MOVEMENT AND POPULATION DYNAMICS OF GREAT LAKES MALLARDS

By

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A DISSERTATION

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ABSTRACT

Mallard (*Anas platyrhynchos*) abundance in the Great Lakes states declined by 30% from 2000 to 2023 based on spring aerial surveys in Michigan, Minnesota, and Wisconsin. Concern among management agencies and uncertainty in the factors contributing to Great Lakes mallard decline led to a regional partnership which initiated this research project. The research objectives were to estimate Great Lakes mallard demographic parameters, determine which parameters had driven declines in abundance, and reduce uncertainty about the ecological and anthropogenic factors affecting movement and population dynamics. We captured, collected genetic and feather samples from, and marked 592 female mallards with GPS-GSM transmitters in Michigan, Wisconsin, Ohio, Indiana, and Illinois, USA from 2021–2023. We also used 32 years of banding, band recovery, and aerial survey data collected from mallards in Michigan and Wisconsin during 1991–2022 to develop an Integrated Population Model (IPM).

Genetic ancestry analysis of GPS-marked female mallards via ddRAD sequencing revealed 44% were wild mallards and 56% were wild x domestic game-farm mallard hybrids. Hybrid mallards had shorter daily movement distances, were less likely to engage in autumn migration, and had higher use and selection of urban developed land cover than did wild mallards. Survival of female GPS-marked mallards was positively related to the proportion of locations in urban developed land cover, regardless of individual genotype, suggesting urban land cover use could be a source of individual heterogeneity in survival. Female mallards with greater domestic ancestry primarily used urban developed land cover, raising questions about their ability to survive in rural habitat types primarily used by wild mallards. Increasing proportion of domestic ancestry was associated with significantly lower probability of initiating nest incubation, indicating early generational hybrids had low productivity. Sedentary behavior, use and selection of urban areas, and low incubation incidence related to domestic ancestry raises concern regarding hybridization between wild and domestic game-farm mallards.

Molting and natal origins estimated from stable hydrogen (δ^2H) isotopes predicted 72%–84% of adult females molted and 59%–77% of juvenile females hatched at the latitudes of the Great Lakes region. Emigration likely contributed little to population decline as 98% of surviving female Great Lakes mallards remained in or returned to the Great Lakes region in subsequent breeding periods. The IPM identified declining productivity and increasing natural mortality in adult and juvenile female mallards as the primary demographic drivers of population decline. Productivity was lowest at urban developed banding sites in the southern Great Lakes region, where prevalence of hybrid mallards was greatest. Productivity declined with loss of area enrolled in the Conservation Reserve Program within Michigan and Wisconsin during 2000–2022. Natural mortality was 3.5–6.7 times and 1.3–4.2 times greater than harvest mortality for adult and juvenile female mallards, respectively, suggesting environmental factors during spring and summer, not harvest, drove annual mortality for female mallards. Attempts to increase or maintain Great Lakes mallard abundance should consider regional quantity and quality of nesting and brood-rearing habitat types and population genetics.

To David Richard Luukkonen, whose life and philosophy were my greatest inspiration.

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The Great Lakes mallard project has been a substantial undertaking and its success relied on the contributions and teamwork of nearly countless people. My guidance committee provided key expertise, advice, and direction throughout the project. Dr. Scott Winterstein was always available to discuss whatever issue I was contemplating. His many stories served as useful examples to guide academics, research, and life. Dr. Dan Hayes' wisdom encouraged deep thinking and to always ask "why". His love for teaching is contagious and I learned much from his engagement with students; I would be lucky to someday be half the educator he is. Dr. Drew Fowler expanded my knowledge of waterfowl life history, population processes, and emerging techniques such as stable isotope analysis. He remained committed to the project from day one despite changing jobs and taking on new responsibilities, and I am grateful for his dedication. Dr. Jerry Urquhart strengthened my ability to consider the big picture in ecology, including the multitude of factors which can interact to affect wildlife populations. I was reminded that before mallards, and not too long ago, American black ducks were the preeminent nesting duck in the Great Lakes region. Dr. Barb Avers has been a longtime mentor and source of encouragement. I am thankful for her in providing many opportunities to discuss findings with wildlife managers and stakeholders. Sharing applied research with practitioners has been one of the most rewarding aspects of the project.

Beginning at its inception and lasting throughout, support for the project was overwhelming. The following organizations provided vital support: Ducks Unlimited, Forbes Biological Station and Illinois Natural History Survey, Franklin College, Indiana Department of Natural Resources, Illinois Department of Natural Resources, Michigan Department of Natural Resources, Michigan State University, United States Fish and Wildlife Service, Upper

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I'd like to thank all current and past waterfowl banders, whose work has contributed to making mallards one of the most highly monitored wildlife species in the world. We would never have been able to deploy 592 transmitters across five states without the help of many banders. I'd like to acknowledge the people who trapped mallards, identified opportunities to capture nesting mallards, helped deploy transmitters, and assisted with other aspects of fieldwork: Don Avers, Taylor Finger, Auriel Fournier, Drew Fowler, Ben O'Neal, Josh Osborn, Amy Shipley, Brendan Shirkey, John Simpson, Jay Winiarski, Jozalynn Boucher, Bailey Marston, Shannon Stemaly, Sierra Avendt, Corey VanStratt, Brandon Blasius, Maddison Allen, Nathan Steelman, Zosha Kuiper, John Darling, Katie Farinosi, John Niewoonder, Tim Riley, Barry Sova, Ron Sting, Rob Hamilton, Tammy Giroux, Nate Levitte, Joe Robison, Brad Johnson, Caleb Eckloff, Brian Roell, Colter Lubben, Karen Sexton, Mike Richardson, Terry McFadden, Randy Knapik, Kaitlyn Barnes, Brandy Dybas-Berger, Pat Brickel, Cameron Dole, Chad Krumnauer, Adam Shook, Zach Cooley, Jeremiah Heise, Amber Frye, Melissa Nichols, Vern Richardson, Trey McClinton, Jessica Jaworski, Josh Martinez, Eric Kroening, Andrew Greenawalt, Austin Ficher, Chelsea Kross, Steven Gurney, Rachel Correia, Samantha Courtney, Marty Johnson, Cheyenne Beach, Andy Gilbert, Chad Creamer, Bryan Woodbury, Tom Cooley, Drew Hawley, Paul Samerdyke, Brenda Kelly, Ben Williams, Brendan Woodall, Kali Rush, Chuck Farrell, Jes Rees Lohr, Jeffrey Edwards, Andrea Spurck, Nate Stott, Alex Hanrahan, Alissa Kakatsch, Allicyn Nelson, Penelope Murphy, Joe Vermeulen, Aaron Wright, Steve Burns, Thomas Carlson, Steven Easterly, Derek Christians, Coleman Nadeau, and Kyle Vandyke. Additionally, Jake Nave, Brady Hannah, and Dan Nelson of USDA APHIS Wildlife Services assisted with transmitter deployments and graciously allowed me to mark several birds despite reducing progress towards their disease sampling quota. Don Avers went above and beyond to ensure the project was a success and I've learned much from his expertise. It is an understatement to say the project would have been unsuccessful without his help. Many people have also assisted with recovering transmitters and carcasses from mallard mortalities despite challenging or unpleasant conditions. Special thanks to staff at the Veterinary Diagnostic Laboratory for performing mallard necropsies, including Tom Cooley, Kelly Straka, Julie Melotti, and Katie Farinosi. Thanks to Paul Link for sharing his insights and experience with transmitter attachment techniques. Pam Garrettson graciously provided preliminary estimates of mallard band reporting probability for chapter 5.

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CHAPTER 1: INTRODUCTION

Mallards (*Anas platyrhynchos*) are a generalist dabbling duck naturally distributed throughout the Holarctic (Johnsgard 1978). In North America, mallards primarily nested west of the Mississippi river prior to the early 1900s (Bent 1923). Mallard nesting density was greatest in the Prairie Pothole and Parkland regions and mallards mainly wintered in the Mississippi alluvial valley (Bellrose 1976). Widespread conversion of forest to agriculture in the eastern United States and Canada by the mid-1900s (Oswalt et al. 2019) increased landscape suitability for nesting mallards. Mallards expanded into eastern North America and likely outnumbered American black ducks (*Anas rubripes*) as the most abundant breeding duck in the Great Lakes region (Michigan, Minnesota, and Wisconsin) by the 1950s (Brewer et al. 1991, Chartier et al. 2013) and were the most-harvested duck in the Atlantic Flyway by 1969 (Huesmann 1974). In addition to breeding range expansion into eastern North America by wild mallards, domestic game-farm mallards, which had been domesticated from wild mallards in Eurasia (Lavretsky et al. 2020), were released in eastern North America beginning in the 1920s (Huesmann 1974, Hepp et al. 1988). Game-farm mallard releases since the 1920s were estimated between >200,000 (U. S. Fish and Wildlife Service 2013) and >500,000 (Huesmann 1974) annually. Wild mallard dispersal from the west and large-scale releases of domestic game-farm birds established mallards in eastern North America.

MIDCONTINENT MALLARD MANAGEMENT

In North America, mallards have been delineated into three populations for harvest management, which are defined by breeding geography and administrative flyway and include eastern, midcontinent, and western mallards (U. S. Fish and Wildlife Service 2023a). The midcontinent mallard population is the largest and comprises mallards nesting from the

Northwest Territories to the Great Lakes region (Figure 1.1). Midcontinent breeding mallard abundance estimates ranged from around 5.5 to 12 million since 1955 (U. S. Fish and Wildlife Service 2022). Beginning in 1995, annual duck hunting season frameworks for the Mississippi and Central flyways were established using Adaptive Harvest Management (AHM) of midcontinent mallards (U. S. Fish and Wildlife Service 2023a). In the AHM framework, regulatory alternatives are based on midcontinent mallard population size and pond (wetland) abundance estimated during the Waterfowl Breeding Population and Habitat Survey (WBPHS; U. S. Fish and Wildlife Service 2023b) with a goal of maximizing long-term sustainable harvest (U. S. Fish and Wildlife Service 2023a). Therefore, the midcontinent mallard population plays an important role in determining Mississippi and Central flyway duck hunting frameworks and considerable resources are devoted to population monitoring via aerial surveys, banding, and harvest surveys.

GREAT LAKES MALLARDS

The U. S. Fish and Wildlife Service (USFWS) added Great Lakes mallards (mallards surveyed during the breeding period in Michigan, Minnesota, and Wisconsin) to the midcontinent mallard population in 1997 under the assumption that Great Lakes mallard population dynamics were equivalent to those of mallards nesting in the U. S. and Canadian prairies (U. S. Fish and Wildlife Service 2023a). Great Lakes mallard abundance historically followed trends in the remainder of the midcontinent population. However, prairie-nesting mallard abundance increased following a decline in the early 2000s while Great Lakes mallard abundance continued to decline (Figure 1.2). Great Lakes region environmental conditions differ from those in prairie ecosystems and some evidence suggests drivers of Great Lakes mallard population dynamics differ than those for mallards nesting in the Prairie Pothole Region (Munro and Kimball 1982, Coluccy et al. 2008). The Great Lakes influence regional temperature and precipitation (Scott and Huff 1996), and wetland hydrology is generally less seasonally dynamic than in the prairies due to a temperate climate and moderating lake effects (Euliss et al. 2004, Simpson et al. 2005). Additionally, harvest rates were generally greater for Mississippi than for Central Flyway mallards, suggesting different anthropogenic and ecological influences on Great Lakes mallard vital rates (Coluccy et al. 2008). Despite extensive annual monitoring and research, wildlife managers are unsure what factors have primarily contributed to declining Great Lakes mallard abundance.

Declining mallard abundance is a concern for wildlife management agencies because mallards and other waterfowl have ecological (Ackerman 2002, Kleyheeg et al. 2019), social (NAWMP 2018), and economic (Carver 2013, 2015, Vrtiska et al. 2013) value. In the Mississippi Flyway and Great Lakes states, mallards are the most-harvested duck species (Raftovich et al. 2020). Locally produced mallards are particularly important for Great Lakes duck hunters with an estimated 58-83% of their mallard harvest derived from mallards hatched within the region (Arnold and De Sobrino 2010). Waterfowl hunters contribute substantial support for conservation (Vrtiska et al. 2013, Carver 2015) through duck stamp purchases and Pittman-Robertson excise taxes which are vital in funding habitat management and research to conserve wetland wildlife. Mallards are also an ecologically important species whose abundance is related to wetland quantity and quality (Soulliere et al. 2017, U. S. Fish and Wildlife Service 2022). As a generalist species, mallards use a variety of wetland types during breeding and the nonbreeding periods (Soulliere et al. 2017) and may serve as an indicator of wetland abundance and function relevant to other wetland wildlife. Therefore, recovering mallards is a priority for waterfowl managers in the Great Lakes region (Soulliere et al. 2017).

RESEARCH QUESTIONS, GOAL, AND OBJECTIVES

Although midcontinent mallards are one of the most highly monitored wildlife populations in the world, Great Lakes mallards are less studied and reasons for population decline are unknown. Previous research (e.g., Simpson et al. 2007, Singer 2014, Singer et al. 2016, Boyer et al. 2018, Palumbo and Shirkey 2022) focused on demographic rates and their relationships to ecological factors and harvest somewhat independently. However, Coluccy et al. (2008) concluded that Great Lakes mallard population growth rate should be most influenced by female nonbreeding survival, ducking survival, and nest survival. Mallard hen and brood survival were inversely related to forest cover in the Great Lakes (Simpson et al. 2007, Boyer et al. 2018). While forest cover remained relatively constant in the upper Midwest over the last three decades (Oswalt et al. 2019), the Upper Mississippi/Great Lakes (UMGL) Joint Venture (JV) region lost an estimated 1.4 million ha of grassland/herbaceous and hay/pasture cover types between 2001 and 2016 (Yang et al. 2018, Soulliere et al. 2020). Upland nesting cover is an important factor in mallard nest success (Stephens et al. 2005, Bortolotti et al. 2022) and productivity (Specht and Arnold 2018). However, long term mallard productivity estimates appeared to be relatively stable in Michigan, Wisconsin, and Minnesota from 1961–2011 (Singer et al. 2016). Long-term adult female mallard survival estimates in Minnesota and Wisconsin were also stable (D. Fowler, Wisconsin Department of Natural Resources, unpublished) and harvest did not appear linked to reduced Great Lakes mallard abundance (Singer 2014). Further, recent work suggested female midcontinent mallards should have the capacity to at least partially compensate for harvest mortality through density dependence in reproduction and mortality (Riecke et al. 2022). Without a clear link between survival, productivity, and population decline, researchers and managers identified several questions that warranted further examination.

Mallard distribution may have changed at one or more spatial scales. Anecdotal observations by wildlife managers and researchers suggested the number of mallards utilizing urban areas increased in the early 2000s and some banding operations began to target these birds (D. Avers, Michigan Department of Natural Resources and B. O'Neal, Franklin College, personal communications). Aerial breeding waterfowl surveys are likely ineffective in detecting mallards using large urban areas, potentially resulting in abundance estimates that are biased low. Additionally, mallards using urban developed land cover during part of the annual cycle may have different demographic rates, possibly resulting in unmeasured individual heterogeneity in population parameters such as survival and productivity. In addition to changing use of land cover types, mallard breeding distribution could be shifting at a regional scale in response to habitat or climatic changes. Breeding period fidelity and hen mallard dispersal were relatively unstudied for Great Lakes mallards and these parameters are difficult to estimate using banding data when live recapture rates are low (Dooley et al. 2019). Capacity to estimate dispersal probability of hen mallards hatched in the Great Lakes to other breeding areas such as the Hudson Bay lowlands (Brook et al. 2021) or prairies was thus limited by available data. Assessing fine-scale and regional movements and fidelity are hence important to obtain a more complete picture of population processes.

Moreover, recent evidence demonstrated introgression of domestic game-farm mallard genes into wild populations in Europe and eastern North America (Söderquist et al. 2017, Lavretsky et al. 2020). Mallards in the U. S. portion of the Atlantic Flyway were a hybrid swarm consisting of ~90% wild x game-farm mallard hybrids (Lavretsky et al. 2020). Hybridization with game-farm mallards may lead to maladaptive traits or behaviors, resulting in lower survival or fecundity for admixed individuals. Using early banding data, Lincoln (1934) suggested that hand-reared domestic mallards released into the wild had lower survival and shorter dispersal distances than did wild mallards. More recent survival estimates have consistently been lower for hand-reared and domestic than for wild mallards (Brakhage 1953, Schladweiler and Tester 1972, Smith 1999, Osborne et al. 2010, Söderquist et al. 2013). Game-farm mallards had a longer breeding period and longer incubation time than wild mallards (Prince et al. 1970, Cheng et al. 1980), traits which may be detrimental in natural settings where nesting hens are exposed to predators. There is concern that releases of domestic mallards are contributing to declines in wild mallard populations (Söderquist et al. 2014, 2017, Lavretsky et al. 2020). Understanding behavioral and demographic consequences of hybridization between wild and domestic game-farm mallards is important given releases of game-farm mallards in eastern North America (Lavretsky et al. 2023). To address these questions and identify factors limiting Great Lakes mallards, a comprehensive view of mallard movements and population dynamics was needed.

The research goal was to estimate hen mallard survival, productivity, resource selection, and fidelity to the Great Lakes region in relation to banding location, genotype, molt and natal location, and age to identify factors limiting abundance and develop management recommendations to recover Great Lakes mallards. Project objectives were to 1) identify the influence of resource selection, genotype, and age on hen mallard breeding and nonbreeding survival using GPS-GSM transmitter data and known-fate models; 2) assess the effects of nest site land cover, predicted suitability, genotype, age, and nest initiation date on nest success and productivity using GPS-GSM transmitter and banding data; 3) quantify differences in nonbreeding season selection of land cover and wetland types between hen mallards marked in urban and rural areas, wild and admixed genotypes, and after hatch year and hatch year birds using location data from GPS-GSM transmitters and remote-sensed spatial data; and 4) determine the relative importance of urban and rural marking location, genotype, molt migration incidence, nest success, and age on probability of hen mallard fidelity to the Great Lakes region using GPS-GSM transmitter data and estimates of molt and natal origin derived from secondary feather stable isotope values.

DISSERTATION CONTENT

This dissertation is comprised of this introductory chapter, four research chapters intended for publication in peer reviewed journals, and a conclusion and management implications chapter. The research chapters include co-author contributions and therefore use plural pronouns; however, I take sole responsibility for their content in this dissertation. Chapter 2 examines movements and resource selection of mallards in relation to individual genotypes. Chapter 3 contains survival estimates for GPS-marked female mallards. Chapter 4 focuses on breeding period ecology including hen mallard incubation initiation, nest survival, and fidelity. Chapter 5 integrates banding, band recovery, and aerial survey data into an integrated population model for Great Lakes mallards. Chapter 6 summarizes the primary findings and management implications of the research.

