

Apparent annual survival of adult *Vermivora chrysoptera* (Golden-winged Warbler) does not differ by sex or region

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ABSTRACT

Understanding range-wide demographic, spatial, and temporal variation in annual survival is essential for managing species of conservation concern. Multi-population models are useful tools for integrating diverse datasets, reducing biases, and deriving survival estimates across differing spatial scales. We conducted a range-wide, multi-population apparent annual survival analysis for a declining songbird, *Vermivora chrysoptera* (Golden-winged Warbler), using data from 18 sites across its breeding and nonbreeding grounds. This Nearctic-Neotropical migrant breeds in 2 disjunct regional populations, the Great Lakes and Appalachian Mountains, which are experiencing different rates of decline. We aimed to quantify regional-, site-, and sex-specific apparent annual survival estimates to identify geographic patterns or demographic factors influencing population declines. We used simulations to assess the precision of our estimates. Our models did not reveal a substantial difference in apparent annual survival between the Great Lakes (0.41, 95% credible interval (CrI): 0.31–0.50) and the Appalachian regions (0.49, 95% CrI: 0.36–0.60), as CrIs overlapped. Site-specific estimates also showed no clear differences in apparent annual survival among sites representing both regional populations. Male apparent annual survival tended to be greater than female apparent annual survival in both regions, though CrI's overlapped. Our study suggests demographic factors other than adult annual survival likely play a larger role in recent regional and range-wide population declines, such as productivity, juvenile/immature survival, or recruitment. Simulations indicate that improving recapture probability and study duration of datasets could lead to more precise apparent annual survival estimates. However, our model produced CrI ranges comparable to the most ideal data collection scenario, suggesting the lack of trends we found was not due to variability in our estimates. We stress the importance of addressing inherent biases in survival datasets and the need for standardized collaborative efforts to inform species conservation on a range-wide scale.

Keywords: annual survival, demographic variability, Golden-winged Warbler, multi-population model, *Vermivora chrysoptera*

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LAY SUMMARY

- *Vermivora chrysoptera* (Golden-winged Warbler) is a declining songbird breeding within 2 disjunct regional populations. The Appalachian Mountains population has undergone significantly higher population declines relative to the Great Lakes population; however, the drivers behind these declines are not well understood.
- We conducted a range-wide apparent annual survival analysis to obtain spatial and demographic survival estimates for adult *V. chrysoptera* and paired this analysis with a simulation exercise to gauge the precision of our estimates.
- Apparent annual survival rates of the Great Lakes and the Appalachian populations were statistically similar. While males tended to have greater apparent annual survival rates than females, overlapping credible intervals made it difficult to infer sex-specific differences.
- Our study suggests that factors such as productivity, juvenile/immature survival, or recruitment may play a more significant role in regional population declines over the past 2 decades than adult annual survival. An integrated population model would help to elucidate specific limiting factors.
- We emphasize the importance of standardizing data collection methods across studies for focal species to improve the precision of multi-population models and to better inform conservation efforts.

La supervivencia anual aparente de adultos de *Vermivora chrysoptera* puede no diferir según el sexo o la región

RESUMEN

Comprender la variación demográfica, espacial y temporal de la supervivencia anual a lo largo de toda la distribución es esencial para manejar especies de interés para la conservación. Los modelos multi-poblacionales son herramientas útiles para integrar diversos conjuntos de datos, reducir sesgos y obtener estimaciones de supervivencia a diferentes escalas espaciales. Realizamos un análisis multi-poblacional de la supervivencia anual aparente en toda la distribución de una especie de ave canora en declive, *Vermivora chrysoptera*, utilizando datos de 18 sitios a lo largo de sus áreas reproductivas y no reproductivas. Este migrante neártico-neotropical se reproduce en dos poblaciones regionales disjuntas, los Grandes Lagos y las Montañas Apalaches, que están experimentando diferentes tasas de declive. Nuestro objetivo fue cuantificar estimaciones de supervivencia anual aparente específicas por región, sitio y sexo para identificar patrones geográficos o factores demográficos que influyen en los declives poblacionales. Utilizamos simulaciones para evaluar la precisión de nuestras estimaciones. Nuestros modelos no revelaron una diferencia sustancial en la supervivencia anual aparente entre las regiones de los Grandes Lagos (0,41, intervalo creíble [ICr] del 95%: 0,31–0,50) y los Apalaches (0,49, ICr 95%: 0,36–0,60), ya que los intervalos creíbles se superponen. Las estimaciones específicas por sitio tampoco mostraron diferencias claras en la supervivencia anual aparente entre los sitios que representan ambas poblaciones regionales. La supervivencia anual aparente de los machos tendió a ser mayor que la de las hembras en ambas regiones, aunque los intervalos creíbles se superponen. Nuestro estudio sugiere que otros factores demográficos distintos a la supervivencia anual de adultos probablemente desempeñan un papel mayor en los recientes declives poblacionales regionales y a escala de distribución, tales como la productividad, la supervivencia de juveniles/inmaduros o el reclutamiento. Las simulaciones indican que mejorar la probabilidad de recaptura y la duración de los estudios de las bases de datos podría conducir a estimaciones más precisas de la supervivencia anual aparente. Sin embargo, nuestro modelo produjo rangos de intervalos creíbles comparables al escenario más ideal de recolección de datos, lo que sugiere que la ausencia de tendencias que encontramos no se debió a la variabilidad en nuestras estimaciones. Destacamos la importancia de abordar los sesgos inherentes en las bases de datos de supervivencia y la necesidad de esfuerzos colaborativos estandarizados para contribuir a la conservación de la especie a escala de toda su distribución.

Palabras clave: modelo multi-poblacional, supervivencia anual, variabilidad demográfica, *Vermivora chrysoptera*

INTRODUCTION

Species experiencing notable population decline often require an understanding of demographic, spatial, and temporal variation in vital rates to identify drivers of decline and to implement effective conservation strategies (Green 1999, Dirzo *et al.* 2014). Understanding variation is of particular significance for species that experience heterogeneous rates of decline based on geographic location (Tilman and Kareiva 1997, Hanski 1999). Teasing apart geographic variation in vital rates can be facilitated in part by implementing multi-population survival models used to obtain survival estimates that are geographically-specific, while accounting for demographic (e.g., age and sex) variation (Paradis *et al.* 2000, Frederiksen *et al.* 2005, Grosbois *et al.* 2008, 2009). Most single-population survival models rely on capture–mark–recapture (CMR) datasets, which involve monitoring individuals over multiple time periods at local spatial scales to estimate survival (Cormack 1964, Jolly 1965, Seber

1965, Lebreton *et al.* 1992). Implementing multi-population models, however, requires numerous CMR datasets from different populations across a species' distribution. Although hierarchical and multi-population studies have become more common in recent years (Papadatou *et al.* 2011, Saracco *et al.* 2012, Rushing *et al.* 2017), relatively few species have been studied comprehensively enough across their geographical range to allow for meaningful spatial, temporal, and demographic comparisons (Koenig 1999, Frederiksen *et al.* 2005, Fayet *et al.* 2021). These data gaps often reflect the difficulty of conducting long-term, geographically distributed studies with sufficient sampling intensity, which requires substantial interest, funding, time, and coordination across time and research teams.

