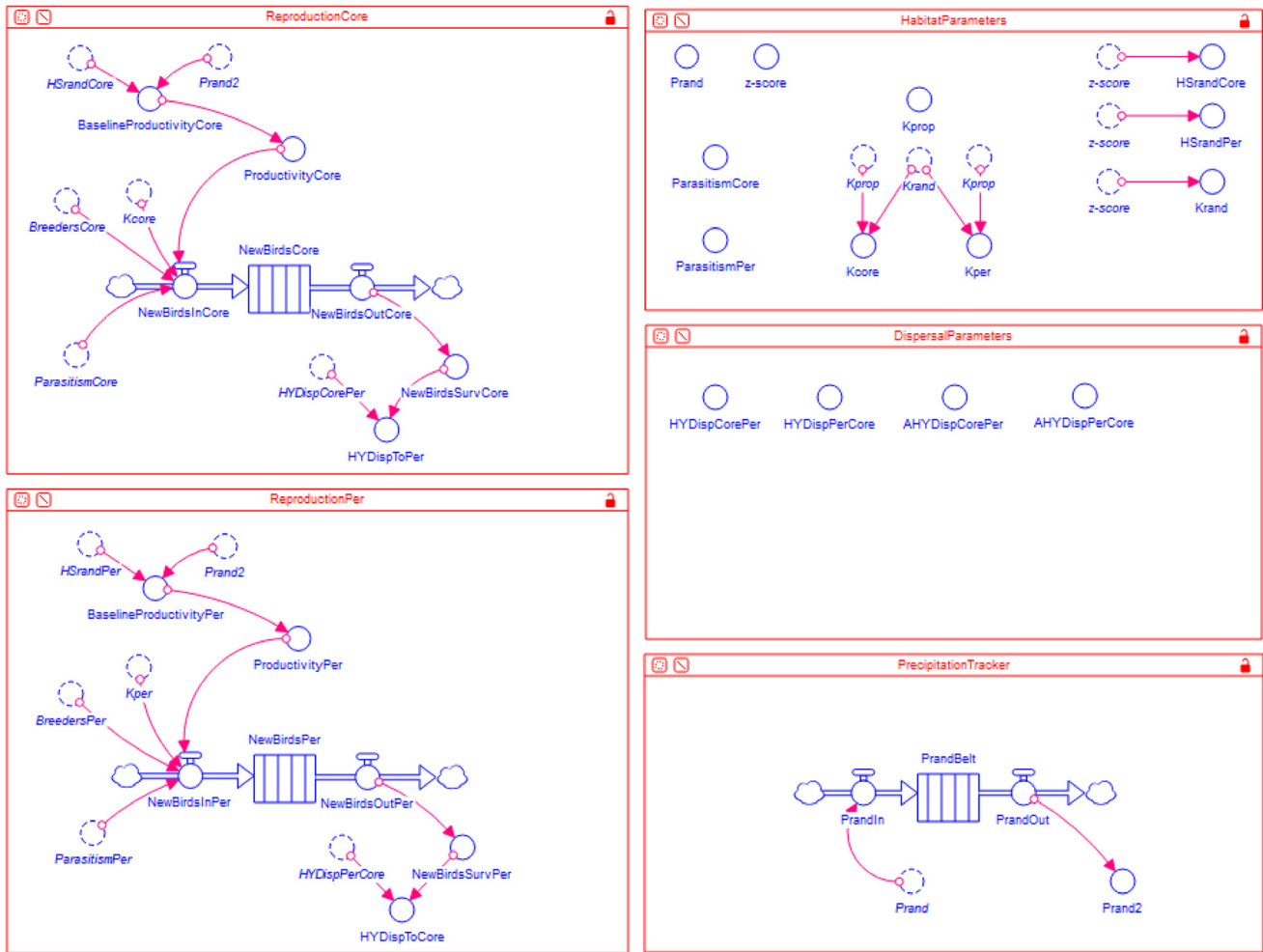
**Fig. 2.** Kirtland’s warbler (*Setophaga kirtlandii*) population simulation model developed using the program STELLA Professional (ver. 1.7.1). The model contains stocks (rectangles) that hold birds during discrete time steps, flows (clouds and regulators connected by arrows) that move birds into and out of stocks (potentially using an equation), converters (circles) that contain values or equations and influence flows, and connectors (arrows) that link the model components. Converters with broken lines indicate ‘ghosts’, where the original converter is located elsewhere in the model. The ‘AdultsCore’ and ‘AdultsPer’ submodels track survival and dispersal of birds in the core and peripheral populations, respectively. Individuals in the sub-populations are able to remain in the population (AHYStayCore/Per, NewBirdsSurvCore/Per), or disperse to the other sub-population (HYDispToCore/Per, AHYDispCorePer/PerCore). Wintering grounds precipitation (Prand; see Fig. 3 for complete description) influences annual survival of individuals in both core (SpringMigSurvCore) and peripheral sub-populations (SpringMigSurvPer).

represents the average estimate under current environmental conditions (0.35; Rockwell *et al.* 2017).