FIGURES

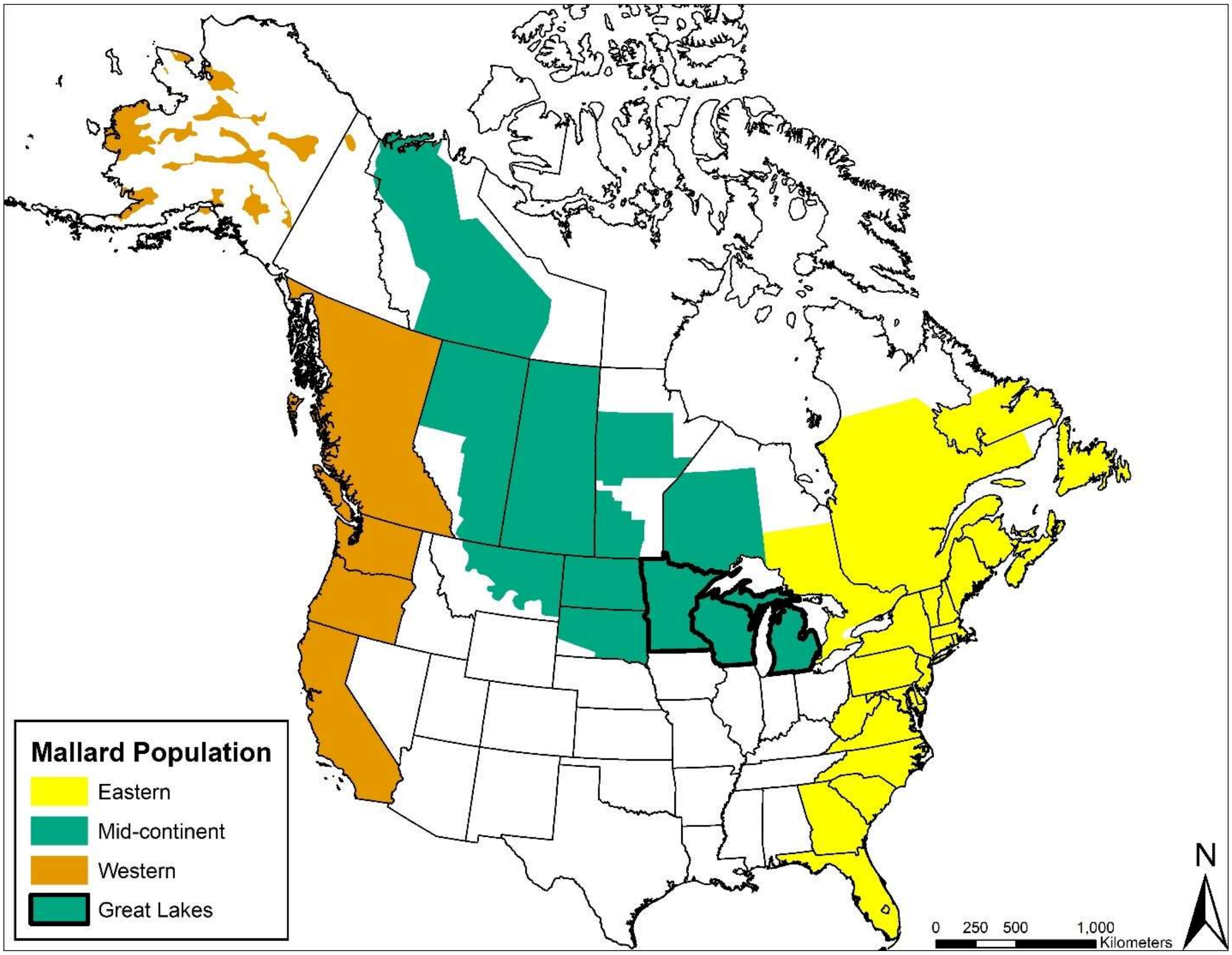

Figure 1.1. North American mallard breeding population survey areas. Data from U. S. Fish and Wildlife Service.

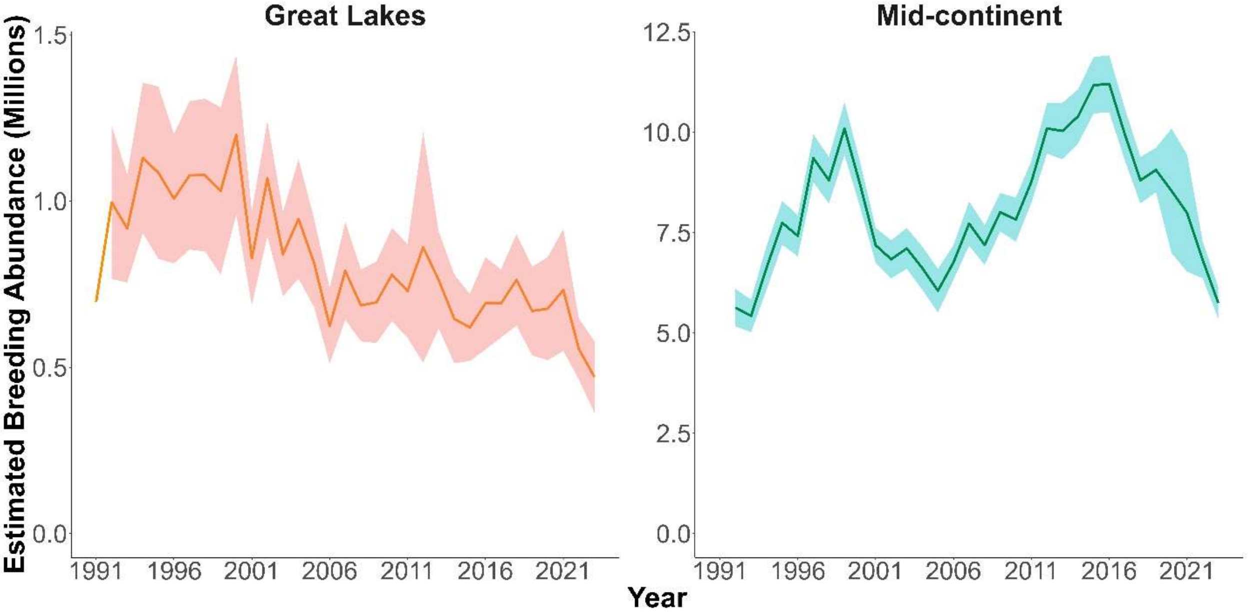

Figure 1.2. Midcontinent and Great Lakes (Michigan, Minnesota, and Wisconsin) breeding mallard abundance estimates (millions) and 95% confidence intervals (shaded region) from the waterfowl breeding population and habitat survey and Great Lakes state surveys, 1991–2023. Data are from the U. S. Fish and Wildlife Service, Michigan Department of Natural Resources, Minnesota Department of Natural Resources, and Wisconsin Department of Natura Resources.

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CHAPTER 2: GENETICS AFFECT GREAT LAKES MALLARD MOVEMENT AND RESOURCE SELECTION

ABSTRACT

Abundance data collected during spring aerial surveys suggested breeding mallard (*Anas platyrhynchos*) populations in the Great Lakes region (Michigan, Minnesota, and Wisconsin, USA) declined by >30% between 2000–2022. Understanding Great Lakes mallard movement ecology in the context of changing environmental and anthropogenic factors could reduce uncertainty in the drivers of declining mallard abundance. Recent detection of widespread introgression of domestic game-farm mallard genes into mallard populations in eastern North America raises concern about the role of hybridization in population declines. Our objective was to examine local and migratory movement and resource selection during the non-breeding period for female Great Lakes mallards in relation to genotype and urban development using GPS-GSM transmitters and remote-sensed spatial data. We captured, obtained a genetic sample, and marked 592 female mallards with GPS-GSM transmitters in Michigan, Wisconsin, Ohio, Indiana, and Illinois, USA from 2021–2023. We used ddRAD sequencing to estimate genotypes of GPS-marked mallards. We used linear mixed models and general linear models to examine factors affecting daily movement distance and autumn migration probability, respectively. We implemented a step-selection function and conditional logistic regression to estimate relative selection strength of land cover types relevant to mallard resource use. Genetic analyses indicated 44% of GPS-marked birds were wild mallards and 56% were wild x domestic game-farm mallard hybrids. Hybrid mallards had shorter daily movement distances, were less likely to migrate, and had higher selection for urban developed land cover than did wild mallards. Sedentary behavior and selection of urban areas raises concerns regarding the ecological fitness of hybrid mallards

and their impact on the regional mallard population.

INTRODUCTION

At the North American scale, mallards have been delineated into 3 populations for harvest management, defined by breeding geography and administrative flyway, including eastern, midcontinent, and western mallards (U. S. Fish and Wildlife Service 2023a). The midcontinent population is the largest and comprises mallards breeding from the Northwest Territories in Canada to the Great Lakes region. The Waterfowl Breeding Population and Habitat Survey (WBPHS) and Great Lakes state (Michigan, Minnesota, and Wisconsin) breeding-period waterfowl surveys are conducted annually to estimate spring waterfowl abundance by species (U. S. Fish and Wildlife Service 2023b). Trends in Great Lakes mallard abundance were historically similar to trends in the midcontinent population. However, prairie-nesting mallard abundance increased following a decline in the early 2000s while Great Lakes mallard abundance continued to decline (Figure 2.1). Breeding population size of Great Lakes mallards peaked near 1.2 million in the year 2000 based on state aerial surveys and declined to around 0.5 million in 2023 (U. S. Fish and Wildlife Service 2023a). Regionally produced mallards are particularly important to hunters in the Great Lakes region as an estimated 58-83% of their mallard harvest is derived from mallards produced within the region (Arnold and De Sobrino 2010). Declining Great Lakes mallard abundance is thus a concern for wildlife management agencies involved in hunting recreation as well as those implementing the North American Waterfowl Management Plan (Soulliere et al. 2017).

Recent research revealed mallards in the U. S. Atlantic Flyway are a hybrid swarm comprised of approximately 90% wild x domestic game-farm mallard hybrids (Lavretsky et al. 2020, 2023). Eastern mallard breeding abundance declined from about 1.4 million in 1998 to 1.2

million in 2023 (U. S. Fish and Wildlife Service 2023b), with the decline driven by mallards occurring in the U. S. portion of the flyway (U. S. Fish and Wildlife Service 2017), and hybridization with game-farm mallards is hypothesized to be a contributing factor (Lavretsky et al. 2020, Roberts et al. 2023). Game-farm mallard releases since the 1920s were estimated between >200,000 (U. S. Fish and Wildlife Service 2013) and >500,000 (Huesmann 1974) annually, although precise estimates are lacking. Historically, game-farm mallards were released primarily in the Atlantic Flyway (Huesmann 1974, Hepp et al. 1988) although 17.5% of captive-reared mallard releases from licensed shooting preserves occurred in the Mississippi Flyway in 2001 (U. S. Fish and Wildlife Service 2013). The proportion of wild x game-farm mallard hybrids detected at a continental scale generally decreases westward, with relatively few hybrids detected west of the Mississippi River (Lavretsky et al. 2023). However, banding data revealed that since 1990, 23% of mallards banded in the U. S. portion of the Atlantic Flyway were recovered in the Mississippi Flyway, revealing a pathway for domestic mallard genes to move westward (Lavretsky and Sedinger 2023). While only 4% of mallards sampled in the southern Mississippi Flyway were hybrids (Davis et al. 2022), 65% of hunter-harvested mallards sampled in northwest Ohio were hybrids (Schummer et al. 2023). Large scale releases of game-farm mallards and declining mallard populations in eastern North America warrant consideration of the effects of hybridization on individual behaviors and population ecology.

Release of artificially selected animals can cause changes in morphology, behavior, and demography that negatively impact wild populations (Champagnon et al. 2012). However, quantifying the population impact of hybridization between captive-bred and wild individuals can be difficult as the additive effects of introgression on fitness may be slow to develop (Tufto 2017). Large-scale, long-term releases of domestic mallards are predicted to negatively impact wild populations if gene flow transfers inheritable traits possessed by domestic ducks that are maladaptive in free-ranging populations (Söderquist et al. 2017, Lavretsky et al. 2020). Gene flow could have maladaptive consequences if domestic traits confer morphological or behavioral characteristics which reduce survival or reproductive capacity for admixed individuals. Using early banding data, Lincoln (1934) posited that hand-reared domestic mallards released into the wild had lower dispersal distances than those of wild mallards. More recent studies found that domestic mallards were typically harvested within three km of release locations (Osborne et al. 2010) and had significantly shorter migration distances (Söderquist et al. 2013) and smaller home range areas (Smith 1999, Bengtsson et al. 2014) than observed in wild mallards (Yetter et al. 2018). Whereas mallards can be considered facultative migrants, migratory decisions have been linked to weather cues that affect energy expenditure and food availability (Schummer et al. 2010, Weller et al. 2022), which have likely evolved to enable selection of areas that enhance survival. If hybridization with game-farm mallards diminishes migration and or the ability to select vital resources, survival could be reduced. Thus, quantifying the effects of hybridization on local movement, migration, and resource selection can aid understanding of factors affecting Great Lakes mallard population dynamics.

Our objective was to examine local and migratory movement and non-breeding period resource selection of hen mallards in relation to their genotype and association to urban development using GPS-GSM transmitters and remotely sensed spatial data. We predicted that hybrid (wild x domestic game-farm) mallards would be more sedentary and less likely to migrate than wild mallards, but that selection of land cover types would be similar for wild and hybrid mallards. Evaluating whether movement and resource selection differs between wild and hybrid mallards would aid understanding of potential consequences of hybridization. Quantifying differences in individual behaviors is important in developing models that examine factors affecting demographic rates and ultimately drivers of population dynamics. In addition to informing Great Lakes mallard population modelling, movement and resource selection information is useful in prioritizing habitat conservation and managing harvest at local and flyway scales.

STUDY AREA

We captured and marked female mallards with GPS-GSM transmitters in Bird Conservation Regions (BCRs; Bird Studies Canada and NABCI 2014) 12 (Boreal Hardwood Transition), 22 (Eastern Tallgrass Prairie), and 23 (Prairie Hardwood Transition) in the Great Lakes states of Michigan, Wisconsin, Ohio, Indiana, and Illinois, USA (hereafter, Great Lakes region; Figure 2.2). Bird Conservation Regions are landscape planning units comprised of similar ecosystems and bird communities and are relevant for landscape conservation planning in the Upper Mississippi/Great Lakes (UMGL) Joint Venture (JV) region (Soulliere and Al-Saffar 2021). The northern UMGL JV is dominated by undeveloped natural communities with extensive upland and wetland forest and lakes (BCR 12) that transition to a mixed landscape of forests, lakes, and more herbaceous wetlands interspersed with agriculture and urban development (BCR 23). The south half of the JV region (BCR 22) is dominated by row crop agriculture and urban landscapes, with smaller proportion coverage in forest and grassland communities; about 90% of historic wetlands have been drained and most remaining wetlands in BCR 22 are associated with riverine systems (Soulliere et al. 2017). Regional temperatures and precipitation across much of the study area are influenced by the Great Lakes and generally consist of cold, snowy winters and hot, humid summers (Scott and Huff 1996). Moderating lake effects result in wetland conditions that are generally more stable and less seasonally dynamic than in the midcontinent prairies and parklands

(Euliss et al. 2004, Simpson et al. 2005). Mallards were the most abundant nesting duck in the Great Lakes region (U. S. Fish and Wildlife Service 2023b) and predicted nesting densities were greatest in BCR 23 (Soulliere et al. 2017). We monitored movements of GPS-marked mallards within North America, which occurred in an area bounded by approximately 51.5ºN and 32ºN, and 75.2ºW, and 99.8ºW.

METHODS

Mallard Capture and Data Collection

We captured ducks using baited traps, rocket- and spring-propelled nets, handheld nets, and via night-lighting from 4 March – 4 October, 2021–2023. We aged ducks as AHY (after hatch year; adult), HY (hatch year; juvenile capable of flight) or L (local; juvenile incapable of flight) and sexed birds via plumage characteristics (Carney 1992). We banded mallards with a size 7 United States Geological Survey (USGS) aluminum leg band. We attached 20 g Ornitela GPS-GSM (global system for mobile communications) transmitters (OrniTrack-E20 4GCT C48; Ornitela, Vilnius, Lithuania) dorsally to female mallards via 4.5 mm-wide elastic straps. Transmitters were attached with two separate elastic loops in 2021 and via an X-shaped design consisting of a single piece of elastic in 2022 and 2023. We weighed each hen mallard to the nearest 10 g and attached transmitters only to individuals >700 g so transmitters comprised <3% of body mass (mean = 1.9%). Transmitters were distributed in approximate proportion to estimated breeding period mallard abundance by BCR (Soulliere et al. 2017). We classified transmitter deployment locations as urban if the proportion of developed land cover (low, medium, or high intensity developed, or developed open space as classified by the 2021 National Land Cover Database [Dewitz 2023]) within a 7 km (mean of maximum daily net displacement) radius of the site was >0.5, or rural if ≤0.5. We measured total head, bill (culmen), total tarsus, and wing chord (Dzubin and Cooch

1992) of GPS-marked females. We drew approximately 0.1 ml of blood from the tarsal vein and clipped approximately 3 mm of the first secondary wing feather of one wing for genetic and isotope analyses, respectively. Ducks were released immediately after processing at capture locations. Approval to capture, band, and attach transmitters was provided by Michigan State University institutional animal care and use committee (IACUC) permit PROTO202100046 and USGS Bird Banding Laboratory permit 03110. Transmitters were programmed to record a location every 30 minutes, 2 hours, or 4 hours when battery charge was >50%, <50% and >25% , or <25%, respectively, and uploaded data once every 24 hours when connected to cell networks.

Transmitter data were forwarded to Movebank (Wikelski and Kays 2019) for storage. We performed data preparation and analyses in Program R (R Core Team 2023) and used the move package (Kranstauber et al. 2018) to retrieve GPS data from Movebank. We defined the non-breeding period as 16 August to 29 February based on Coluccy et al. (2008) and the earliest date of nest incubation observed in this study (13 March) and included data collected during this timeframe from 2021 to 2024 in movement and resource selection analyses. We censored GPS locations where a satellite fix was not obtained or only one satellite was successfully contacted, and/or locations with a horizontal dilution of precision (HDOP) <5 (D'Eon and Delparte 2005). We monitored individuals from marking to reported harvest by a waterfowl hunter, mortality or transmitter loss indicated by transmitter temperature and accelerometer data and verified by field observation when possible, or transmitter failure (transmitter stopped sending data with no indication of mortality). We excluded individuals from analyses that provided GPS data for <7 days after release.

DNA Extraction, Sequencing, and Genetic Ancestry Analyses

We extracted genomic DNA from blood samples using a DNeasy Blood & Tissue kit following the manufacturer's protocols (Qiagen, Valencia, CA, USA). DNA quality was visually assessed on a 1% agarose gel to ensure high molecular weight bands. For mitochondrial DNA (mtDNA), we polymerase chain reaction (PCR) amplified and Sanger sequenced the control region across samples using primers L78 and H774 (Sorenson and Fleischer 1996, Johnson and Sorenson 1999), and following protocols outlined in (Lavretsky et al. 2014b). Final products were sequenced on an ABI 3730 (Applied Biosystems, Life Technologies, Carlsbad, California, USA) machine at the University of Texas at El Paso Border Biomedical Research Centers (BBRC) Genomic Analysis Core Facility. Sequences were then aligned and edited using SEQUENCHER v. 4.8 (Gene Codes Corporation, Ann Arbor, MI, USA). We note that mtDNA control region sequences for reference wild and domestic mallards from previous studies were included in the analyses (Lavretsky et al. 2014a, b, 2019a, Lavretsky 2020a). Reference samples included known wild, domestic game-farm, and domestic Khaki Campbell mallards. We constructed a median-joining haplotype network to visualize mtDNA structure as calculated in the program POPART (Leigh and Bryant 2015). Mallards are characterized by the old world (OW) A and new world (NW) B mitochondrial (mtDNA) haplogroups, which distinguish individuals of Eurasian or North American descent, respectively (Ankney et al. 1986, Avise et al. 1990, Lavretsky et al. 2014a). Importantly, being of Eurasian descent, all domestically-derived mallards carry OW A haplotypes, and thus, are a distinguishing marker when assessing whether game-farm mallard introgression occurred within a wild mallard lineage in North America (Lavretsky 2020b, Lavretsky et al. 2020).

For nuclear DNA, we followed ddRAD-seq (double-digest restriction site associated DNA sequencing) library protocols outlined in DaCosta and Sorenson (2014) and Lavretsky et al. (2015). In short, genomic DNA was enzymatically fragmented using *SbfI* and *EcoRI* restriction enzymes, and Illumina TruSeq compatible barcodes ligated for future de-multiplexing. The barcode-ligated fragments were then size selected using optimized double-sided bead selection protocols (Hernández et al. 2021). Libraries were then quantified with a Qubit 3 Flourometer (Invitrogen, Carlsbad, CA, USA) and pooled in equimolar amounts and sent to Novogenetics LTD (Sacramento, California, USA) for 150 base-pair, single-end chemistry sequencing on an Illumina HiSeq X. Raw Illumina reads were de-multiplexed using the *ddRADparser.py* script of the BU ddRAD-seq pipeline (DaCosta and Sorenson 2014) based on perfect barcode/index matches. Comparable sequences from previously published wild and domestic mallards were included and served as respective references (Lavretsky et al. 2014a, b, 2019b, 2020). For each sample, we first trimmed or discarded sequences of poor quality using TRIMMOMATIC (Bolger et al. 2014), and then remaining quality reads aligned to a chromosomal-level reference wild mallard genome (Lavretsky et al. in press) using the BURROWS WHEELER ALIGNER v. 07.15 (Li and Durbin 2011). Samples were then sorted and indexed in SAMTOOLS v. 1.7 (Bolger et al. 2014) and combined using the *mpileup* function with the following parameters "-c –A -Q 30 -q 30." All steps through *mpileup* were automated using a custom Python script (Lavretsky et al. 2020). Next, we used VCFTOOLS v. 0.1.15 (Danecek et al. 2011) to filter variant call format (VCF) files for any base-pair missing >10% of samples that also included a minimum base-pair depth of 5X (i.e., 10X per genotype) and quality per base PHRED scores of ≥30.