Vermivora chrysoptera (Golden-winged Warbler) has generated considerable interest in its demography because of long-term, range-wide population declines (Rosenberg *et al.* 2016, Hostetler *et al.* 2023). Contemporary *V. chrysoptera* has 2 geographically distinct populations: the Appalachian

Mountains (hereinafter, Appalachian), where ~2.49% of the global breeding population occurs (BBS Region S28), and the Great Lakes, where an estimated 77.7% of the global breeding population occurs (BBS Region S12; Buehler *et al.* 2007, Rosenberg *et al.* 2016, Will *et al.* 2020, Ziolkowski *et al.* 2022). The 2 populations exhibit strong migratory connectivity structure, with individuals from the Great Lakes overwintering in Central America and individuals from the Appalachians overwintering in northern South America (Larkin *et al.* 2017, Kramer *et al.* 2018). These 2 regional populations significantly differ in their rates of decline, with the Great Lakes population declining at a much lesser rate (-0.27% year⁻¹, 95% CL: -1.22 to 0.64 ; Breeding Bird Survey [BBS] Region S12) than the Appalachian population (-6.51% year⁻¹, 95% CL: -7.76 to -5.27 ; BBS Region S28) from 1966 to 2022 (Hostetler *et al.* 2023). Differential rates of declines have been hypothesized to result from several factors, including a greater loss of early-successional habitat in the Appalachians (Buehler *et al.* 2007), historic loss of nonbreeding habitat in South America relative to Central America (Kramer *et al.* 2018), and increased hybridization in the Appalachians due to greater range overlap with *Vermivora cyanoptera* (Blue-winged Warbler) (Rosenberg *et al.* 2016). Additional differential rates of decline have been attributed to variation in vital rates, such as annual survival (Aldinger 2018, McNeil *et al.* 2020a, 2024). Given its rapid decline, *V. chrysoptera* is listed as federally Threatened in Canada under the Species at Risk Act, a tipping point species in the 2022 State of the Birds Report (North American Bird Conservation Initiative 2022), Near Threatened on the IUCN Red List (BirdLife International 2018), and is currently under review for protection under the US Endangered Species Act (Roth *et al.* 2019).

In efforts to elucidate primary drivers of decline, local apparent annual survival rates (which conflate true survival and dispersal rates) for *V. chrysoptera* have been estimated in several CMR studies throughout their range. A significant effect of age has been found, with adults (after-hatch-year [AHY]) exhibiting higher apparent annual survival than juveniles (Aldinger 2018). Alternatively, no site- or region-specific differences in apparent annual survival have been identified (Bulluck *et al.* 2013, Aldinger 2018). Collectively, the range of site-specific mean apparent annual survival estimates from studies depicting the Great Lakes population (0.43–0.62) is similar to the range of mean estimates for studies depicting the Appalachian region (0.48–0.62), suggesting that there may not be regional variation in survival (Chandler 2011, Bulluck *et al.* 2013, Aldinger 2018, Ritterson *et al.* 2021). Lastly, the effect of sex remains unclear, with one study reporting lower apparent annual survival in females (Bulluck *et al.* 2013), and another reporting no difference between sexes (Aldinger 2018).

While site-specific apparent survival estimates have advanced our understanding of individual *V. chrysoptera* populations (Chandler 2011, Bulluck *et al.* 2013, Aldinger 2018, Ritterson *et al.* 2021), they offer an incomplete picture for broader-scale conservation planning. Insights into range-wide population dynamics may be obscured or exaggerated if temporal, spatial, or demographic differences in local population estimates are overlooked (Paradis *et al.* 2000, Grosbois *et al.* 2009, Papadatos *et al.* 2012). Because *V. chrysoptera* breed in 2 allopatric regions and exhibit strong migratory connectivity structure, populations are exposed to different ecological communities and environments that potentially shape distinct behaviors and

demographic trends. Additionally, males and females may differ in habitat use, migratory behavior, or exposure to ecological pressures, which could contribute to sex-specific differences in survival, as observed in other passerines (summarized in Mumme 2024). Thus, range-wide population estimates may be influenced by a suite of biophysical conditions encountered by individuals, emphasizing the need to understand demographic and spatial differences in annual survival.

Because of concern about population declines, extensive research on *V. chrysoptera* has been conducted over the past half-century, with dozens of researchers across the species' distribution capturing, uniquely marking, and reencountering individual warblers to understand fecundity, dispersal, migration, and population demography (summarized by Buehler *et al.* 2007, Roth *et al.* 2019). The resultant species-specific CMR datasets present a unique opportunity to integrate range-wide datasets into a multi-population framework to derive regional estimates of apparent annual survival. There are several advantages of sharing data and implementing multi-population models to gain insights into a species' ecology and conservation, particularly for those experiencing decline. Sharing information across datasets can reduce the influence of site-specific factors, such as vegetation composition and predator communities (e.g., Confer *et al.* 2020). Additionally, by combining data from different studies, statistical power is improved, and data gaps are filled through inferences obtained iteratively by means of conditional likelihoods (Leasure *et al.* 2019).

This study aimed to quantify spatial and sex-specific differences in adult apparent annual survival of *V. chrysoptera* to test the hypothesis that variation in annual survival may be contributing to region-specific population declines. To achieve this, we compiled an array of *V. chrysoptera* CMR datasets for integration into a multi-population survival model, enabling the estimation of apparent annual survival at regional and site-specific scales. Despite prior studies finding no notable differences in apparent annual survival rates among regions or local sites (Bulluck *et al.* 2013, Aldinger 2018), we anticipated that expanding the range-wide sample sizes would reveal greater apparent survival rates in the Great Lakes than the Appalachian region, reflecting the much lower rate of decline (Hostetler *et al.* 2023). We also expected lesser apparent survival estimates for females than males, consistent with patterns observed in other passerine species and given that female *V. chrysoptera* tend to inhabit lower quality habitat on the nonbreeding grounds (Bennett *et al.* 2019). Additionally, we conducted a simulation using model output to assess the precision of our findings and to explore scenarios that could enhance precision and optimize future monitoring protocols for *V. chrysoptera*. Apparent survival estimates from our models could improve our understanding of adult survival as a driver of population trends in *V. chrysoptera* and could support conservation strategies that are responsive to differences in survival across sites, regions, years, and between sexes.