Annual Kirtland’s warbler per capita AHY male production is modelled as a function of wintering and breeding grounds habitat quality, based on estimates from empirical studies on Kirtland’s warbler (Probst 1986; Rockwell *et al.* 2012). To allow both wintering and breeding grounds habitat quality to influence production of birds, the equation includes two predictive components. The first component estimates baseline productivity based on the mean of an annual breeding grounds habitat quality index ( $0.678 + 0.1334[HQ]$ ; HQ index potential

range = 1–3). The second component estimates productivity above the baseline with every 1 cm increase in precipitation ( $0.168[P]$ ). Maximum AHY male production is bounded by the highest empirical estimate (i.e. 2.19 male fledglings per male; Shake and Mattsson 1975).

Annual Kirtland’s Warbler carrying capacity is modelled as a function of quantity and quality of breeding habitat, using temporal variation in mean density of AHY males as a proxy for variation in habitat quality. For habitat quantity, we used the long-term target annual habitat quantity to be suitably-aged for nesting defined by the Kirtland’s Warbler



**Fig. 3.** Kirtland's warbler (*Setophaga kirtlandii*) population simulation model developed using the program STELLA Professional (ver. 1.7.1). The 'ReproductionCore' and 'ReproductionPer' submodels simulate the new breeders produced each year in the core and peripheral sub-populations, respectively. Annual productivity is influenced by precipitation on the wintering grounds, breeding grounds habitat suitability, breeding grounds carrying capacity, and number of potential breeders. The 'PrecipitationTracker' submodel is used for tracking precipitation (Prand) in year X and X – 1. The 'HabitatParameters' submodel contains statistical distributions to draw annual values for wintering grounds precipitation (Prand), breeding grounds habitat suitability for the core (HSrandCore) and peripheral (HSrandPer) sub-populations, breeding grounds carrying capacity in the core (Kcore) and peripheral (Kper) sub-populations, and breeding ground nest parasitism in the core (ParasitismCore) and peripheral (ParasitismPer) sub-populations. Each year, z-score values are drawn and used to obtain the corresponding HSrandCore, HSrandPer, Kcore, and Kper values, whereas Prand is drawn from an independent distribution.

Conservation Team (14 593 ha; U.S. Fish and Wildlife Service (USFWS) 2018). To obtain annual breeding grounds carrying capacity, quantity of breeding habitat is multiplied by mean density of AHY males. The model includes ceiling-type density dependence, which allows populations to grow exponentially until they reach carrying capacity (Akçakaya et al. 2004). When the population exceeds the carrying capacity, reproduction is restricted to the carrying capacity, with the remaining individuals allowed to survive, but not reproduce. Thus, the population can exceed the model carrying capacity, but at the cost of reduced per capita productivity.

The model incorporates demographic and environmental stochasticity. Demographic stochasticity in AHY and HY male annual survival is incorporated by drawing values from a binomial distribution that is parameterised using initial abundance and model-predicted (AHY) or specified (HY) mean annual survival (Akçakaya 1991). Environmental stochasticity in annual carrying capacity is incorporated by drawing mean density values from a Gaussian distribution based on empirical data from 2004 to 2017 (mean = 0.1307/ha, s.d. = 0.0076). Environmental stochasticity in annual productivity is incorporated by drawing breeding grounds habitat quality index values from a Gaussian distribution



based on empirical data from 2004 to 2013 (mean = 2.35, s.d. = 0.05), and wintering precipitation values from a log-normal distribution based on empirical data from 1994 to 2013 (mean = 3.419 cm, s.d. = 2.771). To align annual habitat quality on the breeding grounds, the model draws a habitat quality value from a  $z$ -distribution, and then transforms the  $z$ -score to create the corresponding value for each distribution. To portion the total annual carrying capacity into the two sub-populations, we computed the mean proportion of breeding habitat from 2004 to 2013 in the core (0.79) and peripheral (0.21) sub-populations and assumed this proportion would be similar in future years. The standard deviation for this 10-year period was 0.02, indicating high consistency in proportion of habitat between core and peripheral sub-populations over time.