All nuclear population structure was based on independent bi-allelic ddRAD-seq autosomal single nucleotide polymorphisms (SNPs), and without using *a priori* assignment of individuals to populations or species. The final dataset was obtained by using VCFTOOLS (Danecek et al. 2011) to first extract bi-allelic SNPs, and then PLINK v.1.9 (Purcell et al. 2007) to filter for singletons (minimum allele frequency: 0.0014), any SNP missing ≥10% of data across samples, as well as any SNPs found to be in linkage disequilibrium (LD). We randomly excluded all but one SNP for any positions found to be in significant LD ($r^2 > 0.5$). Population structure was first visualized using a principal components analysis (PCA) as implemented in PLINK v.1.9 (Purcell et al. 2007). Next, the program ADMIXTURE 1.3 (Alexander et al. 2013) was used to attain per sample maximum likelihood estimates of population assignments for each individual, with datasets formatted for the ADMIXTURE analyses using PLINK v.1.9 (Purcell et al. 2007), and following steps outlined in Alexander and Lange (2011). ADMIXTURE analyses were run for population models of *K* of 2 and 3 with a 10-fold cross validation, incorporating a quasi-Newton algorithm to accelerate convergence (Zhou et al. 2011). Each analysis used a block relaxation algorithm for point estimation and terminated once the change in the log-likelihood of the point estimations increased by <0.0001. Finally, standard deviations around each point estimate were calculated based on 1,000 bootstrap replicates. Ancestry assignments and their standard deviation were used to recategorize samples as feral game-farm, wild mallard, and to filial classes of hybrids (Schummer et al. 2023) under expected genotypes in generational backcrosses and uncertainty on assignment probabilities. Thus, we classified individuals with ≥ 0.92 wild assignment probability as wild and all others as hybrids. Assignment probabilities are also interpretable as an estimate of the proportion of an individual's genes that are of wild ancestry, and thus we also considered proportion wild genome as a continuous covariate in movement analyses.

Movement

We modeled the mean sum of step lengths (i.e., movement distance) in each 24-hour period during non-migratory movements in relation to the estimated proportion of wild mallard genes within individuals using linear mixed models in the lme4 package (Bates et al. 2015). First, we inspected the sampling rate of GPS fixes and excluded 6 individuals with a median fix rate >30 minutes (highest programmed location frequency) because estimation of step lengths assumes the length of time between pairs of consecutive locations is equal. We resampled the remaining data to a location every 30 minutes to ensure time between each location was consistent and only used successive locations to calculate step lengths. We calculated step lengths as the linear distance between consecutive GPS locations using the package amt (Signer et al. 2019). Step lengths provide an estimate of movement distance over a given time period and don't require the assumption that individuals are range resident (plots of variance in position over time reach an asymptote, indicating the amount of space used eventually becomes constant), an assumption needed to estimate home range area (Noonan et al. 2019). We excluded step lengths collected during autumn or spring migration that were >30 km when bird trajectories were directed in a northward or southward direction. Thus, the daily sum of step lengths provided an index of total non-migratory distance moved in each 24-hour period and facilitated comparison of local daily movement distances. Inspection of the distribution of step length sums and QQ plots suggested a log transformation of daily movement distance was appropriate because residuals were not normally distributed. We modeled log-transformed daily step length sum (daily movement distance) as a function of proportion wild genotype with a random intercept of mallard ID to account for random individual variation. We included linear and quadratic effects of proportion wild genome as covariates on daily movement distance, resulting in three candidate models. We ranked models using Akaike's Information Criterion (Burnham and Anderson 2002) adjusted for small sample size (AIC_c) using the package MuMIn (Barton 2019). We calculated predicted daily movement distances from the top-ranked model treating proportion wild genome as a continuous variable. To predict how backcrossing of hybrid with wild mallards influences daily movement distance, we also fit a model treating genotype as a discrete predictor where the generational categories of feral, first generation (F1), <F2, F2, <F3, F3, and wild corresponded to 0 to <0.43, 0.43 to <0.63, 0.63 to <0.72, 0.72 to <0.82, 0.82 to <0.86, 0.86 to <0.92, and 0.92 to 1 proportion wild genome, respectively. The <F2 and <F3 categories included hybrids that did not fit into an ordered generational category (unknown generational backcrosses). We used the emmeans package (Lenth 2022) to calculate predicted daily movement distance for each generational category.

We defined autumn migration as a relocation with a total displacement ≥30 km (Weller et al. 2022) during 16 August to 29 February. We estimated the probability of autumn migration, conditional on an individual being alive on 1 January, in relation to genotype and capture site land cover (urban or rural) using general linear models with a binomial response (migrated, did not migrate) and logit link (Bates et al. 2015). Candidate models included all combinations of covariates with additive effects of proportion wild genome, capture site land cover, capture latitude, and capture state (MI, WI, OH, IN, or IL). We examined covariates for multicollinearity prior to modeling. We ranked models using $\mathrm{AIC_c}$ via the package MuMIn (Barton 2019).

Resource Selection

To compare resource selection across mallard genotypes, we implemented a step-selection function analysis to account for resource availability given mallard movement characteristics (Avgar et al. 2016). Modeling movement metrics such as step length and turning angle (angle measured between the previous and current direction of movement) within the time series framework of GPS data provides a method to account for spatial and temporal autocorrelation (de Solla et al. 1999) of animal locations while identifying which resources are biologically available to individuals (Fieberg et al. 2010, Avgar et al. 2016). This approach provides more realistic estimates of availability than using randomly sampled locations because movement patterns affect which resources are available and availability affects how animals move (Avgar et al. 2013). We merged the 2021 USGS National Land Cover Database (NLCD; Dewitz 2023) and 2020 Land Cover of Canada (LCC) database (Latifovic 2022), clipped to the extent of mallard GPS locations, and reclassified the raster into eight cover classes relevant to mallard resource selection. Land cover classes included emergent herbaceous wetland, forested/woody wetland, open water, developed (low, medium, and high intensity developed and developed open space), grassland (grassland/herbaceous and hay/pasture), forest (upland deciduous, evergreen, needleleaf, and mixed forest), agriculture (cultivated cropland), and other (barren, scrub shrub, and shrubland).

We first used Hidden Markov Models (HMMs) to estimate unobserved behavioral states (Langrock et al. 2012, van de Kerk et al. 2015, Patterson et al. 2017) using observed step lengths and turning angles. We fit HMMs in the moveHMM package (Michelot et al. 2016) using a gamma distribution for step length (meters) and a Von Mises distribution for turning angle (radians). Hidden Markov Models had three behavioral states and covariates included all combinations of additive effects of hour of day, genotype, and age, which were hypothesized to affect movement characteristics among individuals and over time (Luukkonen et al. 2022). We ranked HMMs using AIC (Burnham and Anderson 2002) and used the top model to assign the most probable behavioral state to each location. We used the distribution of step lengths and turning angles associated with each behavioral state to randomly sample six available locations for every observed location (Karelus et al. 2019, Luukkonen et al. 2022). Then we extracted the land cover type at each used and available point via the raster package (Hijmans 2020).

We estimated the relative selection strength (Avgar et al. 2017) of land cover types using two-step conditional logistic regression in the TwoStepCLogit package (Craiu et al. 2016).

Relative selection strength (RSS) is analogous to a risk ratio, and in the case where resource units such as habitat types are categorical, RSS is the probability of selecting a given habitat type divided by the probability of selecting a reference cover type (Avgar et al. 2017). Probability of selection is the probability an individual selects a resource unit given the resource unit is encountered (Lele et al. 2013), with selection quantified as an observed GPS location within a given resource unit. In wildlife telemetry, researchers typically only have data to estimate which resource units were used and which units were available, rather than which units were used and unused. When data are in the used versus available format and resource covariates are discrete, the exponential resource selection probability function is inestimable, thus only permitting use of a resource selection function to estimate relative selection and not probability of selection (Lele and Keim 2006). We used models with fixed effects of land cover type and random effects of mallard ID to account for differences in habitat selection between individuals (Karelus et al. 2019, Luukkonen et al. 2022). We set open water as the reference category and calculated odds ratios of selection, or RSS. Relative Selection Strength estimates indicate whether each land cover type was less selected (odds ratio <1 with confidence intervals non-overlapping 1), similarly selected (confidence intervals overlap 1), or more selected (odds ratio >1 with confidence intervals non-overlapping 1) than open water. More importantly, odds ratios of selection allow for comparison of the strength of land cover type selection between mallards of different genotypes, informing if and how selection of land cover types differs by genotype. We considered three genotypic categories in this analysis which corresponded to observed differences in daily movement distance and migration incidence: early generational hybrids (feral and F1 hybrids; <65% wild), late generational hybrids (F2 and F3 hybrids; 65% to 92% wild), and wild (>92% wild).

RESULTS

We attached GPS transmitters to 592 hen mallards in 2021 (n = 194), 2022 (n = 241), and 2023 (n = 157). Mallards were captured using baited traps (n = 331), rocket- and spring-propelled nets (n = 166), hand-held nets (n = 55), and via night-lighting (n = 40). Transmitters were deployed across all states, BCRs, and mallard ages (Table 2.1). Individual mallards were monitored for an average of 189 days (range: 2–1,037 days) during the study. We excluded 24 individuals from analyses for which there were <7 days of GPS monitoring data available following release. Locations collected from 16 August through 28 February in 2021–2022 (n = 744,364), 2022–2023 (n = 1,181,940), and through 29 February in 2023–2024 (n = 1,035,939) were extracted for analysis. After excluding 553 locations (227 in 2021–2022, 147 in 2022–2023, and 179 locations in 2023–2024) that were unreliable or failed fixes, there were 2,968,883 locations available for non-breeding period analyses.

Genetic Ancestry

A total of 590 (of 592) samples provided usable genomic material. First, 592 base-pairs of overlapping mtDNA control region sequence data were attained across all samples, including 580 (of 590) samples specific to this study. Of the 580 sequences, we recovered 63.8% (n = 370) and 36.2% (n = 210) carrying Old World A versus New World B haplogroups, respectively. The proportion of individuals with New World B haplotypes within each state ranged from 6.5% in Indiana to 55.4% in Wisconsin. Interestingly, 46.2% of samples determined to be genetically wild mallard (n = 251) carried Old World A mtDNA haplotypes, suggesting a substantial portion of wild mallards had maternal input from domestic mallards in their ancestral past (Lavretsky et al. 2023).

Next, a total of 33,216 (of 34,230) independent bi-allelic ddRAD-seq SNPs were retained for nuclear population structure analyses. Plotting the first two principal components (Figure 2.3) explained a total of 26.8% of the variance, and clearly separated reference wild mallards, game-farm mallards, and Khaki Campbells, with samples from this study distributed between wild reference mallard set and game-farm mallards (Figure 2.3). Given no evident clustering with Khaki Campbells, we attained assignment probabilities by analyzing a dataset excluding them. Plotting ADMIXTURE assignment probabilities under a *K* population of two distinguished between wild and game-farm mallards, while samples from this study possessed assignment probabilities to either the wild mallard genetic cluster only or had interspecific assignments to both clusters (Figure 2.3). In total, we recovered 44% of GPS-marked mallards as genetically wild, whereas 56% were classified as wild x game-farm mallard hybrids. Total sample sizes for Feral, F1, <F2, F2, <F3, F3, and wild individuals were 22, 37, 63, 61, 60, 92, and 255, respectively. The percentage of wild mallards captured in each state ranged from 8.1% in Indiana to 63.9% in Wisconsin. Generally, fewer hybrids were captured in the northern and western portions of the study area (Table 2.2). Of mallards captured at rural sites (n = 353), 58.4% were wild and 41.6% were hybrids. Mallards captured at urban sites (n = 237) were comprised of 21.9% wild and 78.1% hybrid individuals.

Movement

The top-ranked model predicting log-daily movement distance suggested a positive linear effect of proportion wild genome ($\beta_{\text{pwild}} = 1.33; 95\%\ \text{CI}: [1.06,\ 1.60]$) and received 56% of the model weight (Table 2.3). The proportion of the variance explained by the fixed and random effects (conditional R^2) was 0.289. The second ranked model was 0.52 AIC_c units from the top-ranked model and received 43% of the model weight, however, the 95% CIs on the quadratic effect of proportion wild genome overlapped zero ($\beta_{\text{pwild}^2} = -0.50\ [-1.55,\ 0.54]$). Thus, we report estimates from the top-ranked model. Mallards with a greater proportion of wild genes had greater average daily movement distances, with substantial individual variation (Figure 2.4). The model treating genotype as discrete categories corresponding to estimated generational assignments also predicted an increase in daily movement distance as generational backcrosses approached wild (Figure 2.5). Feral, F1, and <F2 hybrids were predicted to move significantly shorter distances than were wild mallards (non-overlapping CIs). The 95% CIs for F2, <F3, and F3 hybrids overlapped the 95% CIs for wild mallards. Wild mallards were predicted to have 2.52, 1.72, 1.32, 1.20, 1.23, and 1.02 times the daily movement distance compared to Feral, F1, <F2, F2, <F3, and F3 hybrids, respectively.

The top model predicting autumn migration probability included effects of proportion wild genome, banding site type (urban or rural), and capture latitude (Table 2.4). There were positive relationships of proportion wild genome ($\beta_{\text{pwild}} = 2.20\ [0.25,\ 4.16]$) and capture latitude ($\beta_{\text{lat}} = 0.22\ [0.07,\ 0.38]$) with migration probability (Figure 2.6). Mallards marked at rural sites were more likely to migrate than those marked in developed urban areas ($\beta_{\text{site}} = -1.06\ [-1.62, -0.50]$). For rural capture sites at the mean latitude (42.74ºN), wild mallards were 2.12, 1.41, and 1.18 times more likely to migrate than F1, F2, and F3 hybrids, respectively. Mallards that migrated from mid-August through February primarily went to the southern Great Lakes states or mid-latitude states in the Mississippi and Atlantic flyways, with few individuals moving farther south than Tennessee (Figure 2.7).

Resource Selection

The top-ranked HMM describing movement characteristics included three behavioral states and effects of hour of day, genotype, and age (Table 2.5). We used this model to randomly sample available land cover types from the distribution of step lengths and turning angles associated with each individual’s movement state at each observed GPS location. Open water and emergent herbaceous wetland were the most-selected land cover types across all mallard genotypes (Table 2.6; Figure 2.8). The aquatic cover types of open water, emergent herbaceous wetland, and forested wetland were generally more highly selected than were terrestrial cover types (all other land cover types). The Other category (including barren land, scrub-shrub, and shrubland) was highly selected by early generational hybrids. Early generational hybrids had significantly greater selection for urban developed land cover than did late generational hybrids and wild mallards. Early generational hybrids were 1.9 times more likely and late generational hybrids were 1.2 times more likely to select developed land cover than were wild mallards. Early generational hybrids were significantly less likely to select agriculture than were late generational hybrids and wild mallards. Trends in RSS estimates for urban land cover followed trends in the proportion of observed (used) locations in urban land cover (Figure 2.9), with early generational hybrids having the highest proportion of locations in urban land cover and the lowest use of emergent and forested wetlands. Therefore, as the proportion of game-farm ancestry increased, individuals were more likely to select and spend a greater proportion of time in developed areas. Further, hybrid mallards were less likely to use emergent and forested wetlands than were wild mallards (Figure 2.9).

DISCUSSION

Genetic sampling of mallards in the Great Lakes region provided further evidence that large scale releases of game-farm mallards (Huesmann 1974, U. S. Fish and Wildlife Service 2013) in eastern North America during the past century has resulted in flow of domestic genes into wild mallard populations (Lavretsky et al. 2019a). The proportion of hybrids in our sample set was intermediate between the U. S. portion of the Atlantic Flyway where previous research suggested about 90% of mallards were wild x game-farm hybrids (Lavretsky et al. 2019a) and the Central Flyway where sampled mallards were almost entirely comprised of wild individuals (Lavretsky et al. 2023). Previous sampling indicated most releases of game-farm mallards likely occurred in eastern North America (Huesmann 1974, U. S. Fish and Wildlife Service 2013). Our findings support this assumption at a finer spatial scale, with gradually lower proportions of hybrid mallards occurring westward across states in the Great Lakes region.

Regarding genotype distribution relative to developed landscapes, Indiana was an outlier among the states in our sample with hybrids comprising >85% of mallards sampled at both urban and rural locations. Otherwise, hybrids were more prevalent than wild mallards at urban sites, and only five hybrids with <50% wild mallard ancestry were encountered at rural banding locations. Hybrid mallards could be more susceptible to capture than wild mallards when using bait because game-farm mallard bill morphology suggested domestic mallards are better suited to feeding on large grains, such as shelled corn used as bait in this study, than small seeds produced by native wetland vegetation (Champagnon et al. 2010). In addition to being exposed to supplemental feeding (Smith 1999, Söderquist et al. 2024), captive-bred mallards have been shown to settle in urban settings post release (Osborne et al. 2010). Although the behavioral change among captive-bred or hybrid individuals may bias their capture over wild mallards, any increases in hybrids that have such behavior would still reflect prevalence across locations. Consequently, our results support that increases in game-farm mallard ancestry results in individuals significantly selecting urban over rural habitat (Figure 2.8).

Under the assumption that individuals select habitat types to obtain resources required to survive and reproduce, mallards with a higher proportion of domestic ancestry may have morphological, physiological, or behavioral traits that make them better suited to urban landscapes. Artificial selection in captivity may intentionally or unintentionally select for traits that are suited to living in semi-domestic settings or that are maladaptive in wild settings (Lavretsky et al. 2023). Based on previous studies, mallards with more game-farm mallard ancestry are likely to be more susceptible to predation (Schladweiler and Tester 1972), more susceptible to hunter harvest (Hunt et al. 1958, Soutiere 1986, Smith 1999), and have lower annual survival (Osborne et al. 2010, Söderquist et al. 2021). Selection and use of urban areas should generally reduce exposure to predation and harvest pressure and increase access to supplemental feeding (Figley and VanDruff 1982). The inverse relationship between proportion wild genome and relative selection strength and use of developed land cover in this study is consistent with the hypothesis that hybridization of wild with domestic game-farm mallards produces hybrids that are better suited to life in urban settings than in rural habitats used by wild mallards. In addition, we found ancestry cut-offs were associated with shifts from game-farm to wild mallard-like behaviors. Whereas early and late generational hybrids had similar selection of emergent wetlands as did wild mallards, early and late generational hybrids had lower use of emergent wetlands (Figure 2.9) suggesting that hybrids, particularly early generational hybrids, spent little time in emergent wetlands.

Habitat conservation efforts aimed at restoring, enhancing, and protecting rural wetlands benefit wild mallards, but likely provide less benefit to early generational hybrid mallards. Continuous inputs of game-farm mallards since the 1920s (Huesmann 1974, U. S. Fish and Wildlife Service 2013) have increased the proportion of the Great Lakes mallard population comprised of hybrids, resulting in more individuals that select and use urban habitats and spend little time in wetland habitat types used by wild mallards. Decreasing the proportion of the population comprised of hybrid mallards would be expected to increase the effectiveness of traditional habitat conservation techniques as wild mallards were more likely to select and use emergent herbaceous and forested wetlands than were early generational hybrids. Individuals with more domestic than wild genes appear suited to inhabit developed areas. Therefore, developed areas may provide a habitat niche for early generational hybrid mallards. Opportunity for public viewing could be a potential social benefit arising from mallard use of urban areas.