METHODS

Data Collection and Organization

We analyzed *V. chrysoptera* CMR data from 18 sites across the breeding and nonbreeding grounds (Figure 1). We identified and collected applicable datasets through a literature review and through the Golden-winged Warbler Working Group network (www.gwwa.org). Datasets spanned a range

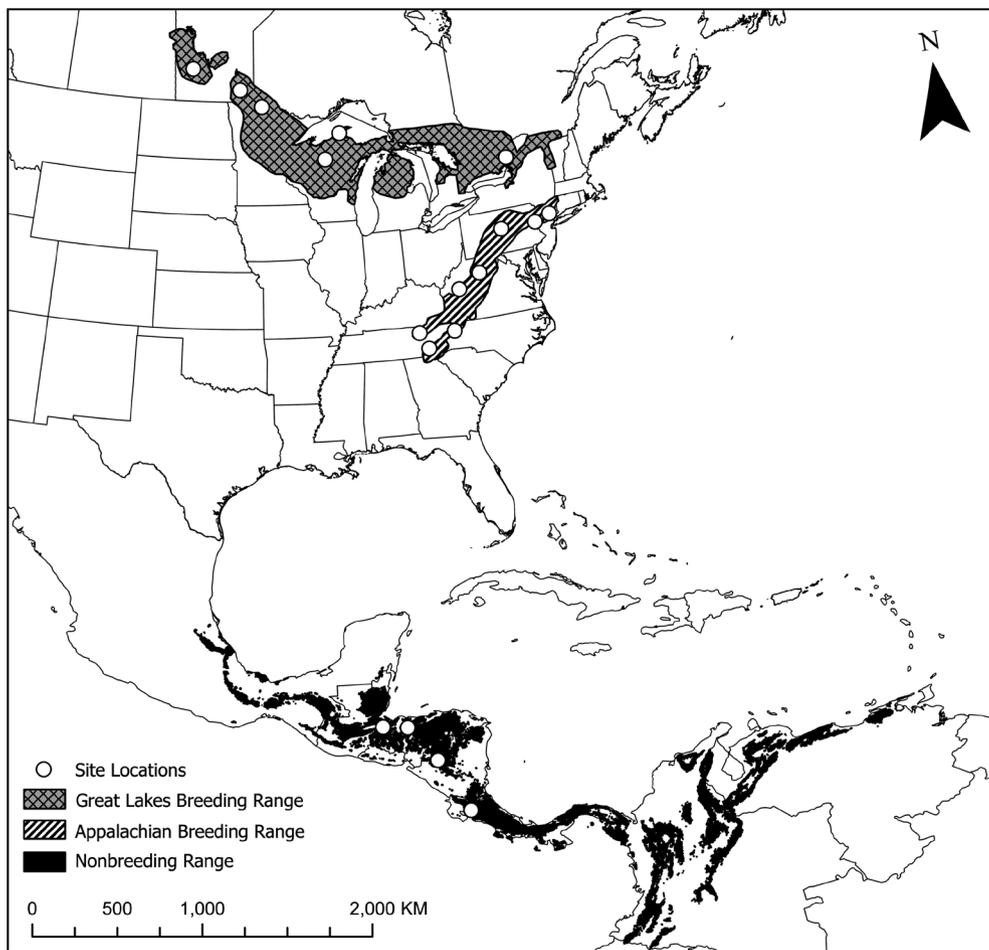


FIGURE 1. Sites where CMR datasets were collected for apparent survival analyses. Breeding range boundaries are approximations and are sourced from the Golden-winged Warbler Working Group (derived from NatureServe; Roth *et al.* 2019). Nonbreeding range boundaries depict the current predicted occupied nonbreeding range of *V. chrysoptera* sourced from eBird observations and supplemented by various georeferenced occurrence datasets (Brodie *et al.* 2024).

of study objectives, including habitat assessment, territory mapping, migration research, and telemetry (Table 1), and contained information regarding the annual detection or non-detection of uniquely marked individuals over a minimum span of 3 consecutive years at each site. Additional metadata included the sex and initial capture coordinates for each individual. There was an inherent male bias in our overall sample size, given the greater difficulty in locating and marking female *V. chrysoptera* compared to males (Bulluck *et al.* 2013, Wood *et al.* 2017, Aldinger 2018). Studies were conducted at different periods and over different durations, with the earliest starting in 2000 and the latest ending in 2022 (Table 1).

An annual capture history matrix was created for each dataset, with individuals in rows and years in columns. Each cell in the capture history matrix contained a 1 or 0 depending on whether an individual was observed (1) or not observed (0) each year, with NA values indicating years when data were not collected at a site. Within each dataset, a site was deemed distinct if all initial capture locations fell within a 40-km radius of one another. This threshold was selected to reflect the spatial clustering of sampling locations observed across studies. Separate studies conducted within the 40-km radius at different or overlapping time periods were combined into a single site to account for overlapping individuals and representation of the same local population. We restricted our analyses to adults (after hatch-year,

AHY) because few sites banded hatch-year (HY) birds, limiting range-wide representation, and sites that did band HY birds lacked sufficient recapture data. Focusing on adults allowed for a more consistent assessment of apparent annual survival across sites and time periods. All HY individuals (born the year of capture on breeding grounds and prior to January 1 on nonbreeding grounds) that were not observed in subsequent years were omitted from capture histories. For HY birds that were recaptured in subsequent years, we excluded their initial year from their capture histories and designated the first year of recapture as their inaugural year as an adult in the analysis. Nonbreeding datasets, where the field season spanned 2 different calendar years, were identified by the first year of a particular nonbreeding field season. To examine regional variation, datasets were grouped by regional breeding population: Great Lakes and Appalachian. Because *V. chrysoptera* has strong migratory connectivity structure (Larkin *et al.* 2017, Kramer *et al.* 2017, 2018), Central American datasets were included in the Great Lakes regional analysis as they likely represented the same breeding population (Larkin *et al.* 2017, Bennett *et al.* 2019).

Statistical Methods

We estimated apparent annual survival and recapture probabilities using 2 identical state-space formulated Cormack-Jolly-Seber (CJS) models (one with Great Lakes datasets and one with

TABLE 1. List of sites included in regional models and respective metadata for each dataset.