To account for the spatial structure in cowbird removal scenarios, we incorporated annual Kirtland's warbler dispersal rates between the core and peripheral sub-populations. We used interannual mark-resight data collected on AHY males during the breeding season from 1985 to 2001, which included 343 breeding dispersal events. We computed the proportion of interannual movement distances that exceeded the minimum distance (14.5 km) between core and peripheral KWMA (0.137), as well as the proportion of movement distances that exceeded the mean distance (49.9 km) needed to move from core to peripheral KWMA (0.047) and the mean distance (34.2 km) from peripheral to core KWMA (0.076). We did not have enough re-sighting data from HY birds to use the same approach for natal dispersal. We therefore used available data on breeding and natal dispersal distances from 47 passerine species (Paradis *et al.* 1998) to calculate the mean magnitude of difference between breeding and natal dispersal across these species, finding that natal dispersal distance was on average 2.58 times greater than breeding dispersal distance. We multiplied each breeding dispersal distance in our dataset by 2.58 to simulate a distribution of plausible natal dispersal distances for Kirtland's warblers. Using this distribution, we computed the proportion of simulated natal dispersal events that exceeded the minimum distance from core to peripheral sites (0.198), and the proportion that exceeded the mean distance from core to peripheral sites (0.122) and from peripheral sites to the core (0.146).

To incorporate varying rates of cowbird parasitism on Kirtland's warbler productivity, we used the level of cowbird removal as a proxy for parasitism in the productivity equation that represented a proportional reduction in annual productivity due to parasitism (hereafter parasitism rate). For the full cowbird removal scenario, we fixed the parasitism rate to 0.54%, based on empirical data that found two of 370 Kirtland's warbler nests were parasitised between 1990 and 2014, the year prior to a reduced-trapping experiment (Bocetti 1994; Rockwell 2013; Cooper *et al.* unpubl. data; Cooper *et al.* 2019). For the remaining scenarios, we increased the parasitism rate until a population decline was

detected based on the mean and 95% CI for  $\lambda$  from 1000 replications.

## Results

### Cowbird abundance and nest parasitism

From 2019 to 2021, we found 326 Kirtland's Warbler nests and five (1.5%) were parasitised by cowbirds. Four parasitised nests were found in 2019, all at the same site, while the fifth was found at a different site in 2021. This represents a slight increase in parasitism rate compared to our previous results with a reduced trapping effort (2015–2017; three of 384 nests [0.8%]) and when trapping was completely suspended (2018; one of 130 nests [0.8%]; Cooper *et al.* 2019). In total, only six of 456 (1.3%) nests have been parasitised since suspension of the trapping program in 2018.

In 2019, we detected a total of 20 cowbirds (16 male, four female) at three sites. Nineteen of 20 (95%) cowbirds were detected at two sites (North and South Tawas) located in the most eastern KWMA. Zero cowbirds were detected in the final period of sampling at the only site where parasitism occurred in 2019, but two cowbirds each were detected in the previous three sampling periods at that site. In 2020, we detected a total of 28 cowbirds (19 male, nine female) at five sites, 16 (57%) of which were at North and South Tawas where nearly all cowbird detections occurred in 2019. In 2021, we detected a total of 48 cowbirds (26 male, three female, 19 unknown) at six sites. Most (33 of 48; 69%) were again detected at North and South Tawas, where the one parasitised nest from 2021 was found.

### Cowbird control model scenarios

Under the full cowbird removal scenario with fixed parasitism rate, the Kirtland's Warbler population was stable over the 50-year simulation period ( $\lambda = 1.0019$  [1.0016–1.0022]) and no simulated populations fell below 1000 males. Under the no cowbird removal scenario, the maximum sustainable parasitism rate throughout the study area was 13–18% depending on the dispersal scenario and confidence limit considered (Table 1). Under the core-only cowbird removal scenario, the maximum sustainable parasitism rate was 57–94% in peripheral areas depending on the dispersal scenario and confidence limit considered (Table 1). The assumed dispersal distance for HY males had the largest impact on model inferences, with a mean and minimum dispersal distance resulting in a sustainable parasitism rate of 57–70% and 83–94%, respectively (Table 1). Using the maximum sustainable parasitism rate to retain  $\lambda \geq 1$  for each scenario, the percentage of simulated populations that fell below 1000 males during the 50-year simulation was

0.2–2.5% for the core-only removal scenario and 1.8–7.3% for the no removal scenario (Table 1).