Sedentary behavior in individuals with greater proportions of domestic genes is consistent with numerous studies examining dispersal or movement distances of domestic game-farm mallards and captive reared mallards released into the wild (Lincoln 1934, Smith 1999, Osborne et al. 2010, Söderquist et al. 2013, 2024). The average daily movement distance for wild mallards in this study of 5.0 km (95% CI: 4.7, 5.4) was similar to mallards marked in California where daily movement distance estimates ranged from 4.9 km to 5.9 km (McDuie et al. 2019) and wild mallards marked in Sweden that moved 5.1 km per day (Söderquist et al. 2024). Our daily movement distance estimate for feral hybrids of 0.7 km (0.5, 0.9) was slightly smaller than for domestic mallards released in a baited wetland in Sweden, which moved on average 1 km per day (Söderquist et al. 2024). However, to our knowledge no study has analyzed movement behavior for hybrid mallards captured in the wild across a gradient of genotypes from primarily domestic to wild. As the proportion of domestic ancestry increased, individuals moved shorter daily distances and were less likely to migrate during autumn and winter. A remaining question is whether lack of migratory behavior in early generational hybrids is due to morphological and or physiological limitations, lack of response to migratory cues, or a combination of factors. Wild mallards captured at urban sites were less likely to migrate than wild mallards captured at rural sites, and access to open water, anthropogenic food sources, and thermal refugia (Grimmond 2007, Meissner et al. 2015) in urban areas could contribute to reduced migration in both wild and hybrid mallards. Lack of migratory behavior could be maladaptive for individuals using rural areas as freezing conditions and snow cover limit access to open water and forage, which are proximate factors associated with mallard migration (Schummer et al. 2009, Weller et al. 2022). Failure of early generational hybrids to migrate could explain why fewer were found in northern latitudes in the Great Lakes region, where migration probability increases in relation to more extreme winter weather. Climate or environmental changes may contribute to individual heterogeneity in migratory behavior in wild mallards. The primary strategies employed by wild mallards were to make short (i.e., within the Great Lakes states) migrations or local movements to areas with open water during the winter. These movements correspond to contemporary northward shifts in dabbling duck band recoveries during January and February (Verheijen et al. 2024), and to the distribution of band recoveries from mallards marked in the Great Lakes states (Chapter 5).

Collectively, sedentary behavior and selection of urban areas raises concern regarding the ecological fitness of wild x domestic game-farm mallard hybrids. Hybridization with game-farm mallards apparently contributes to shorter movement distances, lack of migration, and selection and use of developed land cover. As a result, early generational hybrid mallards may be less available for hunter harvest because they move less and select urban areas where waterfowl hunting is often limited. Waterfowl habitat conservation efforts currently only benefit a portion of the Great Lakes mallard population comprised of late generational hybrids and wild mallards. If early generational hybrids select urban areas because anthropogenic influences (i.e., reduced predation, supplemental feeding) increase survival, then hybridization with game-farm mallards could be a contributing factor to Great Lakes mallard population decline through reduced survival of early generational hybrids outside of developed areas. Our results suggest that third generation (F3) hybrids generally have similar daily movement distances and similar tendencies to migrate as observed in wild mallards, and that resource selection of late generational hybrids approaches that of wild mallards. Therefore, backcrossing of hybrid mallards with wild individuals relatively quickly (i.e., within approximately three mallard generations) results in behaviors equivalent to those observed in wild mallards. Given concern with declining Great Lakes and Eastern mallard populations (U. S. Fish and Wildlife Service 2023b), further research to determine demographic rates of hybrid mallards is warranted.

MANAGEMENT IMPLICATIONS

Results of this study reduce uncertainty in the effects of hybridization between wild and game-farm mallards on movement ecology in the Great Lakes region and provide several considerations relevant to habitat and harvest management. Hybridization and increased proportions of domestic genes were associated with greater sedentary behavior and selection and use of urban areas relative to local movement, migration, and resource selection by wild mallards. Therefore, managers could expect rural wetland habitat conservation efforts for waterfowl to have limited effectiveness for the portion of the Great Lakes mallard population comprised of hybrids. Moreover, shorter daily movement distances and selection of developed land cover, where waterfowl hunting is limited, reduces harvest opportunity provided by hybrid mallards. Additionally, mallard harvest opportunity for hunters in the central portions of the Mississippi and Atlantic flyways, locations historically used during autumn and winter by Great Lakes mallards, will be compromised due to lack of migratory behavior by early generational hybrids and relatively low migration incidence in wild Great Lakes mallards. This study suggests backcrossing of hybrid with wild mallards results in movement behaviors and resource selection similar to that of wild mallards within three generations. Waterfowl and wetland managers with objectives to maintain movement and migration behaviors of wild mallards and the response of mallard populations to traditional wetland habitat conservation could consider regulating game-farm mallard releases. Further research will be required to evaluate the potential negative effects of game-farm mallard releases on mallard demographic parameters.

TABLES

Table 2.1. Number of hen mallards marked with GPS-GSM transmitters by Bird Conservation Region (BCR), state, and age (AHY = after hatch year; HY = hatch year; L = local) in the Great Lakes region from 2021–2023.

	Michigan			**Wisconsin**			**Ohio**			**Indiana**			**Illinois**			
	AHY	**HY**	**L**	**AHY**	**HY**	**L**	**AHY**	**HY**	**L**	**AHY**	**HY**	**L**	**AHY**	**HY**	**L**	**Total**
BCR 23	127	49	3	80	51	10	61	30	0	12	11	2	0	2	0	438
BCR 22	-	-	-	-	-	-	2	2	0	28	9	0	26	10	0	77
BCR 12	12	36	1	7	18	3	-	-	-	-	-	-	-	-	-	77
Total	139	85	4	87	69	13	63	32	0	40	20	2	26	12	0	592

Table 2.2. Sample size (n) and the proportion of wild and hybrid mallards captured by banding site type (urban or rural) within Illinois (IL), Indiana (IN), Michigan (MI), Ohio (OH), and Wisconsin (WI) from 2021–2023.

		Proportion		**n**	
State	**Site Type**	**Wild**	**Hybrid**	**Wild**	**Hybrid**
IL	Rural	0.684	0.316	13	6
	Urban	0.111	0.889	2	16
IN	Rural	0.143	0.857	3	18
	Urban	0.049	0.951	2	39
MI	Rural	0.492	0.508	60	62
	Urban	0.305	0.695	32	73
OH	Rural	0.446	0.554	33	41
	Urban	0.238	0.762	5	16
WI	Rural	0.829	0.171	97	20
	Urban	0.212	0.788	11	41

Table 2.3. Model selection table using Akaike's Information Criterion adjusted for small sample size (AIC_c) for linear mixed models predicting log-transformed daily movement distance (sum of step lengths) as a function of proportion wild genome (pwild; $pwild^2$ denotes a quadratic term) for female Great Lakes mallards marked with GPS-GSM transmitters in Michigan, Wisconsin, Illinois, Indiana, and Ohio from 2021–2023. Table includes model loglikelihood (logLik), difference in AIC_c from the top-ranked model (ΔAIC_c), model weight (ω), and number of parameters (K).

Model	**logLik**	**AIC_c**	**ΔAIC_c**	**ω**	**K**
pwild	-92897.0	185802.1	0.00	0.56	4
$pwild^2$ + pwild	-92896.3	185802.6	0.52	0.43	5
$pwild^2$	-92900.6	185809.1	7.03	0.02	4

Table 2.4. Model selection table using Akaike's Information Criterion adjusted for small sample size (AIC_c) for general linear models (binomial response and logit-link function) predicting autumn migration probability in relation to proportion wild genome (pwild; proportion of wild genome), capture site type (site; urban or rural), capture latitude (lat), and capture state for female mallards marked with GPS-GSM transmitters in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023. Table includes model loglikelihood (logLik), difference in AIC_c from the top-ranked model (ΔAIC_c), model weight (ω), and number of parameters (K).

Model	**logLik**	**AIC_c**	**ΔAIC_c**	**ω**	**K**
site + pwild + lat	-206.59	421.28	0.00	0.82	4
lat + site	-209.41	424.89	3.61	0.14	3
site + pwild	-210.76	427.58	6.30	0.04	3
state + site	-209.88	431.98	10.69	0.00	6
lat + pwild	-213.85	433.76	12.48	0.00	3
site	-216.22	436.46	15.18	0.00	2
pwild	-217.79	439.60	18.32	0.00	2
state + pwild	-213.83	439.89	18.60	0.00	6
lat	-223.14	450.31	29.03	0.00	2
state	-223.00	456.16	34.88	0.00	5
genotype	-227.33	458.69	37.40	0.00	2
age	-232.66	469.34	48.06	0.00	2

Table 2.5. Hidden Markov Model (HMM) selection table using Akaike's Information Criterion (AIC) for models describing step lengths and turning angles associated with unobserved movement states and hour of day, genotype (early generational hybrids, late generational hybrids, and wild), and age (juvenile, adult) effects for female mallards marked with GPS-GSM transmitters in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023. Table includes model loglikelihood (logLik), difference in AIC from the top-ranked model (ΔAIC), and model weight (ω).

Model	**logLik**	**AIC**	**ΔAIC**	**ω**
Hour + Genotype + Age	11440733.1	22825345.0	0.0	1.0
Hour + Genotype	11417106.5	22826619.5	1274.5	0.0
Hour + Age	11436896.4	22831759.0	6414.0	0.0
Hour	11439479.8	22834264.9	8919.9	0.0
Genotype + Age	11413277.8	22872599.4	47254.3	0.0
Genotype	11415847.5	22873844.8	48499.8	0.0
Age	11436267.7	22879011.6	53666.6	0.0
Null	11412634.5	22881506.2	56161.1	0.0

Table 2.6. Resource selection coefficients and 95% confidence intervals (CI) for female mallards marked with GPS-GSM transmitters in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023. Genotype categories include the range of proportion wild genome in parentheses.

Genotype Category	**Land Cover Type**	**Selection Coefficient (95% CI)**
Wild (>92%)	Herbaceous Wetland	0.05 (-0.01,0.11)
Wild (>92%)	Forested Wetland	-0.36 (-0.44,-0.27)
Wild (>92%)	Agriculture	-1 (-1.11,-0.88)
Wild (>92%)	Grassland	-0.65 (-0.77,-0.53)
Wild (>92%)	Forest	-1.34 (-1.48,-1.2)
Wild (>92%)	Urban	-1.09 (-1.21,-0.97)
Wild (>92%)	Other	-0.39 (-0.52,-0.25)
Late Generational Hybrid (65-92%)	Herbaceous Wetland	0.13 (0.06,0.2)
Late Generational Hybrid (65-92%)	Forested Wetland	-0.26 (-0.36,-0.16)
Late Generational Hybrid (65-92%)	Agriculture	-1.05 (-1.18,-0.92)
Late Generational Hybrid (65-92%)	Grassland	-0.68 (-0.79,-0.56)
Late Generational Hybrid (65-92%)	Forest	-1 (-1.12,-0.88)
Late Generational Hybrid (65-92%)	Urban	-0.83 (-0.92,-0.73)
Late Generational Hybrid (65-92%)	Other	-0.44 (-0.58,-0.3)
Early Generational Hybrid (<65%)	Herbaceous Wetland	0.15 (0,0.29)
Early Generational Hybrid (<65%)	Forested Wetland	-0.41 (-0.68,-0.13)
Early Generational Hybrid (<65%)	Agriculture	-1.66 (-2.02,-1.29)
Early Generational Hybrid (<65%)	Grassland	-0.76 (-1.04,-0.48)
Early Generational Hybrid (<65%)	Forest	-1.51 (-1.81,-1.21)
Early Generational Hybrid (<65%)	Urban	-0.4 (-0.58,-0.22)
Early Generational Hybrid (<65%)	Other	-0.07 (-0.32,0.18)

FIGURES

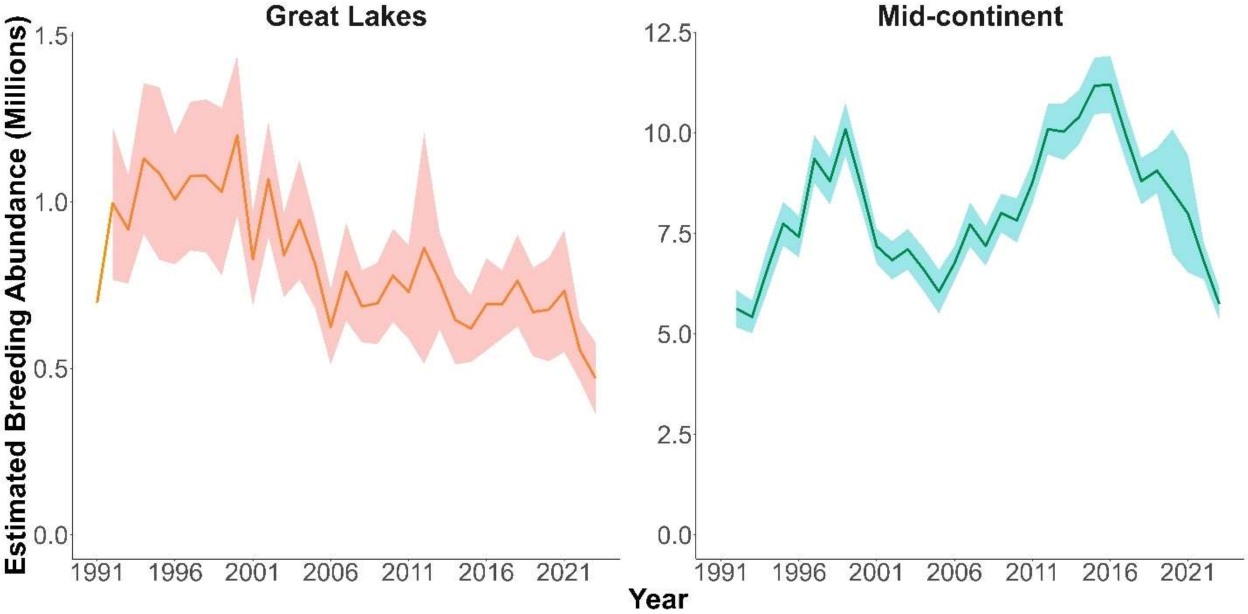

Figure 2.1. Estimated mallard abundance from spring breeding waterfowl surveys in the Great Lakes states (MI, MN, WI combined) and midcontinent population survey area from 1991-2022. Data from United States Fish and Wildlife Service, Michigan Department of Natural Resources, Minnesota Department of Natural Resources, and Wisconsin Department of Natural Resources.

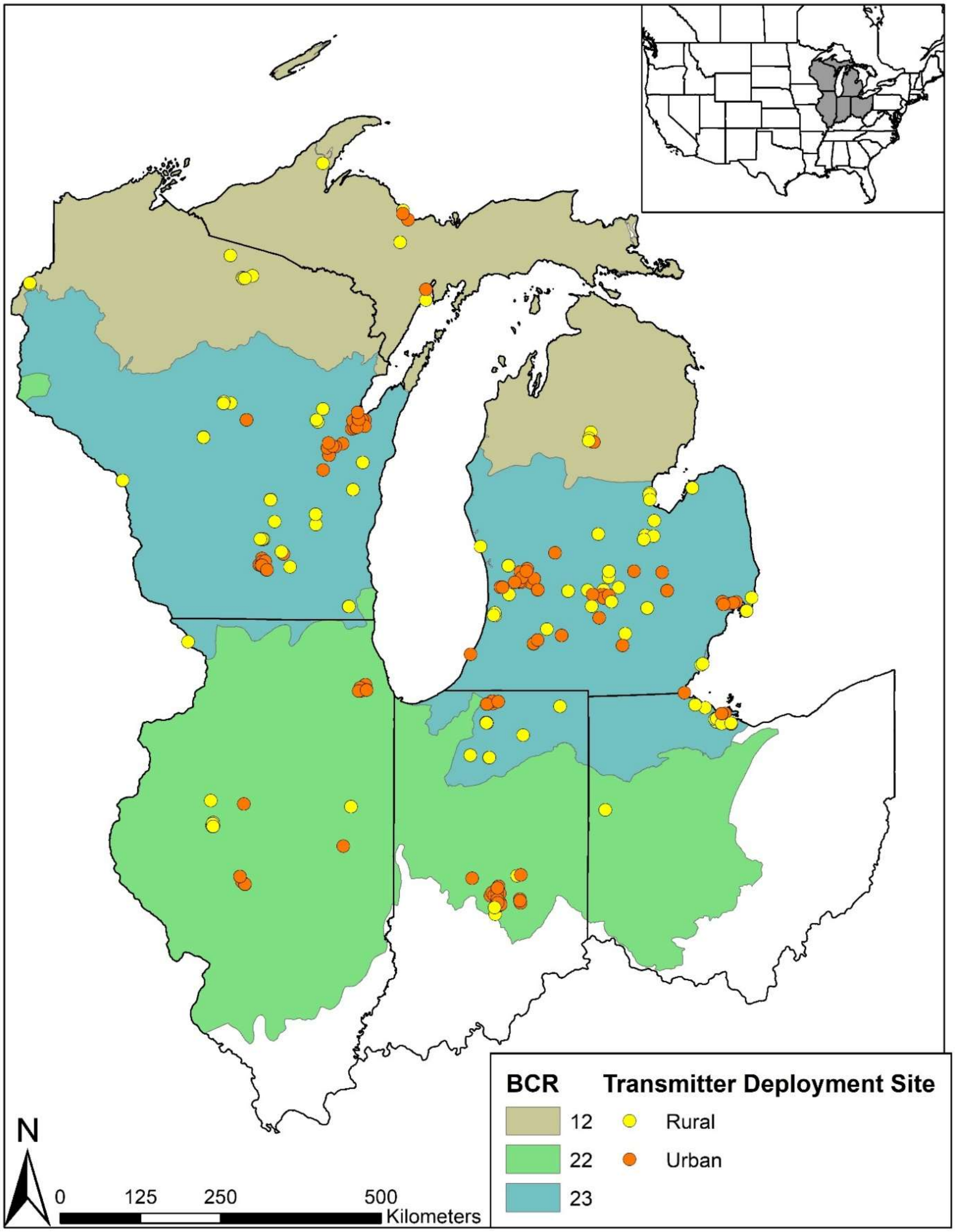

Figure 2.2. Capture and GPS-GSM transmitter deployment locations for female mallards captured in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023 in relation to banding site type (urban or rural) and Bird Conservation Region (BCR) 12, 22, and 23.

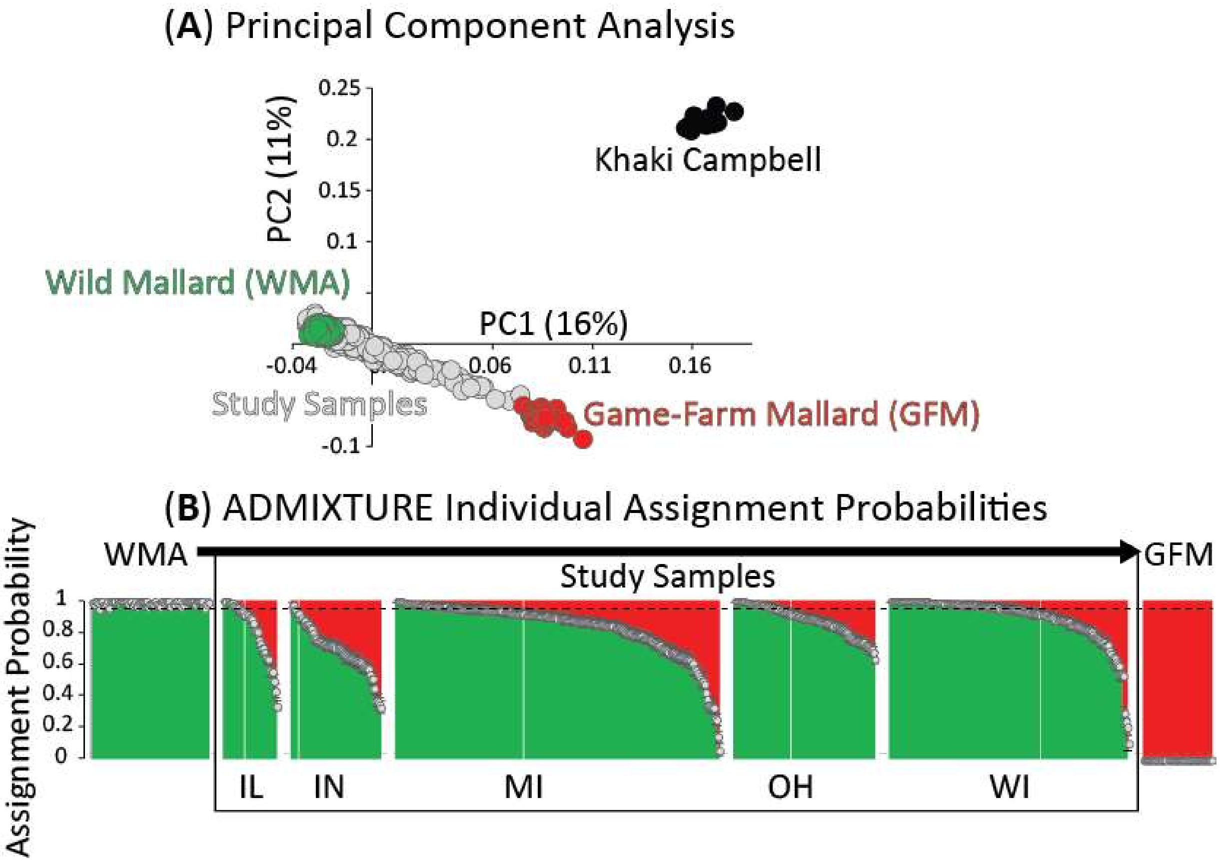

Figure 2.3. Principal component plot (A) of the first 2 principal components explaining variation in nuclear ddRAD sequencing results for reference wild (WMA; green circles), domestic game-farm mallard (GFM; red circles), and Khaki Campbell (black circles) samples and genetic samples collected from female mallards marked with GPS-GSM transmitters in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023 (Study Samples; grey circles). ADMIXTURE assignment probabilities (B) for individual Great Lakes mallard study samples by capture state, and wild and game-farm mallard reference samples.