Site ^a	Study duration	Type of study ^b	Data sources and associated literature	Sample size ^c	Female representation
Great Lakes					
Manitoba (SE)	2008–2014	F, S	Moulton <i>et al.</i> (2017); Van Wilgenburg, <i>unpub.</i>	258	33%
Manitoba (SW)	2008–2010	F, S	Van Wilgenburg, <i>unpub.</i>	271	15%
Ontario (W)	2008–2010	F	Van Wilgenburg, <i>unpub.</i>	29	0%
Wisconsin	2007–2020	TM, G, HA	Buckardt Thomas (2019); Roth, <i>unpub.</i>	198	10%
Michigan	2013–2017	G, HA	Buckardt Thomas (2019); Roth <i>et al.</i> (2014)	64	9%
Ontario (E)	2001–2006	F, S	Bulluck <i>et al.</i> (2013); Vallender <i>et al.</i> (2007)	282	35%
Appalachian					
New York (S)	2002–2010	F, TM	Confer <i>et al.</i> (2010); Confer, <i>unpub.</i>	130	35%
Pennsylvania (C)	2008–2011	T, F	Larkin, <i>unpub.</i>	83	4%
Pennsylvania (E)	2012–2015	T, G, F	Aldinger <i>et al.</i> (2015); Kramer <i>et al.</i> (2017); Fiss <i>et al.</i> (2021)	93	0%
West Virginia (S)	2000–2021	F, HA, TM	Canterbury, <i>unpub.</i>	171	3%
West Virginia (NE)	2008–2015	PC, TM, S, F, HA, T	Aldinger (2018); Aldinger and Wood (2014); Frantz <i>et al.</i> (2016)	188	29%
Tennessee	2003–2011	F, TM, HA, S	Percy (2012); Bulluck <i>et al.</i> (2013); Buebler, <i>unpub.</i>	236	28%
North Carolina (W)	2016–2021	F	Kelly, <i>unpub.</i>	36	8%
North Carolina (NW)	2010–2015	F, TM	Jones <i>et al.</i> (2016); McNeil <i>et al.</i> (2017)	138	7%
Nonbreeding					
Costa Rica	2006–2013	PC, S, HA, T	Chandler and King (2011); Ritterson <i>et al.</i> (2021)	86	8%
Guatemala	2014–2016	G	Bennett, <i>unpub.</i>	20	5%
Honduras	2011–2016	G	Bennett, <i>unpub.</i>	52	12%
Nicaragua	2002–2022	G, BS	Larkin <i>et al.</i> (2017); Chavarría-Duriaux, <i>unpub.</i>	153	24%

^aN = north, E = east, S = south, W = west, C = central.

^bF = fecundity, TM = territory mapping, T = telemetry, G = light-level geolocator, HA = habitat assessment, PC = point count, S = survival, BS = banding station.

^cSample size refers to the number of individual *V. chrysoptera* used in site-specific analysis.

Appalachian datasets) fitted in a hierarchical Bayesian framework (Gilks *et al.* 1996). We elected to model each region separately because their strong migratory connectivity structure and distinct, non-overlapping breeding and wintering areas likely result in region-specific temporal variation in survival. Analyses were implemented in JAGS (Plummer 2003) and run through program R (4.1.0; R Development Core Team 2018) using the *jagsUI* package (Kellner 2015). The CJS model does not distinguish between mortality and permanent emigration and produces estimates of apparent annual survival, which is likely an underestimation of true survival (Lebreton *et al.* 1992, Schaub and Royle 2014). However, several studies have found adult male *V. chrysoptera* exhibit high site fidelity on both their breeding and nonbreeding grounds, suggesting male emigration in subsequent years after establishing a breeding territory may be low (Bulluck *et al.* 2013, Peterson *et al.* 2015, Chandler *et al.* 2016). Our knowledge on site fidelity in females is more obscure, which could result in an underestimate of female survival. Additionally, site fidelity may be influenced by habitat management practices, as these landscapes are not static, and some of the referenced studies were conducted at sites undergoing active management which may have influenced recapture probabilities.

For both models, we used vague prior distributions for all parameters to reflect a lack of prior knowledge on range-wide apparent annual survival and recapture probability, and to minimize biases on posterior distributions (Gelman *et al.* 2000, Gelman 2006). Specifically, we assigned a normal (0, 0.001) prior to the logit-scale overall apparent survival mean, uniform (0, 5) priors for standard deviations of site- and year-level random effects, and independent beta (1, 1) priors for recapture

probabilities, estimated separately for each sex and year within each site. Posterior distributions were collected using 3 Markov chains and 50,000 iterations with a burn-in of 2,500. Year was treated as a random effect to account for unknown and variable search effort throughout the study periods. We were unable to incorporate additional search effort information into our analyses, as most datasets did not include effort metadata, and there was no feasible way to standardize a unit of effort. Model convergence was confirmed by inspecting the potential scale reduction factors (\hat{R} values) proximity to one using the Brooks-Gelman-Rubin criterion (Brooks and Gelman 1998). Ideal \hat{R} values fall below 1.05 for all model parameters, implying that the within-chain and between-chain variances are nearly equal (Gelman and Rubin 1992, Brooks and Gelman 1998).

To obtain site-, region-, and sex-specific apparent annual survival estimates, we implemented a hierarchical structure within each of our 2 regional models (see Figure 2 for an example model structure). At the highest level, we estimated a regional mean apparent annual survival rate on the logit scale, which served as a hyperparameter for all site-level estimates in that region. At the intermediate level, we modeled mean apparent annual survival for each respective site as a random effect drawn from the regional mean to capture among-site variation and to obtain finer-scale spatial estimates. Site-level mean estimates were then summarized by averaging the posterior distributions of apparent annual survival for each respective site. At the lowest level, we estimated apparent annual survival for each year at each site to account for temporal variation, treating year as a random effect that followed a normal distribution with mean 0 and variance Σ^2 . To account for a potential effect of sex in

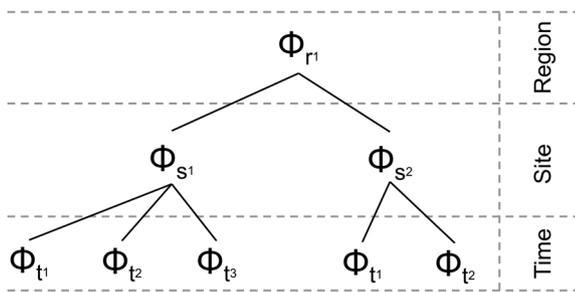


FIGURE 2. Example of the model structure for our hierarchical regional apparent annual survival model. This example represents one region (i.e., Great Lakes or Appalachian).

detection, we modeled recapture probability as sex-specific. Within each site, we allowed recapture probability to vary by both sex and year, with time- and sex-specific estimates assigned independent beta-distributed priors. This structure helped account for the possibility that differences in recapture probability between sexes could bias apparent survival estimates.