## Discussion

Our cowbird population monitoring and Kirtland's warbler nest searching efforts confirmed that despite complete suspension of the cowbird trapping program since 2018, both cowbird abundance and nest parasitism continue to remain low in the northern Lower Peninsula of Michigan (~1.3%). Our simulation model indicates that if cowbird populations recovered and trapping was not reinstated, Kirtland's warblers could withstand a maximum rate of 13–18% reduction in annual reproduction due to parasitism before the population would begin to decline. However, a much higher rate of parasitism in peripheral areas could be withstood as long as trapping was fully reinstated in the core area. By incorporating spatial design in the cowbird control program, managers can consider the tradeoffs between risk of parasitism and cost of implementing the program to best manage the Kirtland's warbler population post-delisting.

While relaxing cowbird control measures appears to have no noticeable negative effects on Kirtland's warblers currently, monitoring will be crucial to verify whether cowbird abundances and parasitism rates continue to remain low and thus have minimal impacts on the Kirtland's warbler population. In contrast to our study, at Fort Hood, Texas, USA, parasitism rates of black-capped vireos increased ~2 years after managers eliminated removal of cowbirds, indicating the possibility of a delayed effect of trapping suspension (Kostecke *et al.* 2010). However, differences in responses observed at Fort Hood and what we report may be attributed to land cover. Fort Hood is surrounded by agriculture, while forested land in Michigan has increased by over 800 000 ha since 1980 (Pugh 2018), much of which is the reversion of agriculture to forest land. The reduced presence of agriculture, which is a primary feeding cover type for cowbirds, can strongly limit the distribution of cowbirds, and removing feeding areas has been suggested as a key cowbird control measure (Chace *et al.* 2005). Thus, increased proportions of forest cover in northern Lower Michigan landscapes has likely reduced cowbird abundance independent of cowbird control measures (Cooper *et al.* 2019). However, future consideration should be given to the possibility that increased urbanisation and associated changes in land cover in the region could supplement cowbirds in lieu of agriculture. An important consideration for the continual monitoring efforts of cowbirds and their impact on Kirtland's warbler is the correlation between cowbird abundance and nest parasitism rates, and nest parasitism rates and Kirtland's warbler productivity. Assessing cowbird abundance via point counts could act as a cost-effective surrogate for estimating nest parasitism rates, which would eliminate the need

for intensive demographic field studies. The relationship between cowbird removal, parasitism rate, and productivity has been defined for this population (Kelly and DeCapita 1982), but the cowbird abundance threshold where trapping should be reimplemented to reduce the effect of nest parasitism has yet to be determined. Continued monitoring of cowbird abundances and Kirtland's warbler reproductive success should provide greater insight into this relationship and help managers determine if and when cowbird control measures need to be reinstated.

If cowbird populations increase over time, a spatially structured control design seems to be a promising alternative to the historical trapping approach that places traps near all nesting Kirtland's warblers. Our results are similar to previous simulation models that found trapping only in the core breeding area was effective at preventing rapid population decline as long as cowbird parasitism reduced Kirtland's warbler productivity by  $\leq 41\%$  in patches where trapping was not implemented (Brown *et al.* 2017). Our results indicate that the Kirtland's warbler population may be able to withstand much greater rates of parasitism in peripheral breeding habitat. One of the primary differences between our model and Brown *et al.* (2017) was that we retained the ability of floaters (i.e. individuals beyond carrying capacity) to survive (but not breed), whereas floaters were killed in Brown *et al.* (2017). Thus, in our model, floaters are able to buffer the impact of reduced reproductive success (Barabás *et al.* 2004; Robles and Ciudad 2017) and increase resilience from demographic and environmental stochasticity (Harrison 1991; Hanski and Gyllenberg 1993). Our decision to keep floaters in the population is consistent with territoriality patterns in birds (Newton 1992; Penteriani *et al.* 2011). Additionally, growth rates from population models may have limited practical use if floaters are ignored (Lee *et al.* 2017), indicating that incorporating floaters into our modeling framework provided a more realistic representation of population dynamics, as long as floaters can become breeders if habitat is available (Newton 1992; Marra and Holmes 1997; Cooper *et al.* 2009). Moreover, floaters create surplus individuals that can disperse from core to peripheral management areas or vice-versa. This movement between sub-populations allowed surplus immigrants to offset losses from cowbird parasitism and is likely why dispersal had the greatest influence on maximum sustainable parasitism rates in our study. However, there is currently much to learn about dispersal and the processes that inform it for the Kirtland's warbler (Cooper and Marra 2020) and birds more generally (Ponchon *et al.* 2013). Accounting for species-specific dispersal and the processes that inform it will continue to advance these types of population models (Ponchon *et al.* 2015).