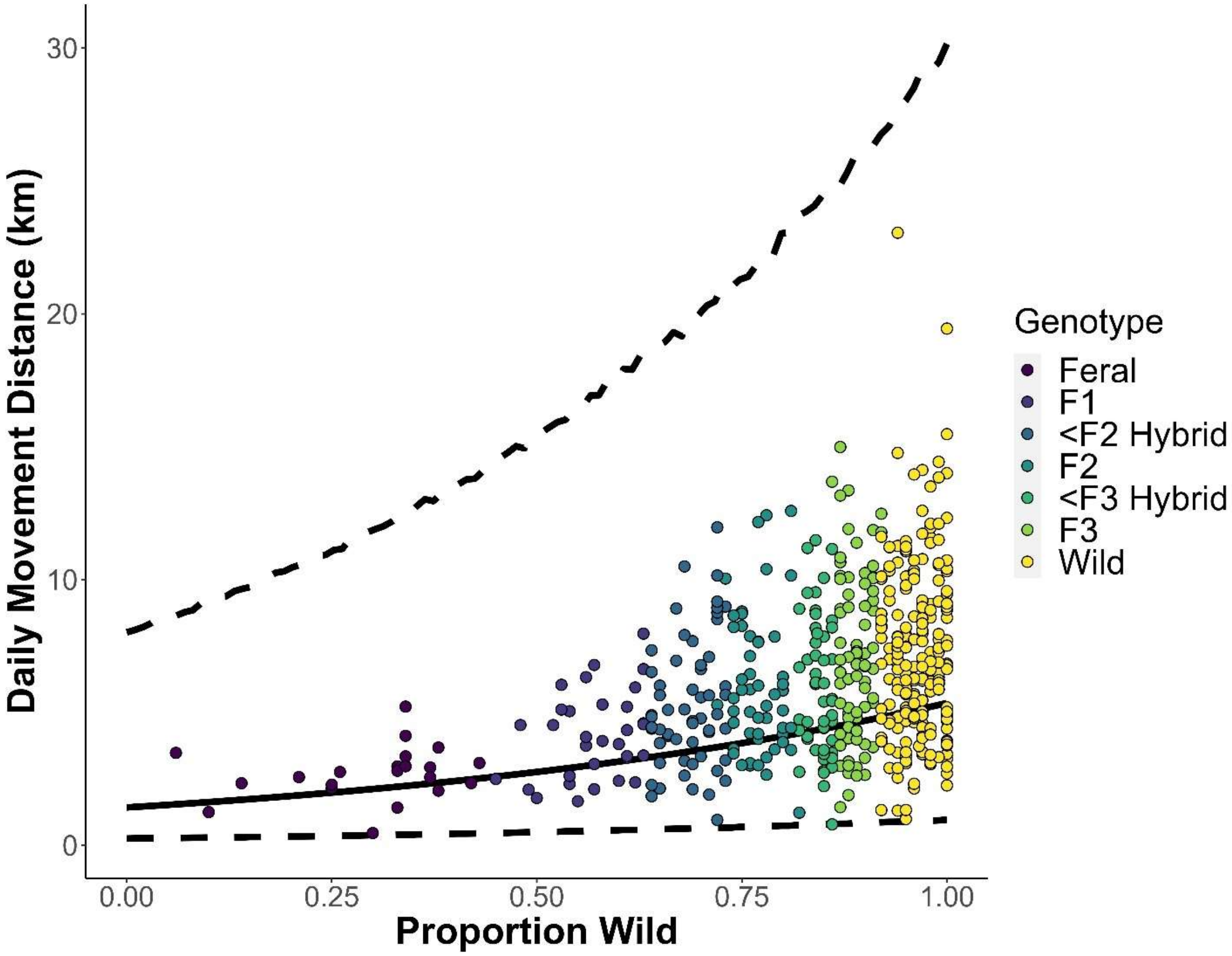

Figure 2.4. Predicted average daily movement distance (solid line) and 95% confidence intervals (dashed lines), and average individual daily movement distance (points) for female mallards marked with GPS-GSM transmitters in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023. Point color corresponds to estimated ancestry assignment where feral, first generation (F1), <F2, F2, <F3, F3, and wild corresponded to 0 to <0.43, 0.43 to <0.63, 0.63 to <0.72, 0.72 to <0.82, 0.82 to <0.86, 0.86 to <0.92, and 0.92 to 1 proportion wild genome, respectively.

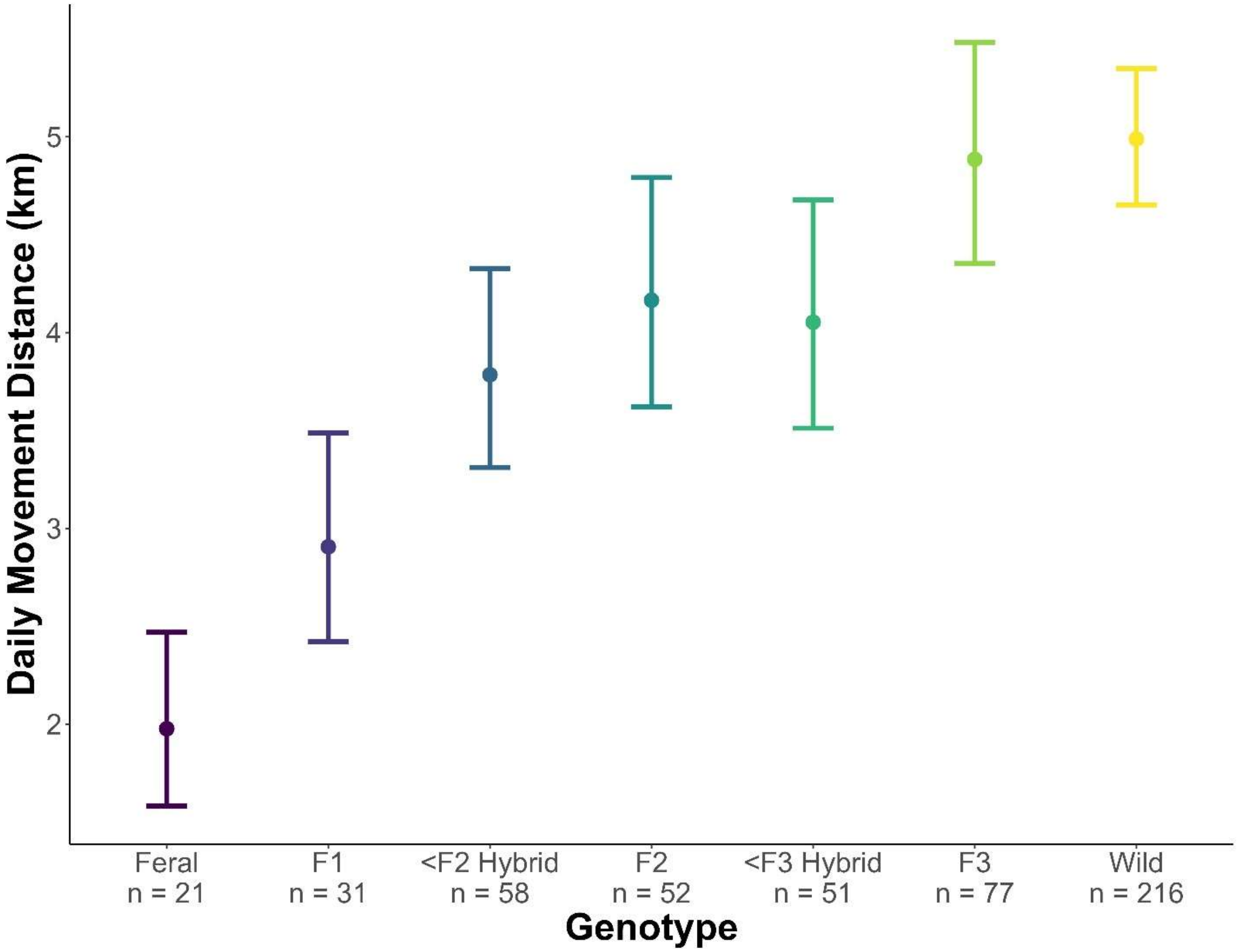

Figure 2.5. Predicted mean daily movement distance (points) and 95% confidence intervals (error bars) in relation to mallard ancestry assignment for mallards marked with GPS-GSM transmitters in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023. Color corresponds to estimated ancestry assignment where feral, first generation (F1), <F2, F2, <F3, F3, and wild corresponded to 0 to <0.43, 0.43 to <0.63, 0.63 to <0.72, 0.72 to <0.82, 0.82 to <0.86, 0.86 to <0.92, and 0.92 to 1 proportion wild genome, respectively.

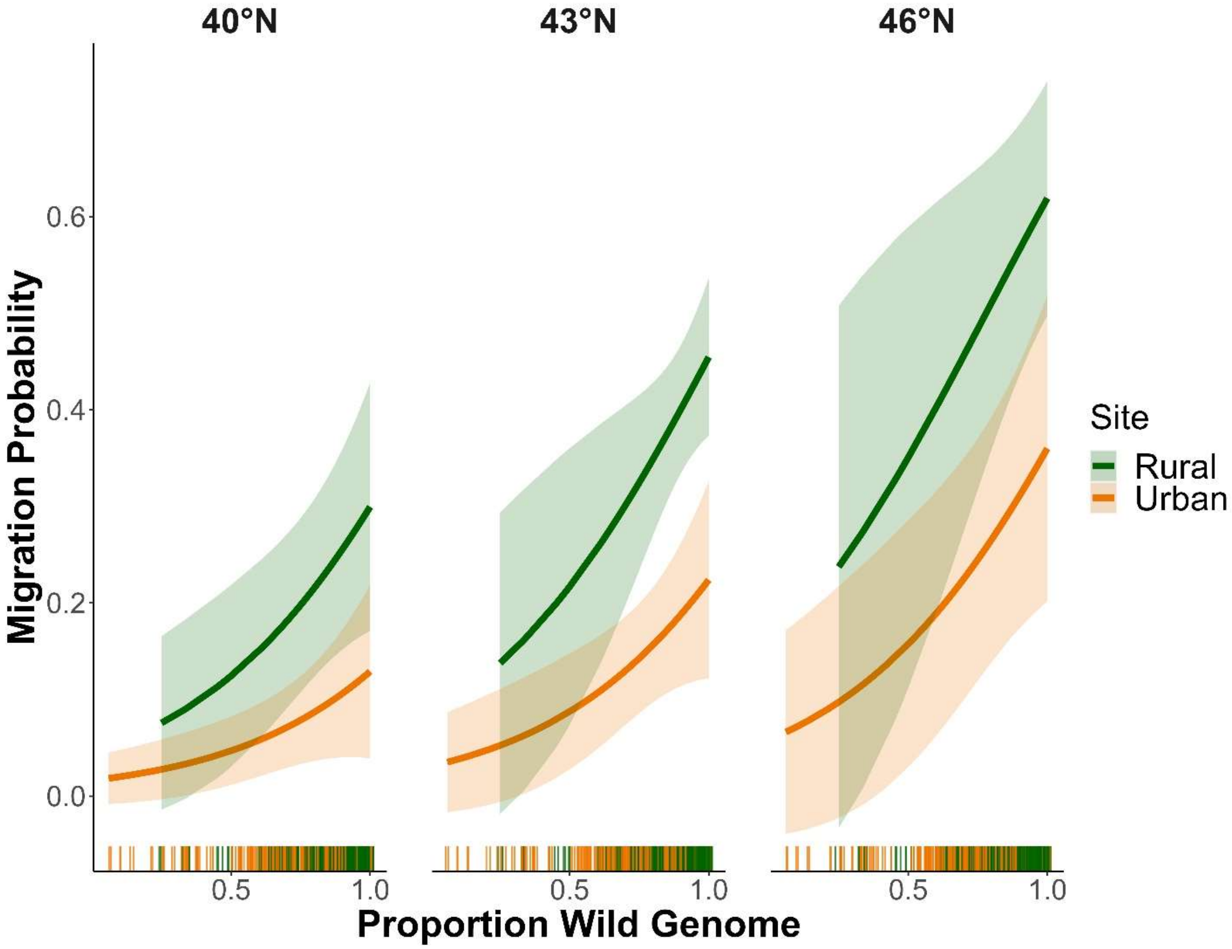

Figure 2.6. Predicted autumn (16 August – 29 February) migration probability as a function of capture latitude (panels), capture site land cover (urban or rural), and proportion wild genome for female mallards marked with GPS-GSM transmitters in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023. Vertical lines on x-axis (rug) denote proportion wild genome and capture site types of individual GPS-marked female mallards.

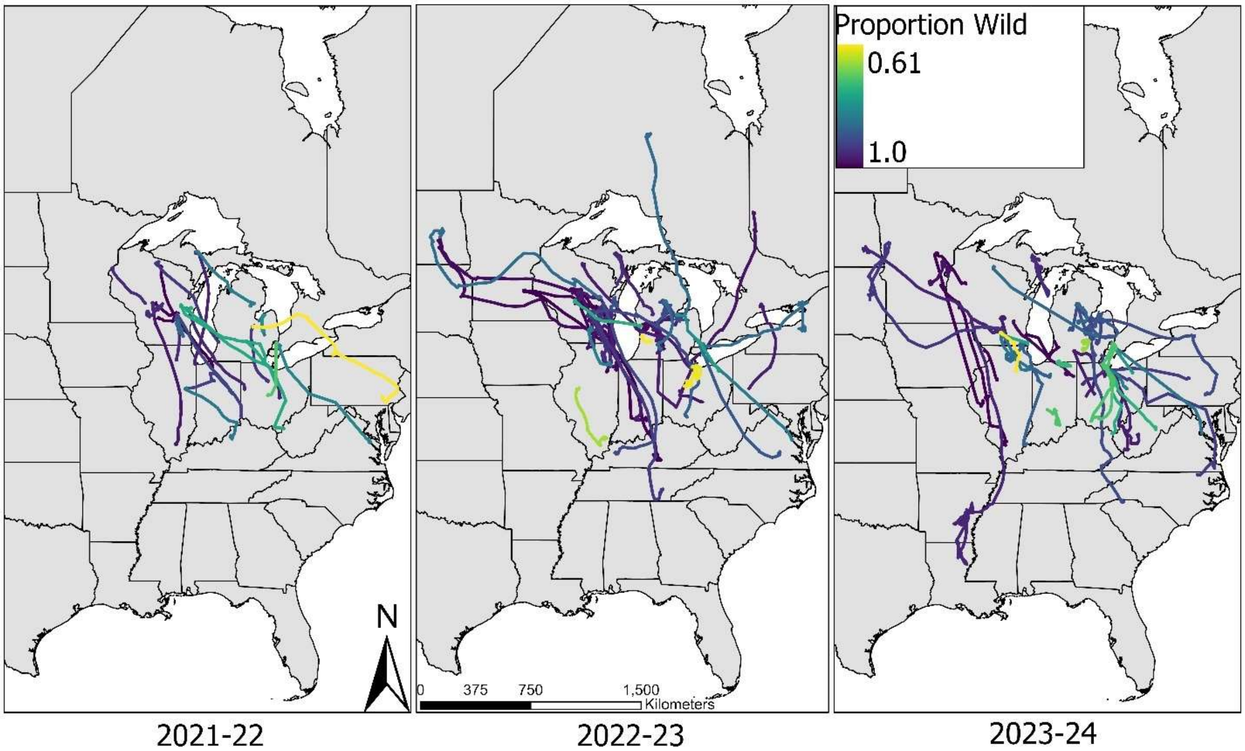

Figure 2.7. Autumn (16 August – 29 February) migration paths of female mallards marked with GPS-GSM transmitters in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023 which moved ≥30 km. Line color indicates the proportion of wild ancestry of the individual.

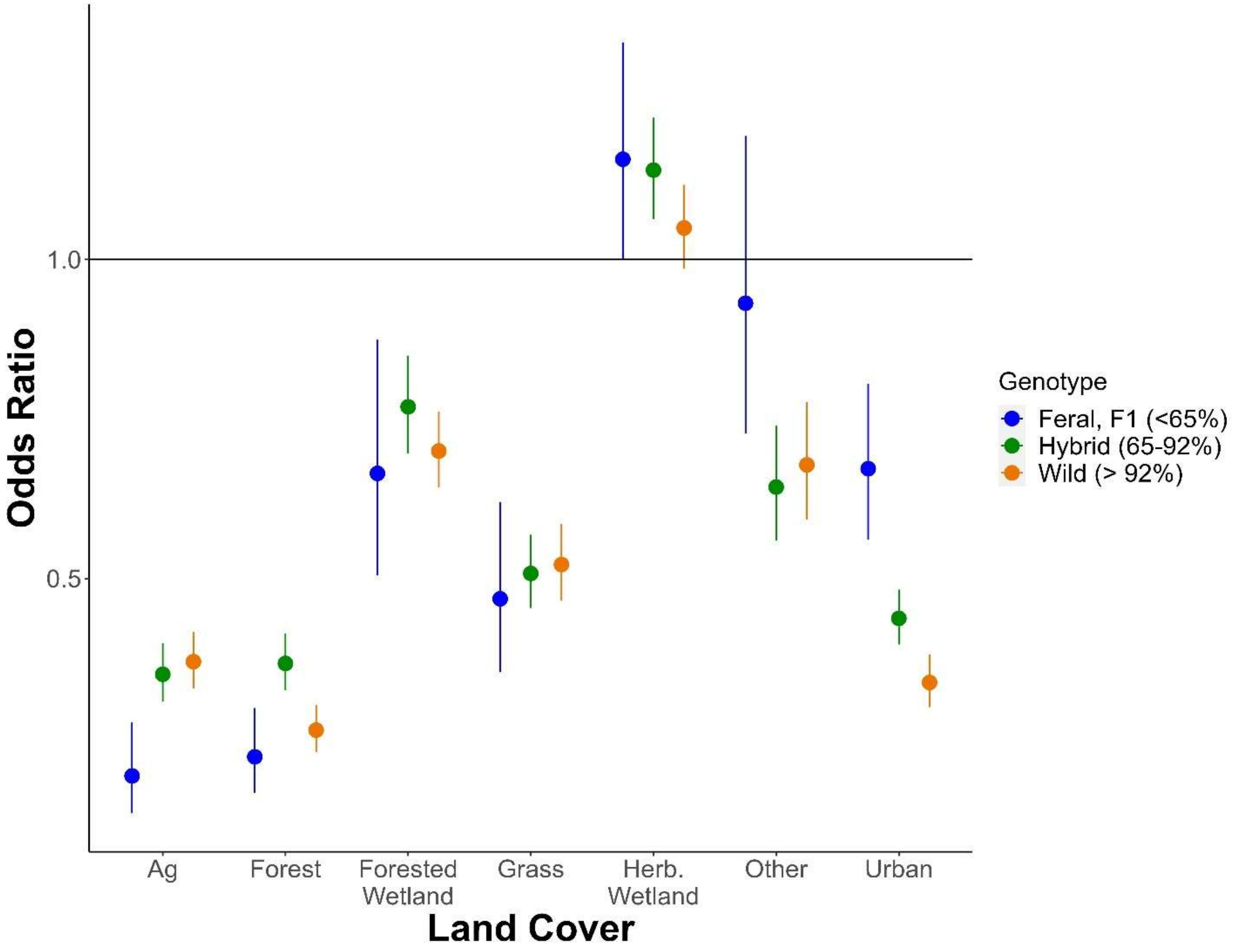

Figure 2.8. Estimated odds ratios representing relative selection strength (probability of selecting the given land cover type divided by the probability of selecting open water) and 95% confidence intervals (CI) for female mallards marked with GPS-GSM transmitters in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023. Open water was the reference category, designated by the solid horizontal line. An odds ratio less <1 with CIs excluding 1 indicate that land cover type was less selected than open water, CIs overlapping 1 indicate that land cover type was selected similarly to open water, and estimates >1 with CIs excluding 1 indicate the land cover type was more selected than open water. Genotype categories correspond to the percentage wild genome.