To evaluate whether sex explained variation in apparent annual survival, we indexed the survival and recapture parameter by sex in both regional models for all sites with female representation. We calculated the difference in sex-specific posterior apparent survival means (delta estimates) as a derived parameter to obtain respective 95% credible intervals (CrI) of each difference. We examined site- and region-specific sex differences but elected to not include temporally and sex-specific apparent survival estimates for each site, given that annual sample sizes were often low, and in several cases, there were years with no female representation.

Simulations of Survival Estimate Precision

We conducted a series of simulations to explore how data quality and study design choices could influence precision in apparent survival estimates. Retaining the multi-level, multi-population structure of our Appalachian apparent survival model, we ran 30 simulations that considered 56 different scenarios involving 3 scenarios for the number of primary sampling occasions (3, 6, and 9 year), 2 levels of female representation (30% and 50%), 3 sample sizes of initial capture at each occasion (10, 30, and 50), and 3 recapture probabilities (30%, 60%, and 90%). The selected variations in parameters reflect common study design considerations and constraints, with values ranging from those typical of *V. chrysoptera* studies to what we would consider the maximum reasonable scenarios. We elected to only run a simulation on our Appalachian model due to the similarity in model structures between both regional models, under the assumption that results would be applicable to the Great Lakes region as well. Therefore, credible interval ranges for overall region- and site-specific apparent survival estimates were analyzed only for this population. In addition to gauging precision in our spatial estimates, we wanted to know ideal scenarios that would increase our confidence in potential sex-specific variations for each site. Capture histories were created for each combination using a modified implementation of the *simul.cjs* function created by Kéry and Schaub (2012). Apparent annual survival probabilities used to generate the capture histories were sampled from a normal distribution produced with the site-specific mean posterior estimates and respective standard errors that we obtained from our original models. Model results were evaluated by comparing the width

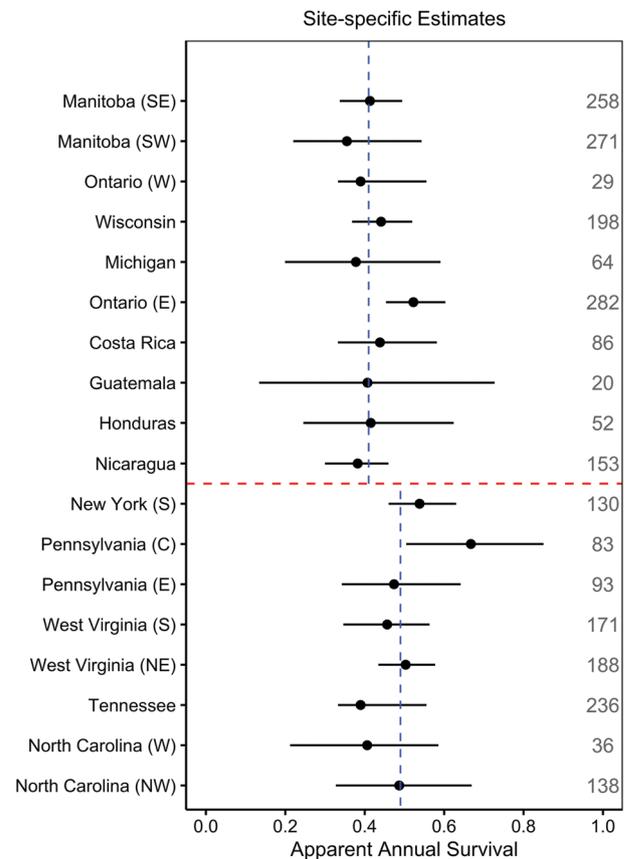


FIGURE 3. Site-specific apparent annual survival estimates for both populations of *V. chrysoptera*. The horizontal red dashed line separates sites representing the Great Lakes population (above) and the Appalachian population (below). Gray numerical values on the right denote the sample size used for each respective site analysis. Vertical dashed blue lines represent the regional mean respective to each regional population for reference. Points represent the posterior means, and lines represent 95% CrIs.

of the credible interval among the scenarios and with our original model output. We calculated the width of the 95% CrI by subtracting the 2.5% quantile from the 97.5% quantile of posterior distributions of the parameters of interest. Smaller CrI widths indicated greater precision.

RESULTS

We compiled from 18 sites a total of 2,488 individual CMR records (1,413 records for the Great Lakes population and 1,075 for the Appalachian population). Sampling occasions averaged 7.6 year with 141 individuals per site for the Great Lakes population, and 8.5 year with 134 individuals per site for the Appalachian population. Females represented 20% of the total range-wide records ($n=487$). One site in each regional apparent survival model was omitted from the sex-specific analysis due to the absence of females in the datasets (Table 1). Posterior apparent annual survival estimates showed no meaningful temporal variation within individual sites, with overlapping CrI's across years at each site (first level; Supplementary Material Figures S1 and S2). Site-specific mean posterior apparent annual survival estimates (second level) ranged from 0.36 to 0.52 in the Great Lakes and from 0.41 to 0.67 in the Appalachians; however, site-specific estimates did not differ from one another (Figure 3). Site-specific mean posterior recapture probabilities ranged

TABLE 2. Mean apparent annual survival (Φ) and recapture probability (p) estimates with 95% CrI's and standard deviations (SD) for the Great Lakes and Appalachian populations. Male (M) and female (F) apparent annual survival estimates are included for each respective region. \bar{R} is an indicator of successful convergence.

Parameter	Mean	SD	95% CrI	\bar{R}
$\Phi_{\text{Great Lakes}}$	0.41	0.05	0.31–0.50	1.00
Φ_{M}	0.43	0.04	0.36–0.50	1.00
Φ_{F}	0.40	0.04	0.33–0.49	1.00
$p_{\text{Great Lakes}}$	0.53	0.03	0.47–0.60	1.00
p_{M}	0.58	0.04	0.49–0.66	1.00
p_{F}	0.49	0.05	0.39–0.59	1.00
$\Phi_{\text{Appalachian}}$	0.49	0.06	0.36–0.60	1.00
Φ_{M}	0.50	0.03	0.45–0.56	1.00
Φ_{F}	0.49	0.04	0.41–0.57	1.00
$p_{\text{Appalachian}}$	0.53	0.03	0.47–0.59	1.00
p_{M}	0.58	0.03	0.52–0.65	1.00
p_{F}	0.48	0.05	0.39–0.58	1.00

from 0.39 to 0.83 for males and from 0.31 to 0.63 for females, with males tending to have higher recapture probabilities for sites that had at least 10% female representation (Supplementary Material Figure S3). At the regional level, mean apparent annual survival estimates for the Great Lakes population (posterior mean 0.41, 95% CrI: 0.31–0.50) did not differ from the mean apparent annual survival estimates for the Appalachian population (posterior mean 0.49, 95% CrI: 0.36–0.50; Table 2). Additionally, the Great Lakes recapture probability estimate (posterior mean 0.53, 95% CrI: 0.47–0.60) was not different from the Appalachian recapture probability estimate (posterior mean 0.53, 95% CrI: 0.47–0.59; Table 2). All model parameters had \bar{R} values that confirmed successful convergence (Table 2).