Our model assumed that habitats in the peripheral KWMA were equally suitable for colonisation, and breeding success in these patches was only constrained by brood parasitism, which may be a simplification of the extrinsic growth

factors exerted on populations. Density of Kirtland's warblers was historically different among jack pine regeneration methods (e.g. wildfire, plantation, and natural regeneration following disturbance) with the higher stem density wildfire-regenerated habitat being considered optimal habitat (Probst and Weinrich 1989; Bocetti 1994). However, most nesting habitat since the mid-1990s has been regenerated through high-stem density plantations interspersed with small openings (i.e. traditional management; Donner *et al.* 2008) regardless of where within the primary breeding range, which likely minimises differential habitat quality across the Kirtland's warbler breeding area. However, it is important to note that we assumed land management agencies can meet habitat regeneration goals established in the current memorandum of understanding (Michigan Department of Natural Resources (MDNR), United States Fish and Wildlife Service, and United States Forest Service 2015), and habitat availability and corresponding carrying capacity of the Kirtland's warbler population will remain relatively consistent in the future. If regeneration of jack pine habitat goals are not met, however, the Kirtland's warblers may be less resilient to increases in cowbird parasitism than our models indicate.

Even if habitat regeneration goals are met in the near future, the overall quality of habitat may still change. Under the current conservation plan, 25% of newly created nesting habitat will be regenerated through non-traditional stocking techniques, such as reduced planting density of jack pine or interplanting of red pine (*Pinus resinosa*) and jack pine (Michigan Department of Natural Resources (MDNR), United States Fish and Wildlife Service, and United States Forest Service 2015). Planting red pine in combination with jack pine has been suggested to provide the structural characteristics at a lower cost and to offset lost timber revenue from dense jack pine stands with slower growth. Kirtland's warbler has used jack pine-red pine stands historically (Buech 1980; Probst 1988; Van Dyke *et al.* 2022) and within areas outside of their core breeding habitat (Anich *et al.* 2011; Olah *et al.* 2022), when adequate amounts of suitable nesting habitat (i.e. pure jack pine stands) was not available on the broader landscape in context to the population level. Brown *et al.* (2017) simulated the effects of current management (constant habitat suitability across breeding range) and experimental jack pine management (i.e. non-traditional, reduced habitat suitability across 25% of breeding range) on the Kirtland's warbler population and concluded that population growth was similar between both scenarios ( $\bar{\lambda} = 0.995$  for current management,  $\bar{\lambda} = 0.994$  for experimental management) over a 50-year period. However, the implications of potentially reduced habitat quality in mixed forests (relative to jack pine plantations) on colonisation and parasitism rates for the long-term productivity of Kirtland's warbler remains unclear.

Climate changes on the breeding and wintering grounds, particularly changes in precipitation, could also influence long-term population viability of Kirtland's warbler. Donner

*et al.* (2018) projected that climatic suitability for jack pine will decrease in Michigan this century, although core KWMA were projected to be less impacted than peripheral KWMA. Additional studies using a variety of modelling techniques generally agree that climate change will likely negatively impact jack pine in the Upper Midwest (Iverson *et al.* 2008; Handler *et al.* 2014). In a precursor to this study, Brown *et al.* (2019) projected that spring precipitation changes on the wintering grounds could result in the decline or extinction of Kirtland's warbler, based on empirical studies linking wintering grounds precipitation to survival and productivity (Rockwell *et al.* 2012, 2017). However, current climate models dramatically differ in future precipitation projections for the Bahamas, and the population remained stable for the majority of the climate models. For this study, we chose not to incorporate climate change because of the high uncertainty in future precipitation dynamics. However, the status of the Kirtland's warbler will depend largely on the continued creation of high-quality habitat into the future, and our results continue to support that some level of cowbird control may be necessary in mixed forest patches to offset any reduced productivity associated with mixed forests stands and climate change (Brown *et al.* 2019).

Our simulation study indicated that different cowbird control scenarios have varying effects on the rate of parasitism that the Kirtland's warbler population is able to withstand before declining. While each cowbird control measure that we assessed has its benefits and drawbacks, an approach that accounts for the spatial structure of the host species distribution seems to be a promising initial step towards an effective and efficient cowbird control program in the future. Continued development and testing of similar adaptive management strategies for the Kirtland's warbler and other cowbird host species will provide managers with better insight on how to design cowbird control programs across large landscapes.

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**Data availability.** Data are available upon request from the corresponding author.

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