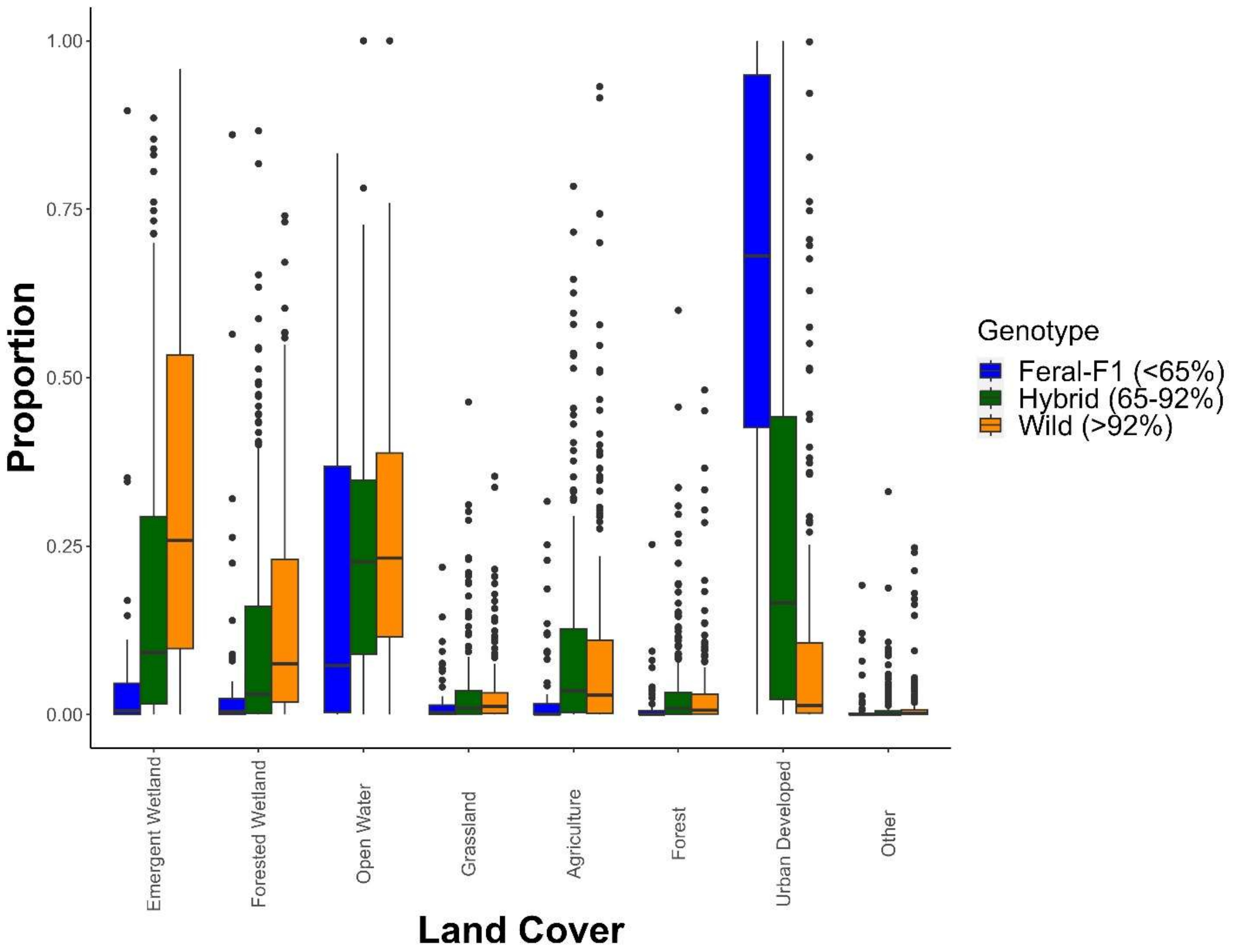

Figure 2.9. Boxplots of the proportion of GPS locations in each land cover type collected from 16 August – 29 February, 2021–2024 from female mallards marked with GPS-GSM transmitters in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023. Land cover types include the following categories from the 2021 National Land Cover Database and the Land Cover of Canada database: emergent herbaceous wetlands, forested wetlands, open water, developed (low, medium, and high intensity developed and developed open space), grassland (grassland and pasture), forest (deciduous, evergreen, needleleaf, and mixed forest), agriculture, and other (barren, scrub shrub, and shrubland). Medians are shown by the bold horizonal line, boxes denote the 25th and 75th percentiles, whiskers are 1.5 times the interquartile range, and points denote individual values more extreme than the whiskers.

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CHAPTER 3: GREAT LAKES MALLARD SURVIVAL

ABSTRACT

Long-term, large-scale releases of game-farm mallards (*Anas platyrhynchos domesticus*) in the eastern United States has resulted in introgressive hybridization with wild mallards (*A. platyrhynchos*) that raises questions surrounding ecological consequences. Given a decline in Great Lakes (Michigan, Minnesota, and Wisconsin, USA) mallard abundance from 2000–2023, determining the effects of hybridization on mallard survival is of interest to waterfowl and wetland managers. Our objective was to identify the influence of genotype, age, and urban land cover use on female survival in Great Lakes mallards using GPS-GSM transmitter data and known fate survival models. We captured, obtained a genetic sample from, and marked 592 female mallards with GPS-GSM transmitters in Michigan, Wisconsin, Ohio, Indiana, and Illinois, USA from 2021–2023. Genetic ancestry of GPS-marked mallards was assessed using thousands of nuclear loci, and we examined the effects of individual and temporal covariates on mallard survival using known-fate models. Genetic analyses indicated 44% of GPS-marked birds were wild mallards and 56% were wild x domestic game-farm mallard hybrids. Female mallard survival was positively related to the proportion of GPS locations in urban land cover and adult females had greater survival than did juvenile females. Modeling results did not support differences in survival related to individual genotypes, although early generational hybrid mallards were primarily associated with urban areas, suggesting developed landscapes enabled hybrid mallards to survive at similar rates as those of wild mallards. Use of urban land cover is likely one source of individual heterogeneity in female mallard survival, and managers should consider further examining effects of urban landscapes on the survival and geographic spread of wild x domestic game-farm mallard hybrids in the Great Lakes region.

INTRODUCTION

Individual heterogeneity, or any observed or unobserved variation in a trait among individuals (Hamel et al. 2018b), represents both a challenge and opportunity in demographic parameter estimation and population analysis. Individual heterogeneity may result from measured individual traits such as body size (Black et al. 2007), nutrient reserves (Fowler et al. 2020a, 2020b), or genetics (Niewoonder et al. 1998). However, failure to account for unmeasured individual heterogeneity may lead to biased demographic parameter estimates (Otis et al. 1978, Rexstad and Anderson 1992) or spurious conclusions about the effects of environmental conditions or management actions on a population (Arnold 2021). While accounting for unmeasured individual heterogeneity can reduce bias, greater understanding of selective pressures and individual responses is possible through modeling sources of individual heterogeneity (Gimenez et al. 2018, Hamel et al. 2018a). Conservation of gamebird populations often requires estimating effects of environmental and anthropogenic factors on survival probability (Brasher et al. 2006, Sedinger et al. 2007, Johnson et al. 2015). In many waterfowl species, changes in population growth rate are most sensitive to variation in adult female survival (Koons et al. 2014). As such, there is opportunity to improve models, such as midcontinent mallard (*Anas platyrhynchos*) Adaptive Harvest Management (AHM) survival models, through incorporation of individual heterogeneity (Koons et al. 2022, U. S. Fish and Wildlife Service 2023a).

An emerging question is whether long-term, large-scale releases of domestic game-farm mallards in eastern North America and subsequent hybridization with wild mallards has contributed to population declines in the eastern population and Great Lakes component of the midcontinent mallard population (U. S. Fish and Wildlife Service 2023b). Game-farm mallard releases since the 1920s were estimated between >200,000 (U. S. Fish and Wildlife Service 2013) and >500,000 (Huesmann 1974) annually, although the true magnitude of releases is unknown. Historically, game-farm mallards were released primarily in the Atlantic Flyway (Huesmann 1974, Hepp et al. 1988) and recent sampling revealed mallards in the U. S. portion of the Atlantic Flyway are a hybrid swarm comprised of approximately 90% wild x domestic game-farm mallard hybrids (Lavretsky et al. 2020).

Gene flow from domestic game-farm to wild mallards could have maladaptive consequences if domestic traits confer morphological or behavioral characteristics that reduce survival or reproductive capacity for admixed individuals. Several studies have estimated survival of captive-reared mallards after release and found survival probabilities from autumn to spring to be ~0.25 (Osborne et al. 2010), 3-week survival post release to be 0–0.75 (Schladweiler and Tester 1972), and annual survival to be 0.1–0.25 (Söderquist et al. 2013). Captive-reared mallards released for hunting in Maryland were estimated to have survival probabilities 0.23–0.54 from release to post-hunting (seven weeks), but were observed to have higher survival where supplemental feeding occurred, suggesting energetic or nutritional deficiency contributed to reduced survival (Smith 1999). However, studies estimating survival for wild x game-farm mallard hybrids are lacking. Given the importance of female survival to population dynamics and evidence suggesting genotype may contribute to individual heterogeneity in survival, quantifying the impact of mallard genotype on survival is warranted.

Our objective was to identify the influence of mallard genotype, age, and urban land cover use on female survival in Great Lakes mallards using GPS-GSM (global positioning system-global system for mobile communications) transmitter data and known fate survival models. Understanding the demographic consequences of hybridization can inform whether genotype is a source of individual heterogeneity in survival. We predicted that wild x game-farm mallard hybrids would have lower survival than wild mallards, consistent with studies suggesting lower survival for domestic or hand-reared mallards. Specifically, we expected that survival would increase with wild mallard ancestry among individuals. Additionally, we expected survival to be positively related to use of urban developed land cover for hybrid and wild mallards due to lower rates of predation and harvest within urban areas.

STUDY AREA

We captured and marked female mallards with GPS-GSM transmitters in Bird Conservation Regions (BCRs; Bird Studies Canada and NABCI 2014) 12 (Boreal Hardwood Transition), 22 (Eastern Tallgrass Prairie), and 23 (Prairie Hardwood Transition) in the Great Lakes states of Michigan, Wisconsin, Ohio, Indiana, and Illinois, USA (hereafter Great Lakes region; Figure 3.1). Bird Conservation Regions are landscape planning units comprised of similar ecosystems and bird communities and are relevant for landscape conservation planning by the Upper Mississippi/Great Lakes (UMGL) Joint Venture (JV; Soulliere et al. 2017). The Great Lakes region is dominated largely by forests and forested wetlands in the north, transitioning to heavily human-modified in the southern portion where agriculture is most prevalent (Yang et al. 2018). Regional temperatures and precipitation are influenced by the Great Lakes and generally consist of cold, snowy winters and hot, humid summers (Scott and Huff 1996). Moderating lake effects result in wetland conditions that are generally more stable and less seasonally dynamic than in the Prairie Pothole Region (Euliss et al. 2004, Simpson et al. 2005). Mallards were the most abundant breeding duck in the Great Lakes region (U. S. Fish and Wildlife Service 2023b) and densities were estimated to be greatest in BCR 23 during the breeding period (Soulliere et al. 2017). We monitored movements and land cover use of GPS-marked mallards within North

America, which occurred in an area bounded by approximately 51.5ºN and 32ºN, and 75.2ºW, and 99.8ºW.

METHODS

Mallard Capture and Marking

We captured ducks using baited traps, rocket- and spring-propelled nets, handheld nets, and via night lighting from 4 March –4 October, 2021–2023. We aged ducks as AHY (after hatch year; adult), HY (hatch year; juvenile capable of flight) or L (local; juvenile incapable of flight) and sexed birds via plumage characteristics (Carney 1992). We banded mallards with a size 7 United States Geological Survey (USGS) aluminum leg band. We attached 20 g Ornitela GPS-GSM transmitters (OrniTrack-E20 4GCT C48; Ornitela, Vilnius, Lithuania) dorsally to female mallards via 4.5 mm wide elastic straps. Transmitters were attached with two separate elastic loops in 2021 and via an X-shaped design consisting of a single piece of elastic in 2022 and 2023. Transmitters were distributed in approximate proportion to estimated breeding period mallard abundance by bird conservation region (Soulliere et al. 2017). We classified capture and transmitter deployment locations as urban if the proportion of developed land cover within a 7 km (mean of maximum daily net squared displacement) radius of the site was >0.5, or rural if ≤0.5. We weighed each hen mallard to the nearest 10 g and attached transmitters only to individuals >700 g so transmitters comprised <3% of body mass (mean = 1.9%). We measured total head, bill, total tarsus, and wing chord (Dzubin and Cooch 1992) of GPS-marked females. We drew approximately 0.1 ml of blood from the tarsal vein for genetic analysis. Ducks were released immediately after processing at capture locations. Transmitters were programmed to record a location every 30 minutes, 2 hours, or 4 hours when battery charge was >50%, <50% and >25%, or <25%, respectively, and uploaded data once every 24 hours when connected to cell networks. Approval to capture, band, and attach transmitters was provided by Michigan State University institutional animal care and use committee (IACUC) permit PROTO202100046 and USGS Bird Banding Laboratory permit 03110.

DNA Extraction, Sequencing, and Genetic Ancestry Analyses

We extracted genomic DNA from blood samples using a DNeasy Blood & Tissue kit following the manufacturer's protocols (Qiagen, Valencia, CA, USA). DNA quality was visually assessed on a 1% agarose gel to ensure high molecular weight bands. We amplified mitochondrial DNA (mtDNA) via polymerase chain reaction (PCR) and Sanger sequenced the control region across samples using primers L78 and H774 (Sorenson and Fleischer 1996, Johnson and Sorenson 1999), and following protocols outlined in Lavretsky et al. (2014b). Final products were sequenced on an ABI 3730 (Applied Biosystems, Life Technologies, Carlsbad, California, USA) machine at the University of Texas at El Paso Border Biomedical Research Centers (BBRC) Genomic Analysis Core Facility. Sequences were then aligned and edited using SEQUENCHER v. 4.8 (Gene Codes Corporation, Ann Arbor, MI, USA). We note that mtDNA control region sequences for reference wild and domestic mallards from previous studies were included in the analyses (Lavretsky et al. 2014a, b, 2019a, Lavretsky 2020a). Reference samples comprised known wild, domestic game-farm, and domestic Khaki Campbell mallards. We constructed a median-joining haplotype network to visualize mtDNA structure as calculated in the program POPART (Leigh and Bryant 2015). Mallards are characterized by the old world (OW) A and new world (NW) B mitochondrial (mtDNA) haplogroups, which distinguish individuals of Eurasian or North American descent, respectively (Ankney et al. 1986, Avise et al. 1990, Lavretsky et al. 2014a). Importantly, being of Eurasian descent, all domestically-derived mallards carry OW A haplotypes, and thus, are a distinguishing marker when assessing whether game-farm mallard introgression occurred within a wild mallard lineage in North America (Lavretsky 2020b, Lavretsky et al. 2020).

For nuclear DNA, we followed ddRAD-seq (double-digest restriction site associated DNA sequencing) library protocols outlined in DaCosta and Sorenson (2014) and Lavretsky et al. (2015). In short, genomic DNA was enzymatically fragmented using *SbfI* and *EcoRI* restriction enzymes, and Illumina TruSeq compatible barcodes ligated for future de-multiplexing. The barcode-ligated fragments were then size selected using optimized double-sided bead selection protocols (Hernández et al. 2021). Libraries were then quantified with a Qubit 3 Flourometer (Invitrogen, Carlsbad, CA, USA) and pooled in equimolar amounts and sent out to Novogenetics LTD (Sacramento, California, USA) for 150 base-pair, single-end chemistry sequencing on an Illumina HiSeq X. Raw Illumina reads were de-multiplexed using the *ddRADparser.py* script of the BU ddRAD-seq pipeline (DaCosta and Sorenson 2014) based on perfect barcode/index matches. Comparable sequences from previously published wild and domestic mallards were included and served as respective references (Lavretsky et al. 2014a, b, 2019b, 2020). For each sample, we first trimmed or discarded sequences of poor quality using TRIMMOMATIC (Bolger et al. 2014), and then remaining quality reads aligned to a chromosomal-level reference wild mallard genome (Lavretsky et al. in press) using the BURROWS WHEELER ALIGNER v. 07.15 (Li and Durbin 2011). Samples were then sorted and indexed in SAMTOOLS v. 1.7 (Bolger et al. 2014) and combined using the *mpileup* function with the following parameters "-c –A -Q 30 -q 30." All steps through *mpileup* were automated using a custom Python script (Lavretsky et al. 2020). Next, we used VCFTOOLS v. 0.1.15 (Danecek et al. 2011) to filter variant call format (VCF) files for any base-pair missing >10% of samples that also included a minimum base-pair depth of 5X (i.e., 10X per genotype) and quality per base PHRED scores of ≥30.

All nuclear population structure was based on independent bi-allelic ddRAD-seq autosomal single nucleotide polymorphisms (SNPs), and without using *a priori* assignment of individuals to populations or species. The final dataset was obtained by using VCFTOOLS (Danecek et al. 2011) to first extract bi-allelic SNPs, and then PLINK v.1.9 (Purcell et al. 2007) to filter for singletons (minimum allele frequency: 0.0014), any SNP missing ≥10% of data across samples, as well as any SNPs found to be in linkage disequilibrium (LD). We randomly excluded all but one SNP for any positions found to be in significant LD ($r^2 > 0.5$). Population structure was first visualized using a principal components analysis (PCA) as implemented in PLINK v.1.9 (Purcell et al. 2007). Next, the program ADMIXTURE 1.3 (Alexander et al. 2013) was used to attain per sample maximum likelihood estimates of population assignments for each individual, with datasets formatted for the ADMIXTURE analyses using PLINK v.1.9 (Purcell et al. 2007), and following steps outlined in Alexander and Lange (2011). ADMIXTURE analyses were run for population models of *K* of 2 and 3 with a 10-fold cross validation, incorporating a quasi-Newton algorithm to accelerate convergence (Zhou et al. 2011). Each analysis used a block relaxation algorithm for point estimation and terminated once the change in the log-likelihood of the point estimations increased by <0.0001. Finally, standard deviations around each point estimate were calculated based on 1,000 bootstrap replicates. Ancestry assignments and their standard deviation were used to recategorize samples as feral game-farm, wild mallard, and to filial classes of hybrids (Schummer et al. 2023) under expected genotypes in generational backcrosses and uncertainty on assignment probabilities. Thus, we classified individuals with ≥ 0.92 wild assignment probability as wild and all others as hybrids. Assignment probabilities are also interpretable as an estimate of the proportion of an individual's genes that are of wild ancestry, and thus we also considered proportion wild genome as a continuous covariate in survival analysis. To quantify differences in the number of hybrid mallards across banding site types, we used a chi-square goodness of fit test to assess if hybrid mallards were more likely to be encountered at rural or urban banding locations.

Survival Data and Analyses

Data collected by transmitters were forwarded to Movebank (Wikelski and Kays 2019) for storage. We performed data preparation and analyses in Program R (R Core Team 2023) and used the move package (Kranstauber et al. 2018) to retrieve GPS data from Movebank. We censored GPS locations where a satellite fix was not obtained or only one satellite was successfully contacted, and/or locations with a horizontal dilution of precision (HDOP) <5 (D'Eon and Delparte 2005). Individual ducks with <7 days of monitoring data were censored from analyses (Brasher et al. 2006).

Transmitter data were monitored daily to identify potential mortalities. We determined that a mortality likely occurred when GPS location and accelerometer (ACC) data indicated lack of transmitter movement (~24 hours), and when temperature data recorded by transmitters declined below the minimum temperature observed for live ducks (~10ºC). When suspected mortalities were identified, we navigated to the average coordinates of locations collected after movement ceased, or to the last known GPS location, when feasible. We recovered located transmitters and collected bird remains for necropsy. Necropsies were performed by Michigan Department of Natural Resources (DNR) Wildlife Disease Laboratory staff at the Diagnostic Center for Population and Animal Health in East Lansing, MI. Mortality cause was classified as predation, hunter harvest, vehicle strike, powerline strike, window strike, interspecific (male mallard) aggression, starvation/exposure, poaching, or unknown. When transmitters or bird remains could not be located, we assumed a mortality occurred and assigned unknown cause when ACC data characteristics were not consistent with two cases of confirmed transmitter loss. In the cases of confirmed transmitter loss, examination of the ACC data showed the transmitter becoming loose and increasing physical movement while the GPS data indicated typical bird movements, which contrasted with data observed from known mortalities. Location and mortality dates were converted to week number and fates (i.e., alive or dead) were assumed known when transmitters provided at least one GPS location, or when a mortality was recorded within each weekly interval. When a transmitter did not provide GPS data and no mortality was detected, individual fate was unknown. We converted weekly known alive, known dead, and unknown fate data into individual encounter histories.