No substantial differences in sex-specific apparent annual survival were supported for each site, with all 95% CrIs overlapping zero (Supplementary Material Figure S4). At the regional scale, males tended to have greater overall apparent annual survival than females in both populations, but overlapping 95% CrIs indicate no clear difference (Table 2 and Figure 4).

Results from our simulation analysis showed that the most precise scenario for estimating overall apparent annual survival in the Appalachians (CrI range: 0.170) included 9 sampling occasions for each site, 50 newly marked individuals at each occasion, and a 60% recapture probability (Supplementary Material Figure S5). The CrI ranges for the 20 most precise scenarios (CrI range: 0.17–0.20) all involved scenarios where recapture probability ≥ 0.6 and the number of occasions ≥ 6 , indicating that precision stabilizes with considerable CMR efforts (Supplementary Material Figure S5). Reducing the number of sampling occasions to 3 while retaining high recapture probabilities and sample sizes resulted in comparatively wider CrIs (Figure 5). The difference in the CrI range between our original model output (CrI range: 0.24) and the most precise simulation scenario (CrI range: 0.17) was 0.07. While the narrower intervals from the simulation highlight the potential value of more intensive sampling designs, the relatively modest reduction in precision that the simulation produced suggests that our original data provided reasonably precise estimates, given logistical constraints (Supplementary Material Figure S5). Additionally, within the set of simulated scenarios, there was no meaningful difference in the precision of sex-specific

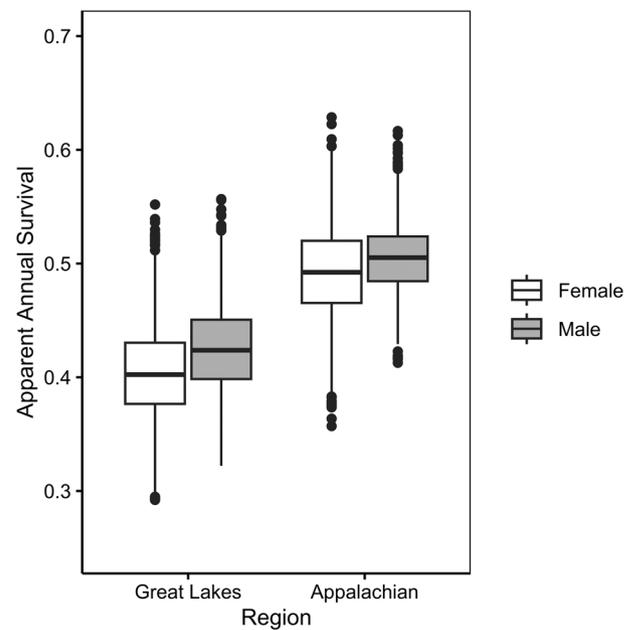


FIGURE 4. Sex-specific apparent annual survival estimates for the Great Lakes and Appalachian populations. Boxes represent the interquartile range (IQR) between 1st and 3rd quantiles. Horizontal lines inside boxes indicate respective medians. Whiskers represent 1.5 times the respective IQR. Dots beyond whiskers indicate outliers.

apparent annual survival estimates in simulations with 30% vs. 50% female representation if recapture probabilities and the number of occasions were high (Figure 5).

DISCUSSION

Spatial and Temporal Variation

Despite the Appalachian population facing greater declines than the Great Lakes population, we found that apparent annual survival for adults was similar for both regional populations. This result aligns with previous spatial findings in single-population apparent annual survival models (Bulluck *et al.* 2013, Aldinger 2018) and suggests adult mortality may not be the primary driver of recent variation in range-wide population trends over the past 2 decades. Instead, regional variations in population trends could reflect other demographic factors influencing population size, such as juvenile/immature survival, productivity, and recruitment (McNeil *et al.* 2020a, Keele *et al.* 2024, McNeil *et al.* 2024), or differences in breeding habitat availability.

We elected not to include HY records in our analyses as natal dispersal for *V. chrysoptera* is suggested to be greater than dispersal for adults (Koonce 2005, Bulluck *et al.* 2013, Aldinger 2018, López-Calderón *et al.* 2019), and we did not want to conflate our apparent annual survival analyses by not accounting for this heightened dispersal. Additionally, HY was a widely underrepresented cohort in our compiled dataset, with representation at only a few sites. Although juveniles were excluded from our models, their survival may play a critical role in population dynamics. In passerines, juvenile apparent survival is often substantially lower than that of adults, which has important implications for population growth (King *et al.* 2006, Cox *et al.* 2014, Rockwell *et al.* 2017, Rushing *et al.* 2017). Our study provides no information to evaluate whether

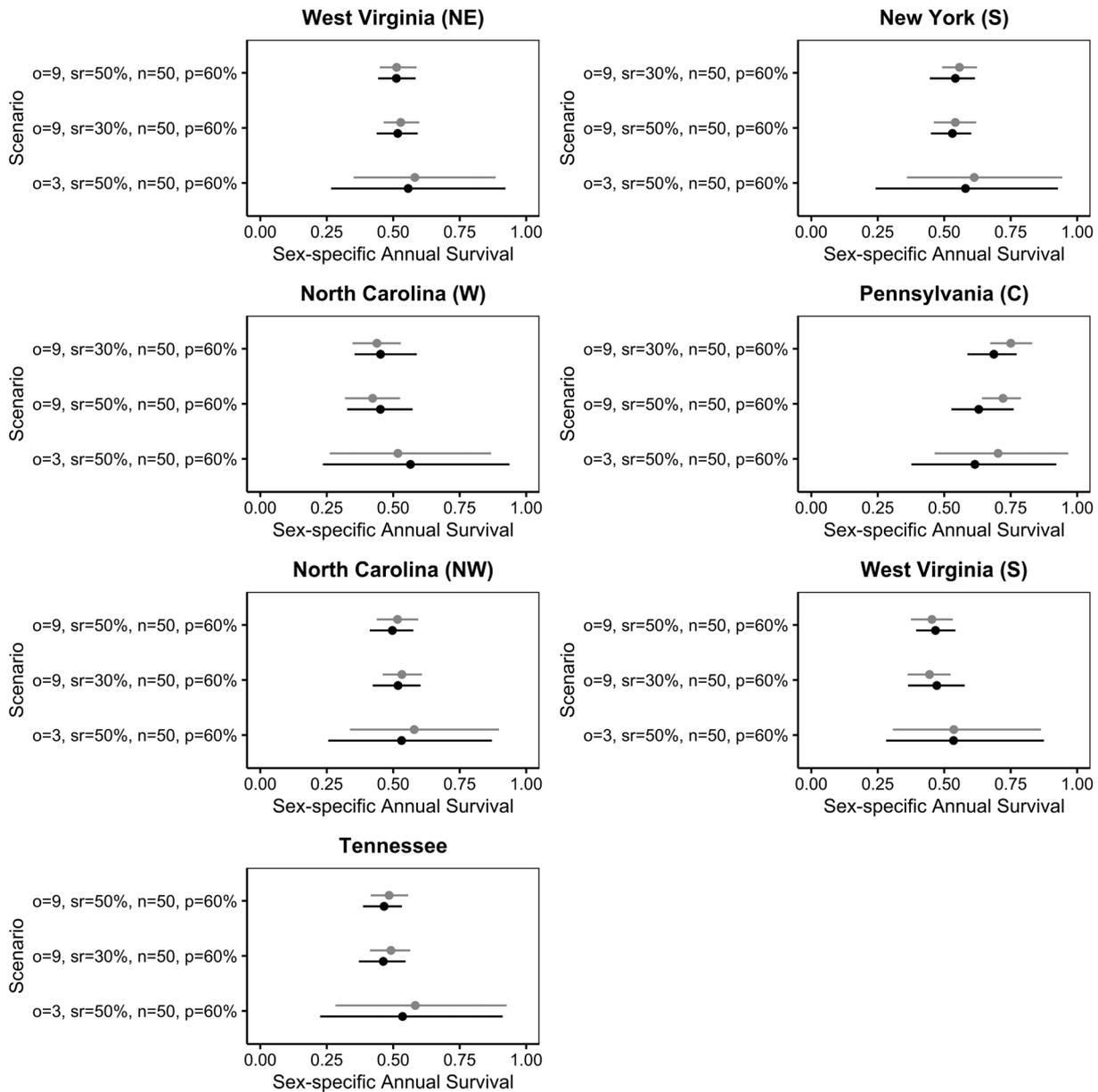


FIGURE 5. Sex-specific apparent annual survival and 95% quantile estimates for the Appalachian population taken from mean posterior estimates of 30 simulations for 3 selected scenarios. Each plotted scenario represents a particular number of occasions (o), female sex representation (sr), number of new individuals banded per year (n), and recapture probability (p). Male estimates are depicted in gray, and female estimates are depicted in black.

region-specific differences in juvenile survival could contribute to differences in rates of decline between Great Lakes and Appalachian populations.

Recruitment into the adult breeding population is influenced by several factors, including nest success, post-fledging survival, and survival during migration and the nonbreeding period. While regional differences in nest success rates have not been consistently identified (Bulluck et al. 2013; see Roth et al. 2019 for a selection of site-specific estimates), productivity varies among study sites and may be driven by multiple factors. For example, brood parasitism by *Molothrus ater* (Brown-headed Cowbird) can significantly reduce fledging success (Roth et al. 2019), and smaller average clutch sizes have been associated with lower productivity in some Appalachian sites (Bulluck et al. 2013). Additionally, local food availability can limit reproductive output, particularly where arthropod prey is scarce

(Keele et al. 2024, McNeil et al. 2024). Such variation in productivity can result in different population responses to conservation efforts for the species (McNeil et al. 2020a). For example, poor food availability in parts of the Appalachian region has been linked to lower post-fledging survival, especially within the first 5 days after fledging when birds are highly vulnerable (Keele et al. 2024, McNeil et al. 2024). Predation pressure from snakes in the Appalachian population has also been hypothesized to cause regional differences in post-fledging survival (Lehman 2017). These early-life threats may contribute to the demographic disparities observed between regions.

Beyond the breeding season, immature birds (ie, those in their first year of life prior to their first breeding season) must also survive migration and the nonbreeding season to be recruited into the breeding population. While strong migratory connectivity structure could lead to region-specific risks during

migration, there is currently no evidence that differences in adult migration explain variation in population trends (Kramer *et al.* 2023). Additionally, survival from the end of the first nonbreeding season to the start of the following one (ie, from approximately March–October) does not appear to differ significantly between first-year individuals and adults (Ritterson *et al.* 2021). These studies highlight the pivotal role that first-year cohorts may play in driving demographic disparities among regions with differing ecological drivers, such as predator pressure, resource availability, and habitat quality. In addition to these factors, skewed sex ratios or variation in the frequency of unpaired males could also influence regional differences in productivity. Further understanding of immature cohort survival could help elucidate trends, and the use of integrated population models could provide deeper insights into how productivity and recruitment shape regional population dynamics.

Although we found no substantial regional differences in apparent annual survival between the 2 populations, these estimates may still be influenced by adult dispersal rates, which were unaccounted for as our CJS models were not able to distinguish between mortality and permanent emigration. Recapture probabilities were similar between the Great Lakes (0.53, 95% CrI: 0.47–0.60) and the Appalachian population (0.53, 95% CrI: 0.47–0.59), suggesting comparable availability for recapture across regions. However, this does not preclude the possibility of region-specific dispersal behaviors that influence apparent survival in more subtle ways.

We found that males tended to have higher recapture probabilities than females, a pattern that could bias apparent survival estimates if sex ratios are uneven across regions or if female dispersal or detectability differs. This is particularly relevant for the Appalachian region, where population densities are lower and females may be less likely to be encountered or resighted, due to either true absence or reduced detectability. Additionally, *V. chrysoptera* are adapted to seek out ephemeral early successional habitat, often dispersing to nearby unoccupied patches (McNeil *et al.* 2020b). In the Appalachian region, breeding habitat—such as reclaimed surface mines, overgrown pastures, and wetland edges—is increasingly fragmented and restricted by topography, potentially limiting dispersal distances and contributing to higher site fidelity (Canterbury *et al.* 1993, Buehler *et al.* 2007, Aldinger *et al.* 2015, McNeil *et al.* 2018, Lin and Bulluck 2023). In contrast, the Great Lakes region offers abundant, contiguous nesting habitats—such as expansive aspen forests and shrub wetlands—which may facilitate broader movement, particularly among unpaired individuals (Roth and Lutz 2004, Martin *et al.* 2007, Peterson *et al.* 2015, Buckard Thomas *et al.* 2023). If adult dispersal is indeed more common in this region, true annual survival may be higher than suggested by our apparent annual survival estimates. Thus, while recapture probabilities were similar, potential differences in landscape connectivity and population density across regions could still introduce bias into apparent annual survival estimates.