We estimated weekly survival probability (S; probability an individual alive at the start of week i survives to the start of week i+1) using known fate models in program MARK (White and Burnham 1999) and using package RMark (Laake and Rexstad 2018). Models included individual covariates of proportion wild genotype, age at capture (adult [AHY] or juvenile [HY and L]), attachment type (2 loop or X harness), and proportion of GPS locations in urban land cover identified using the 2021 National Land Cover Database (NLCD; Dewitz 2023) and 2020 Land Cover of Canada (Latifovic 2022) database. We used the raster package (Hijmans 2020) to extract the land cover type at each GPS location and calculated the proportion of urban (low, medium, or high intensity developed or developed open space) locations used for each individual. We included time (week number) as a temporal covariate. There was little variation in the total proportion and distribution of mortalities throughout each year (2021–2024), thus we did not include year as a covariate. We constructed 28 candidate models *a priori* that addressed our primary research questions of the effect of individual mallard genotype and urban land cover use on survival. We preformed model selection using Akaike's Information Criterion (Burnham and Anderson 2002) adjusted for small sample size (AIC_c). For top models, we calculated annual survival probability and corresponding standard errors using the Delta method via the msm package (Jackson 2011). We report survival estimates and 95% confidence intervals. We also plotted the Kaplan-Meier survival curve (Kaplan and Meier 1958) and 95% confidence intervals for the combined (2021–2024) data by age at capture to assess how survival varied throughout the annual cycle and to estimate annual survival for adult and juvenile females. Finally, we calculated the annual direct recovery rate for GPS-marked mallards harvested by hunters to assess whether birds with transmitters had higher recovery rates than reported for banded mallards. The direct recovery rate is the proportion of birds marked in the pre-season (1 July – 30 September) that are shot, retrieved, and reported by hunters in the hunting season immediately following banding.

In known fate models, the fully parameterized model is biologically sensible and fits the data perfectly, precluding use of a goodness of fit test based on comparison of model deviance. As no goodness of fit test exists for known fate models (White and Burnham 1999), we assessed the influence of overdispersion in the data on model selection by adjusting the variance inflation factor estimate ($\hat{c}$). We increased $\hat{c}$ from 1 (no overdispersion) to 3 (high overdispersion) by increments of 0.25 (Brasher et al. 2006) and determined if model ranking by quasi-Akaike's Information Criterion (QAIC_c) and subsequent inference changed.

RESULTS

We attached GPS transmitters to 592 hen mallards in 2021 (n = 194), 2022 (n = 241), and 2023 (n = 157). Mallards were captured using baited traps (n = 331), rocket- and spring-propelled nets (n = 166), hand-held nets (n = 55), and via night-lighting (n = 40). Transmitters were deployed across all Great Lakes states, BCRs, and ages (Table 3.1). Individual mallards were monitored for an average of 189 days (range: 2–1,037 days) during the study. We excluded 24 individual mallards from analyses for which there were <7 days of GPS monitoring data available following release.

Genetic Ancestry

A total of 590 (of 592) samples provided usable genomic material. First, 592 base-pairs of overlapping mtDNA control region sequence data were attained across all samples, including 580 (of 590) samples specific to this study. Of the 580 sequences, we recovered 63.8% (n = 370) and 36.2% (n = 210) carrying Old World A versus New World B haplogroups, respectively. The percentage of individuals with New World B haplotypes within each state ranged from 6.5% in Indiana to 55.4% in Wisconsin. Interestingly, 46.2% of samples determined to be wild mallard (n = 251) via nuclear DNA carried Old World A mtDNA haplotypes, suggesting a substantial portion of sampled wild mallards had maternal input from domestic mallards in their ancestral past (Lavretsky et al. 2023).

Next, a total of 33,216 (of 34,230) independent bi-allelic ddRAD-seq SNPs were retained for nuclear population structure analyses. Plotting the first two principal components (Figure 3.2) explained a total of 26.8% of the variance, and clearly separated reference wild mallards, game-farm mallards, and Khaki Campbells, with samples from this study distributed between wild reference mallard set and game-farm mallards (Figure 3.2). Given no evident clustering with Khaki Campbells, we attained assignment probabilities by analyzing a dataset excluding them. Plotting ADMIXTURE assignment probabilities under an assumption of two population clusters distinguished between wild and game-farm mallards, while samples from this study possessed assignment probabilities to either the wild mallard genetic cluster only or had interspecific assignments to both clusters (Figure 3.2). In total, we identified 44% of GPS-marked mallards as genetically wild, whereas 56% were classified as wild x game-farm mallard hybrids. The proportion of wild mallards captured in each state ranged from 8.1% in Indiana to 63.9% in Wisconsin. Generally, fewer hybrids were captured in the northern and western portions of the study area. Of mallards captured at rural sites (n = 353), 58.4% were wild and 41.6% were hybrids. Mallards captured at urban sites (n = 237) were comprised of 21.9% wild and 78.1% hybrid individuals. Significantly more hybrids were captured at urban than rural sites ($\chi_1^2 = 74.9; \mathrm{p} < 0.0001$).

Survival and mortality

Cause of mortality could not be confirmed for 47% of all mortalities (n = 138) due to inconclusive evidence or inability to locate GPS transmitters. Among the 158 individuals where cause of mortality could be determined, hunter harvest accounted for 56% and predation accounted for 39% of mortalities. However, collisions with vehicles or anthropogenic structures, poaching, aggressive behavior by male mallards, and starvation combined for 5% of known-cause mortalities (Table 3.2). Annual direct recovery rates ranged from 0.11 to 0.20 for adult (mean = 0.14) and from 0.13 to 0.30 for juvenile (mean = 0.22) female GPS-marked mallards. Direct recovery rates generally increased from 2021–2023 for adults and juveniles (Figure 3.3).

Manipulation of the variance inflation factor estimate ($\hat{c}$) revealed that model ranking was sensitive to changes at low values of $\hat{c}$. Under no ($\hat{c} = 1$) and slight ($\hat{c} = 1.25$) overdispersion, more complex models where survival was a function of additive effects of age, proportion urban land use, time (week), and proportion wild genome were favored. Predictions from the top five models when ($\hat{c}$ was assumed to be 1) were plotted against the Kaplan-Meier survival curve fit to the observed data (Figure A.1). Model predictions of juvenile female survival were generally lower than annual survival from the Kaplan-Meier curve fit to the observed data (Figure A.1). Under $\hat{c} \geq 1.5$, the top two models both included additive effects of age and proportion urban land use, with the second-ranked model also including the additive effect of proportion wild genome (Table A.1). The second-ranked model was ≈2 $\mathrm{QAIC_c}$ units from the top model, and both the 95% (-1.22, 0.69) and 85% (-0.98, 0.44) CIs (Arnold 2010) on the additional parameter (proportion wild genome) estimate overlapped zero, suggesting proportion wild genome was an uninformative parameter. Thus, we report model ranking by $\mathrm{QAIC_c}$ assuming $\hat{c} = 1.5$ (Table 3.3).

The top model indicated adult female survival was greater than juvenile female survival ($\beta_{\mathrm{Age}} = -0.48, 95\%\ \mathrm{CI}: [-0.71, -0.25]$) and survival for both age classes increased ($\beta_{\mathrm{p\_urban}} = 1.42\ [0.99, 1.84]$) with an increasing proportion of locations in urban land cover (Figure 3.4). Support for a survival difference in relation to the proportion of wild ancestry was lacking, however, on average 71% of locations collected from mallards with ≤50% wild ancestry were in urban land cover. The Kaplan-Meier survival curves (Figure 3.5) estimated adult female survival declined from 0.94 (0.91, 0.97) to 0.66 (0.61, 0.72) and juvenile female survival declined from 0.87 (0.82, 0.91) to 0.43 (0.35, 0.50) from the last week in September through the last week in January (corresponding to open duck seasons in the Mississippi Flyway). From the first week of April to the first week of June, adult female survival declined from 0.63 (0.57, 0.69) to 0.50 (0.44, 0.56), while juvenile female survival declined from 0.40 (0.33, 0.47) to 0.34 (0.27, 0.42). Annual (53 week) survival estimates were 0.46 (0.40, 0.51) and 0.31 (0.24, 0.38) for adult and juvenile female mallards, respectively (Figure 3.5).

DISCUSSION

Genetic Ancestry

Our molecular data corroborates and further demonstrates the extent of gene flow in the Great Lakes region resulting from large-scale releases of game-farm mallards (Huesmann 1974, U. S. Fish and Wildlife Service 2013, Lavretsky et al. 2023). The proportion of admixed individuals in our sample was intermediate between the U. S. portion of the Atlantic Flyway where previous research found about 90% of mallards were wild x game-farm hybrids (Lavretsky et al. 2019a) and the Central Flyway where sampled mallards were almost entirely comprised of wild individuals (Lavretsky et al. 2023). While variation in the distribution of hybrid mallards within the Great Lakes region generally followed this pattern with few hybrids captured at western and northern sites, there was also variation at finer spatial scales.

Indiana was an outlier among the states in our sample with hybrids comprising >85% of mallards sampled at both urban and rural locations. Hybrids were more prevalent than wild mallards at urban sites across other Great Lakes states, and only five hybrids (1.5%) with <50% wild mallard ancestry were encountered at rural banding locations. Hybrid mallards could be more susceptible to capture than wild mallards when using bait, such as shelled corn used in this study (Champagnon et al. 2010). In addition to being exposed to supplemental feed (Smith 1999, Söderquist et al. 2024), captive-bred mallards may settle in urban areas post release (Osborne et al. 2010). Although the behavioral difference among captive-bred or hybrid individuals may bias their capture over wild mallards, any increases in hybrids that have such behavior would still reflect prevalence across locations. Therefore, a higher proportion of hybrid mallards in captures at urban sites likely reflects greater prevalence of hybrid mallards in developed areas.

Survival and mortality

Whereas the leading source of known-cause mortalities was hunter harvest, the source of mortality for nearly half (47%) of all detected (via GPS and accelerometer data or field observation) mortalities could not be determined. This was primarily due to recovery of scavenged remains where cause of death could not be verified, or inability to locate transmitters sending a mortality signal. As transmitter technology improves and hardware becomes smaller and lighter, inclusion of both a GPS-GSM and very high frequency (VHF) transmitter in a single unit would improve recovery ability as VHF signals could be used to locate transmitters more easily after receiving a mortality signal. However, a transmitter containing both VHF and GPS capability was not an option for this study because of size and weight constraints for transmitters. Under the assumption that most unknown-cause mortalities were likely due to predation, the proportion of known-cause mortalities attributed to predation is likely an underestimate and would exceed harvest mortality. There were two cases of transmitter loss which were confirmed by resighting or recapturing banded individuals after the transmitter slipped off the bird and was recovered. The difference in data characteristics between transmitter loss and birds that were depredated, scavenged, or shot by hunters suggests that few mortalities assigned unknown cause were likely to be undetected transmitter losses, and thus were truly mortalities. Detection and reporting of GPS-marked hens harvested by hunters is likely high due to a trophy effect (Arnold et al. 2020), but the proportion of mortalities due to predation is likely biased low. The single confirmed instance of poaching occurred in an urban park where the marked bird could be easily observed, and this illegal take could have been related to the presence of a band and/or transmitter.

Direct recovery rates of GPS-marked hen mallards harvested by hunters in this study were greater than Brownie dead recovery (Brownie et al. 1978) probability estimates for adult (range: 0.03–0.08) and juvenile (range: 0.05–0.16) female mallards banded in Michigan and Wisconsin, 1991–2022 (Chapter 5). Additionally, GPS-marked female Great Lakes mallards had higher direct recovery rates than estimated for female mallards banded at western Lake Erie, USA (range: 0.05–0.07; Palumbo and Shirkey 2022), but direct recovery rates observed in this study were relatively similar to those for female mallards banded at Lake St. Clair, Ontario (range: 0.10–0.14; Palumbo and Shirkey 2022). Transmitters or other auxiliary markers (e.g., neck or tarsal bands) can increase visibility of marked birds and result in targeted harvest of marked individuals by hunters (LeTourneux et al. 2022, Sedinger et al. 2022), although targeting of birds with auxiliary markers may be more common in geese than in ducks. Alternatively, auxiliary markers could make birds more susceptible to harvest via other mechanisms, such as increased likelihood of decoying, without visual selection for marked individuals by hunters (Caswell et al. 2012). Harvest of GPS-marked mallards in this study is likely biased high relative to harvest of mallards marked with bands only, however we have little reason to suspect conscious targeting by hunters because transmitters were usually preened into the bird’s feathers, making them difficult to observe. Factors other than targeted hunter harvest may have increased direct recovery rates of GPS-marked mallards in this study relative to band-only mallards.

Model rankings were sensitive to the choice of variance inflation factor ($\hat{c}$) value, suggesting there was greater variability in the data than expected. However, the models with most support (model weight) and subsequent inference remained the same after $\hat{c}$ was adjusted to 1.5, suggesting only moderate lack of fit in the data. The main assumptions of known-fate models are that fate (i.e., alive or dead) of each individual is known at each time period (detection probability is assumed to be one), censoring of individuals is independent of fate, fates of individuals are independent of one another, survival probability is homogenous within a group, and individuals released in different occasions are accounted for using a staggered entry design (White and Burnham 1999). We expect that individuals marked during the same banding capture could have similar movements and be exposed to similar mortality sources, potentially resulting in partial dependency of fates. Whenever possible, we marked ≤5 hens with GPS transmitters at a single banding site in a single year. Further, 22% of mallards were marked during spring (1 March–30 June), and these individuals may have had different survival probabilities than mallards marked during the pre-season banding period (1 July–30 September). Although there was evidence for moderate overdispersion, we believe ranking models by $\mathrm{QAIC_c}$, examining support for parameters in the top models, and examining temporal effects on survival during the annual cycle by plotting the Kaplan-Meier survival curve provided useful inference regarding the effects of the examined variables on mallard survival.

The top models indicated support for higher survival among adult than juvenile female mallards, and a positive relationship of proportion urban land use and survival for both age classes. Mallards that spend more time in urban areas likely encounter fewer predators and waterfowl hunters (Figley and VanDruff 1982), reducing their exposure to primary sources of mallard mortality. Although female Great Lakes mallards with more domestic ancestry had greater use and selection of urban developed land cover, wild female mallards also used urban land cover, but to a lesser degree than hybrid mallards (Chapter 2). Previous work provided evidence that domestic and hand-reared mallards were likely to be more susceptible to predation (Schladweiler and Tester 1972), more susceptible to hunter harvest (Hunt et al. 1958, Soutiere 1986, Smith 1999), and had low annual survival (Osborne et al. 2010, Söderquist et al. 2021). Additionally, supplemental feeding in urban areas (Figley and VanDruff 1982) could enhance survival of early generational hybrids which may rely more on anthropogenic than naturally available forage (Smith 1999, Söderquist et al. 2024). Whereas we predicted that the proportion of wild genes would be directly related to survival, our results did not align with that hypothesis. However, because hybrid mallards with <50% wild ancestry primarily used and selected (Chapter 2) urban land cover, the ability to estimate survival for early generational game-farm mallard hybrids in undeveloped or rural landscapes was limited. Further, because few early generational hybrids were captured at rural banding sites and game-farm mallard releases likely occur primarily on private shooting preserves and not in urban areas (U. S. Fish and Wildlife Service 2013), we suspect they have relatively short lifespans in rural landscapes. We hypothesized that a greater proportion of game-farm ancestry would be associated with lower survival, however, individual genes could code for traits or behaviors that were uncorrelated with survival. Therefore, simply measuring the relationship between the proportion of wild ancestry and survival could fail to account for only certain domestic genes having an influence on survival, and further studies could explore this question.

Midcontinent mallards had similar to slightly higher annual survival in juvenile compared to adult female cohorts (Riecke et al. 2022), whereas annual survival was greater for adult than for juvenile female eastern mallards (Roberts et al. 2023) and Great Lakes mallards (Chapter 5). Estimates of juvenile female harvest mortality have typically been greater than that of adult female harvest mortality (Singer 2014, Riecke et al. 2022), suggesting juvenile females are more susceptible to harvest. In contrast, breeding season survival was similar or higher for juvenile female than for adult female midcontinent mallards (Reynolds et al. 1995, Devries et al. 2003), whereas breeding survival of Great Lakes mallards has been greater for adult than for juvenile mallards (Coluccy et al. 2008). Our results suggested that adult female mallards had greater annual survival than did juvenile mallards. Annual survival estimates of GPS-marked adult females were comparable (range in survival difference: 0.01–0.08) to survival of adult female mallards marked with bands only in Michigan and Wisconsin, 2021–2022 (Chapter 5; Figure A.2). Annual survival estimates of GPS-marked juvenile females were lower (range in survival difference: 0.10–0.14) than survival estimates for banded-only juvenile female mallards in Michigan and Wisconsin, 2021–2022 (Chapter 5; Figure A.2). Adult female annual survival in this study was similar to annual survival estimates reported for midcontinent (Hoekman et al. 2002) and Great Lakes (Coluccy et al. 2008) mallards. Few studies have estimated annual (365-day interval) survival for GPS- or radio-transmitter marked female mallards, although our survival estimates were similar to annual survival of breeding-age female mallards marked with prong and suture transmitters in Saskatchewan (Arnold and Howerter 2012). Although our annual survival estimates for adult females deviated little from expectation based on banded-only adult females, our estimates of juvenile female annual survival may be biased low. We note that 8.7% of mallards marked as juveniles were local-age (juveniles incapable of flight), which may result in lower survival estimates than expected for the juvenile age class if local-age females have lower survival than hatch year (flighted) females, although we lacked sufficient sample size of local-age mallards to test for a difference. Previous assessments of transmitter effects on avian taxa demonstrated potential for reduced survival for birds marked with transmitters relative to those which are marked with bands only (Barron et al. 2010, Bodey et al. 2018). Additionally, mallards marked with external prong and suture transmitters had lower survival than mallards with abdominally implanted transmitters (Arnold and Howerter 2012). We tested for survival differences between two configurations of elastic straps (2 separate loops vs a single X loop design) used to attach transmitters, with modeling results suggesting a slight but nonsignificant advantage of the X loop design (Figure A.3). The risk of mortality for adult female mallards marked with transmitters was 1.45 times the risk of mortality for mallards marked with a band only in the Mississippi Flyway from 2013–2022 (Setash et al., in press). Weighing the costs and benefits of transmitter use in context with study objectives and required data is important to decide if transmitters are necessary. We elected to use transmitters in this study because daily and migratory movements, resource selection (Chapter 2), and fine-scale breeding fidelity (Chapter 4) were of interest, and this information could not be obtained or would be of inadequate detail without deploying transmitters. We caution interpretation of the magnitude of survival estimated for juvenile female mallards in this study and recommend against using these survival estimates for population modeling. However, if a survival bias induced by transmitters is consistent across individuals and random with respect to covariates, the relative differences in survival still provide valuable information (in this case, differences within an age class but across values of other covariates). Under that assumption, there is likely a positive effect of urban land cover use on female Great Lakes mallard survival.

The size of urban areas in the Great Lakes region is predicted to expand (Soulliere et al. 2020), creating a growing source of refuge for mallards if using these areas confer benefits that enhance survival. Notably, urban areas appear to allow wild x game-farm mallards to survive at rates similar to those of wild mallards. Urban areas may play an important role in creating opportunities for contact between domestic and wild mallards and could potentially be areas where increased hybridization occurs. Whereas female mallard survival was higher in urban areas, developed landscapes may be less suitable for nesting and brood rearing (Figley and VanDruff 1982, Dykstra et al. 2024), resulting in lower productivity (Chapter 5). Thus, female mallards could experience tradeoffs between survival and fecundity related to their choice of habitat type throughout the annual cycle. Further work will be required to better understand the effects of hybridization between wild and game-farm mallards on demography. Our results suggest potential for individual heterogeneity in Great Lakes female mallard survival related to use of urban areas.