Sex Effect

Although apparent annual survival tended to be greater among males than females, this pattern lacked statistical support in regional- and site-specific assessments. This lack of support was congruent with previous findings of apparent annual survival for populations of *V. chrysoptera* (Aldinger 2018) but contradicted findings for other populations (Bulluck *et al.* 2013). At the site level, wider 95% CrIs for sex-specific differences in

apparent annual survival often corresponded with lower female representation (e.g., North Carolina (NW): female representation = 7%, CrI range: 0.43) compared to those with greater female representation (e.g., New York (S): female representation = 35%, CrI range: 0.19; Supplementary Material Figure S4). However, regional 95% CrI ranges for sex-specific apparent survival estimates showed no substantial difference, likely because of the balance of sites with low and high female representation in both regions (average of 15% female representation in the Great Lakes and 14% in the Appalachians).

Future efforts should aim to enhance female representation in datasets to increase precision in estimates, although doing so will be difficult to achieve as females are harder to catch and recapture and may have smaller population sizes than males (Breitwisch 1989). Across most sites, posterior recapture probability estimates tended to be lower for females than males, which may further contribute to underestimates of female survival. Our simulation results suggest that increasing site-specific female representation beyond 30% may not significantly improve parameter precision in regional models. Instead, focusing on refining data collection methods, such as increasing recapture rates by searching during key windows of female detectability (e.g., before incubation or while feeding nestlings) or by incorporating tracking technology to better recapture elusive females, may better increase confidence in sex-specific survival differences.

The tendency for females to have lower apparent annual survival than males in migratory passerines (summarized in Mumme 2024) makes our finding of similar apparent survival rates between adult male and female *V. chrysoptera* particularly interesting. An unexplored factor in our study was the interaction between sex and age, which could contribute to variability in apparent survival rates. Given that immatures experience lower overwinter survival than adults (Ritterson *et al.* 2021), and that females occupy lower quality habitat on nonbreeding grounds (Chandler *et al.* 2016, Bennett *et al.* 2019, King *et al.* 2023), these factors could contribute to lower survival for females during their first year of life. Additionally, the lack of supported sex differences in apparent annual survival may be influenced by females exhibiting lower site fidelity and higher dispersal than males, or by unbalanced sex ratios in the population. Since female survivorship has a strong influence on population demography, obtaining true sex-specific annual survival estimates through spatial CJS (s-CJS) approaches (Schaub and Royale 2014) to reduce conflation with dispersal, improving our understanding of sex-specific survival in juveniles, and focusing efforts on marking and recapturing females could provide clearer insights into factors driving population declines.

Data Collection Standardization

The abundance of *V. chrysoptera* CMR data collected in the last half-century allowed for the use of a multi-population approach to obtain regional apparent annual survival estimates for adults. This analytical approach is not common for migratory birds, likely due to the logistical challenges of collecting sufficient range-wide CMR data for migratory songbirds with large distributions (Dhondt 2001, Frederiksen *et al.* 2005; Grosbois *et al.* 2009). While we succeeded in obtaining estimates of apparent annual survival at 2 spatial scales (regional and site), the lack of standardized data collection across datasets produced noise and uncertainty in our models. At most sites, CMR datasets were

not collected for survival-specific objectives. Instead, capture histories were gathered incidentally as a by-product of capturing birds to pursue a variety of unrelated field objectives using different methodologies such as telemetry and territory mapping. Additionally, study sites were selected for various reasons depending on study objectives, with some sites identified due to the abundance and reliability of *V. chrysoptera* populations and other sites identified through habitat assessment of forest characteristics with no previous knowledge of *V. chrysoptera* occupancy (e.g., Roth *et al.* 2014, Buckardt Thomas 2019). Along with inconsistencies in field methods and site selection criteria across datasets, search effort (ie, time spent and distance traveled looking for marked individuals) was not consistently reported nor consistent across sites/years, which could skew site-specific recapture probabilities and affect our models.

Results from our simulation analysis demonstrated that the most precise regional- and sex-specific apparent survival estimates were achieved when CMR efforts included high recapture probabilities ($\geq 60\%$) and a high number of sampling occasions (≥ 6 year), suggesting that prioritizing sustained recapture efforts over a longer timeframe is more effective than focusing solely on marking many individuals within a shorter period. While on average our studies exceeded 6 sampling occasions (7.4 year for Great Lakes, 8.5 year for Appalachians), the average recapture probability for all sites (53%) fell short of these standards. Additionally, our simulations indicate that changes in sample size between 30 and 50 are unlikely to significantly affect parameter estimates of regional apparent annual survival, likely due to inherent variation in search effort, temporal effects, and site effects.

Conclusions

Our simulation results suggest that the lack of differences in apparent annual survival that we detected among sites and between regions was not an artifact of low precision. Instead, regional differences in *V. chrysoptera* population trends in the past 2 decades are more likely attributed to factors other than adult mortality, such as productivity, juvenile/immature survival, and recruitment. Reduced reproductive output, due to low nest success, limited food availability, and declining nesting habitat availability, may play a significant role in shaping these trends. Studies that aim to elucidate the mechanisms driving variability in productivity and recruitment could provide a more complete picture of this species' demography. Integrating more advanced modeling techniques (e.g., integrated population models) could further elucidate the complex interplay of factors influencing *V. chrysoptera* demographics and enhance our understanding of the mechanisms driving population trends in both regions.

Supplementary material

Supplementary material is available on *Ornithology* online.

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Ethics statement

Collaborators on this project obtained the appropriate permits for fieldwork in their respective locations.

Conflict of interest statement

The authors declare they have no conflicts of interest.

Author contributions

E.N.F., A.M.R., and W.E.T. conceived of and planned the study; E.N.F., E.J.R., and S.J.C. conducted data analyses; K.R.A., R.E.B., D.A.B., L.B., R.A.C., R.C., C.J.F., K.H., J.A.J., D.K., G.R.K., J.L.L., D.J.M., J.D.R., A.B.T., R.V., S.L.V., and P.W. contributed datasets and provided edits; E.N.F. wrote the first draft and made final edits. A.M.R. and W.E.T. were responsible for securing funding to support this study.

Data availability

Analyses reported in this article can be reproduced using the data and code provided by Filiberti *et al.* (2025).

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