MANAGEMENT IMPLICATIONS

Over half of female mallards sampled in the Great Lakes region were wild x game-farm mallard hybrids, with hybrid mallards more prevalent at urban capture sites. There was a positive relationship between urban land cover use and female mallard survival, suggesting developed areas could serve as a form of refuge from predation and harvest. Urban areas can provide conditions enabling hybrid mallards to survive at rates equivalent to those of wild mallards. These locations also have relatively high human concentrations, often with elevated human-waterfowl interactions and potential to inform and influence stakeholder opinions regarding waterfowl conservation. Further research is needed to better understand the effects of landscape change and hybridization on Great Lakes mallard population dynamics, with the goal of increasing efficacy of waterfowl habitat management decisions. Lastly, our results suggest researchers should use caution when applying transmitters as transmitter-marked ducks may survive at lower rates than ducks marked only with bands, and we encourage researchers to report these effects to provide transparency in inferences and to help inform the methodological choices of other researchers.

TABLES

Table 3.1. Number of hen mallards marked with GPS-GSM transmitters by Bird Conservation Region (BCR), state, and age (AHY = after hatch year; HY = hatch year; L = local) in the Great Lakes region from 2021-2023.

	Michigan			**Wisconsin**			**Ohio**			**Indiana**			**Illinois**			
	AHY	**HY**	**L**	**AHY**	**HY**	**L**	**AHY**	**HY**	**L**	**AHY**	**HY**	**L**	**AHY**	**HY**	**L**	**Total**
BCR 23	127	49	3	80	51	10	61	30	0	12	11	2	0	2	0	438
BCR 22	-	-	-	-	-	-	2	2	0	28	9	0	26	10	0	77
BCR 12	12	36	1	7	18	3	-	-	-	-	-	-	-	-	-	77
Total	139	85	4	87	69	13	63	32	0	40	20	2	26	12	0	592

Table 3.2. Number of mortalities for adult (AHY; after hatching year) and juvenile (HY; hatching year and L; local) female mallards marked with GPS-GSM transmitters in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023. Mortalities of unknown cause include mortalities identified using GPS and accelerometer data and mortalities identified by field observation for which cause could not be determined.

	Number of Mortalities		
Mortality Cause	**Adult**	**Juvenile**	**Total**
Unknown	82	56	138
Hunter harvest	38	50	88
Predation	32	29	61
Vehicle strike	3	1	4
Drake aggression	1	0	1
Poaching	1	0	1
Powerline strike	1	0	1
Window strike	0	1	1
Starvation/Exposure	0	1	1

Table 3.3. Loglikelihood (logLik), quasi-Akaike's Information Criteria adjusted for small sample size (QAIC_c), difference in QAIC_c from the top model (ΔQAIC_c), model weight (ω), and number of parameters (K) for models predicting survival of female mallards marked with GPS-GSM transmitter in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023 in relation to age (adult or juvenile), proportion of GPS locations in urban land cover (p_urban), proportion wild genome (pwild), attachment type (2-loop or X harness), and week (week of the year as a factor). Models are adjusted for the variance inflation factor ($\hat{c}$) value of 1.5.

Model	**logLik**	**QAIC_c**	**ΔQAIC_c**	**ω**	**K**
age + p_urban	1987.71	1993.71	0.00	0.68	3
age + pwild + p_urban	1987.51	1995.51	1.80	0.28	4
age × pwild × p_urban	1984.70	2000.71	7.00	0.02	8
p_urban	1998.89	2002.89	9.18	0.01	2
p_urban + attachment	1997.10	2003.10	9.39	0.01	3
pwild + p_urban	1998.06	2004.06	10.35	0.00	3
p_urban × attachment	1996.98	2004.98	11.27	0.00	4
pwild × p_urban	1997.50	2005.50	11.79	0.00	4
age + p_urban + week	1897.78	2008.15	14.44	0.00	55
age + p_urban + pwild + week	1897.58	2009.97	16.26	0.00	56
age + pwild	2005.11	2011.11	17.40	0.00	3
p_urban + week	1909.76	2018.12	24.41	0.00	54
pwild	2017.07	2021.07	27.36	0.00	2
pwild + attachment	2016.53	2022.53	28.82	0.00	3
pwild × attachment	2016.53	2024.53	30.82	0.00	4
age	697.49	2025.31	31.61	0.00	2
age + pwild + week	1915.10	2025.48	31.77	0.00	55
age + attachment	697.45	2027.27	33.56	0.00	3
age × attachment	696.15	2027.97	34.26	0.00	4
pwild + week	1927.34	2035.70	41.99	0.00	54
age + week	607.02	2039.20	45.49	0.00	54
Null	716.17	2041.99	48.28	0.00	1
attachment	716.14	2043.96	50.25	0.00	2
week	625.75	2055.92	62.21	0.00	53
age × week	562.69	2099.90	106.19	0.00	106
age × p_urban × week	1734.36	2163.93	170.22	0.00	212
age × pwild × week	1806.17	2235.74	242.03	0.00	212
age × p_urban × pwild × week	1596.93	2467.44	473.73	0.00	424

FIGURES

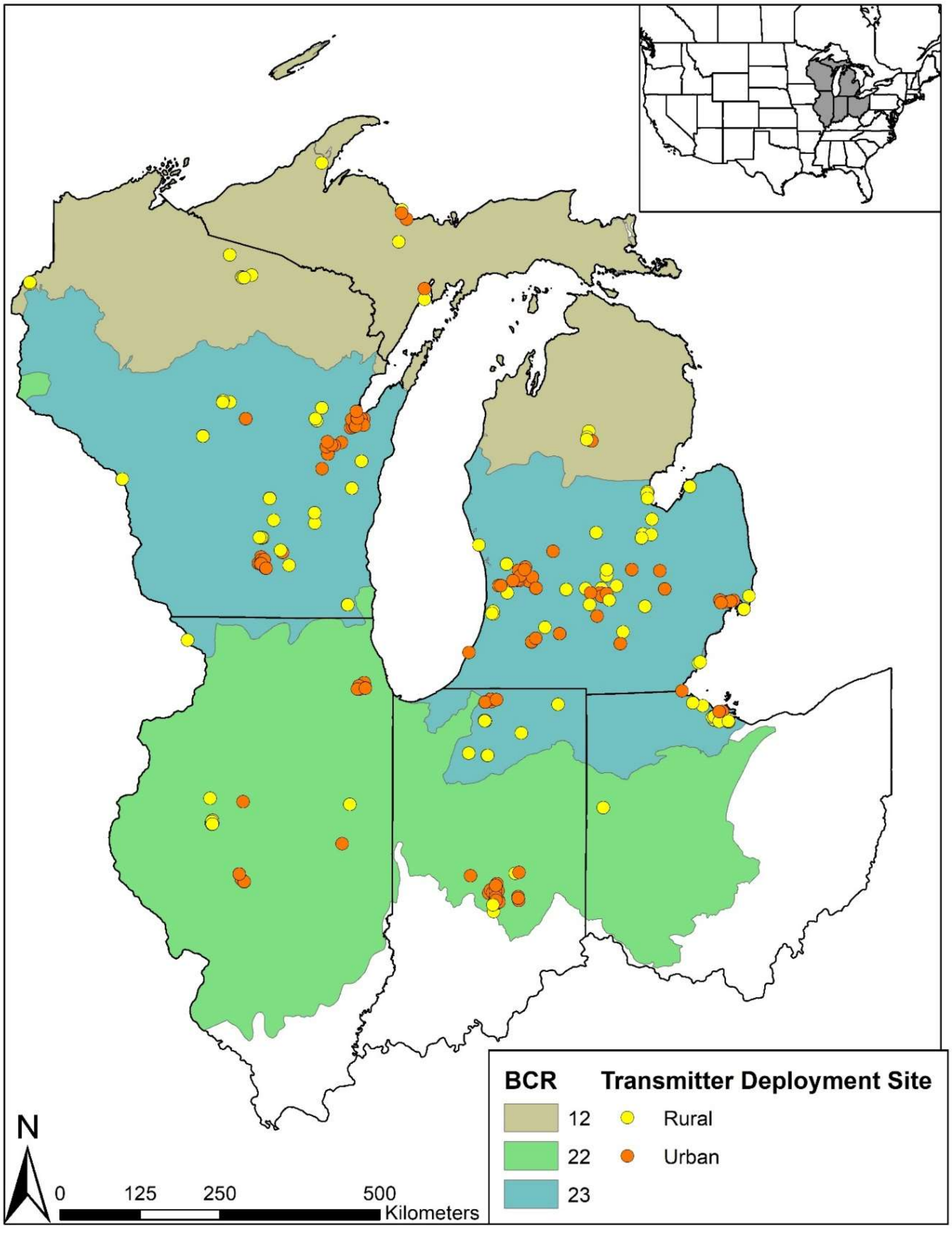

Figure 3.1. Capture and GPS-GSM transmitter deployment locations for female mallards captured in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023 in relation to banding site type (urban or rural) and Bird Conservation Region (BCR) 12, 22, and 23.

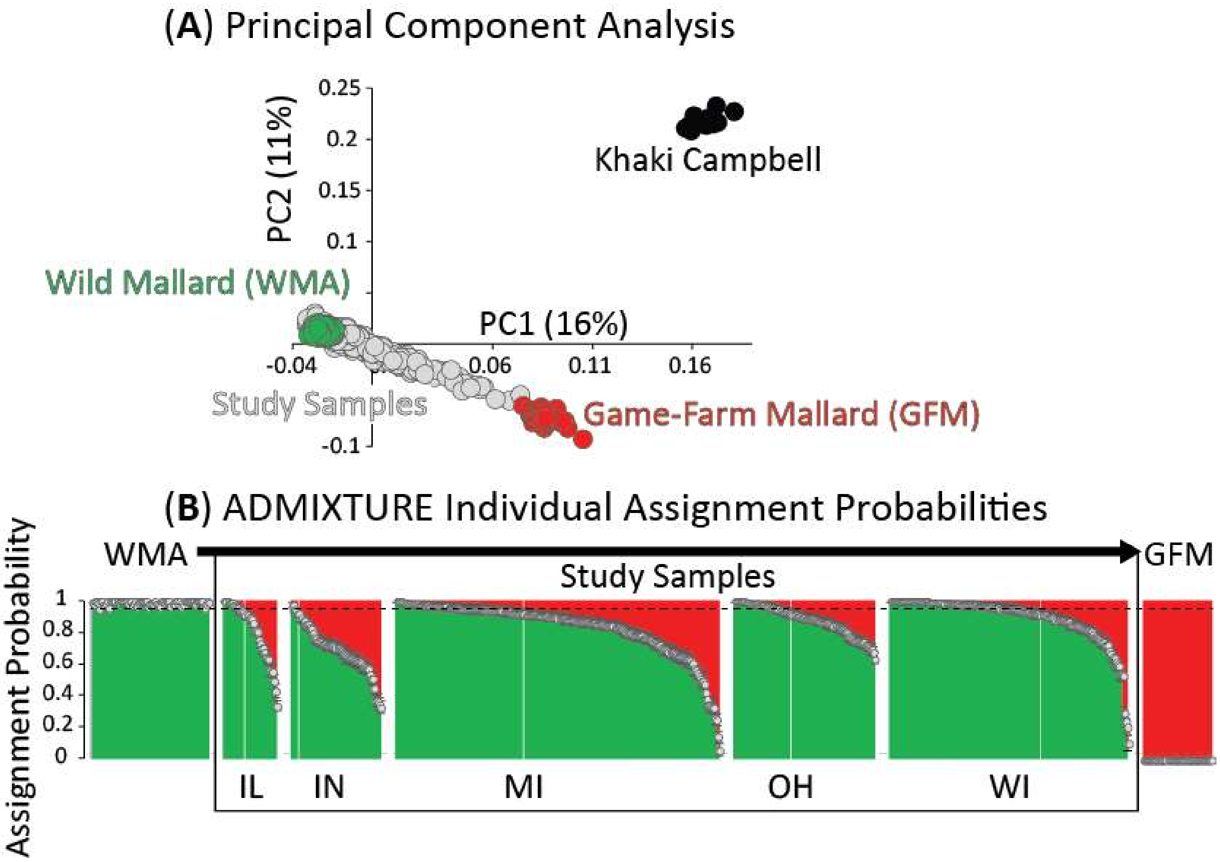

Figure 3.2. Principal component plot (A) of the first 2 principal components explaining variation in nuclear ddRAD sequencing results for reference wild (WMA; green circles), domestic game-farm mallard (GFM; red circles), and Khaki Campbell (black circles) samples and genetic samples collected from female mallards marked with GPS-GSM transmitters in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023 (Study Samples; grey circles). ADMIXTURE assignment probabilities (B) for individual Great Lakes mallard study samples by capture state, and wild and game-farm mallard reference samples.

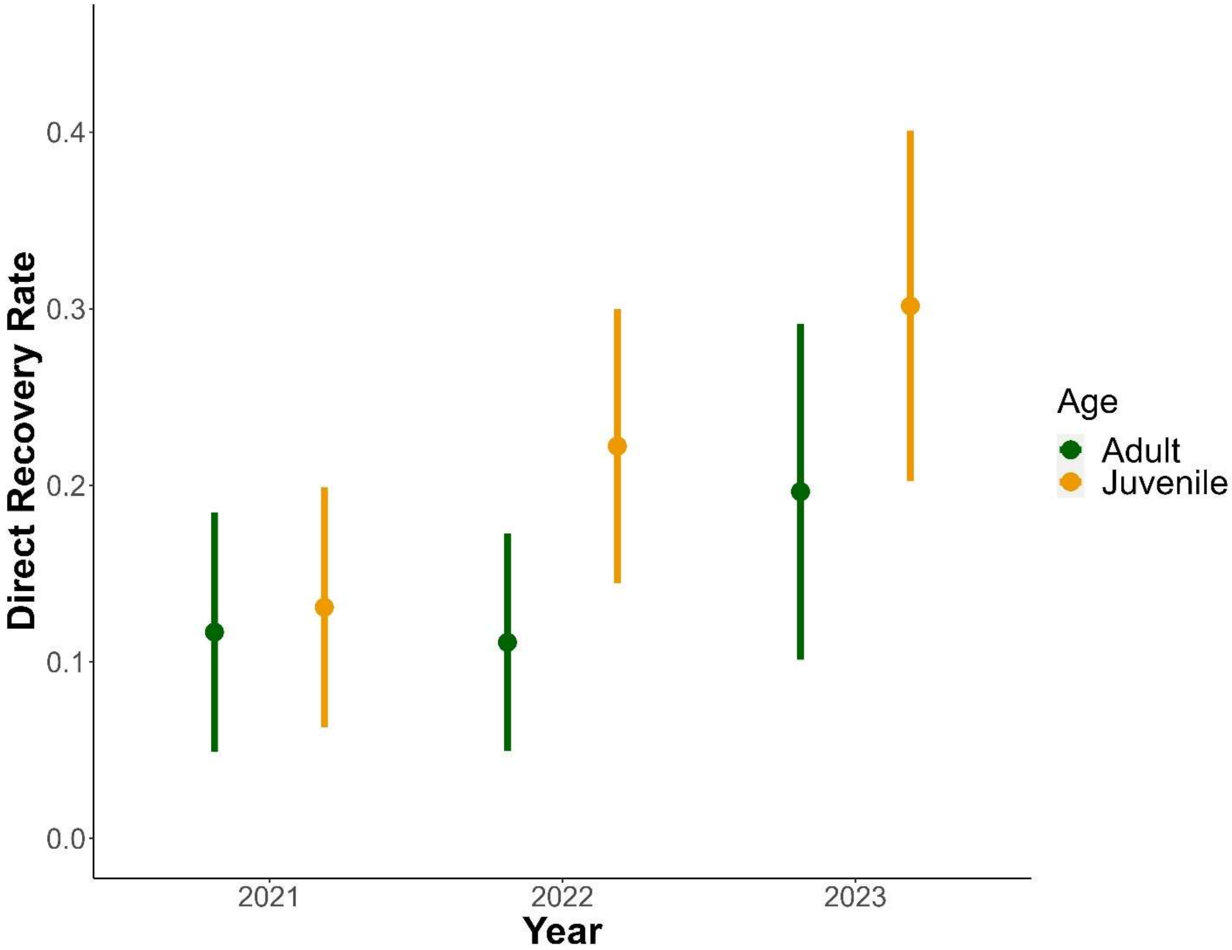

Figure 3.3. Direct recovery rate estimates (points; probability a marked bird is shot, retrieved, and reported during the hunting season immediately following banding) and 95% confidence intervals (error bars) for adult (AHY; after hatching year) and juvenile (HY; hatching year and L; local) female mallards marked with GPS-GSM transmitters in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023.

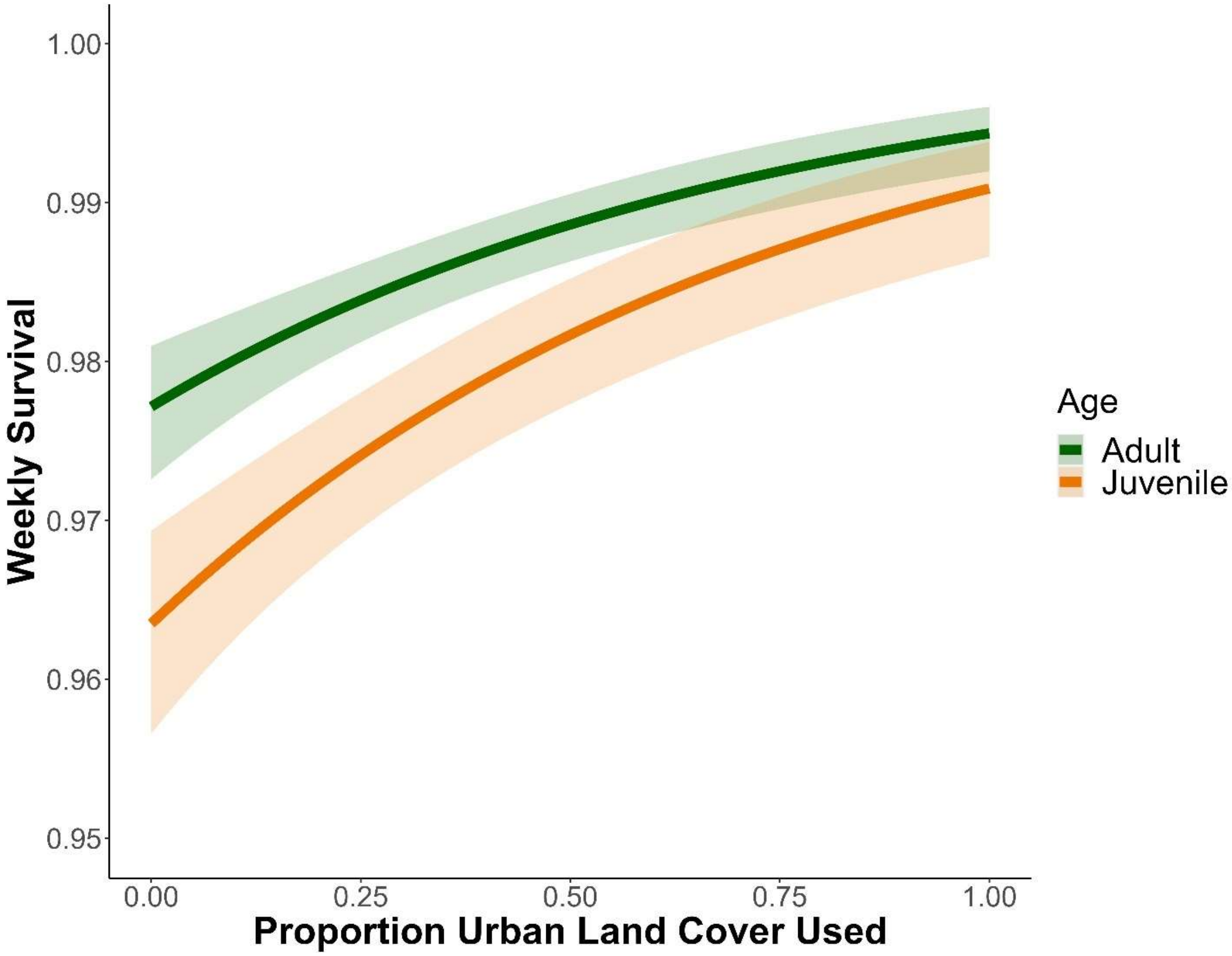

Figure 3.4. Predicted weekly survival probability in relation to the proportion of GPS locations in urban land cover for adult (AHY; after hatching year) and juvenile (HY; hatching year and L; local) female mallards marked with GPS-GSM transmitters in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023.

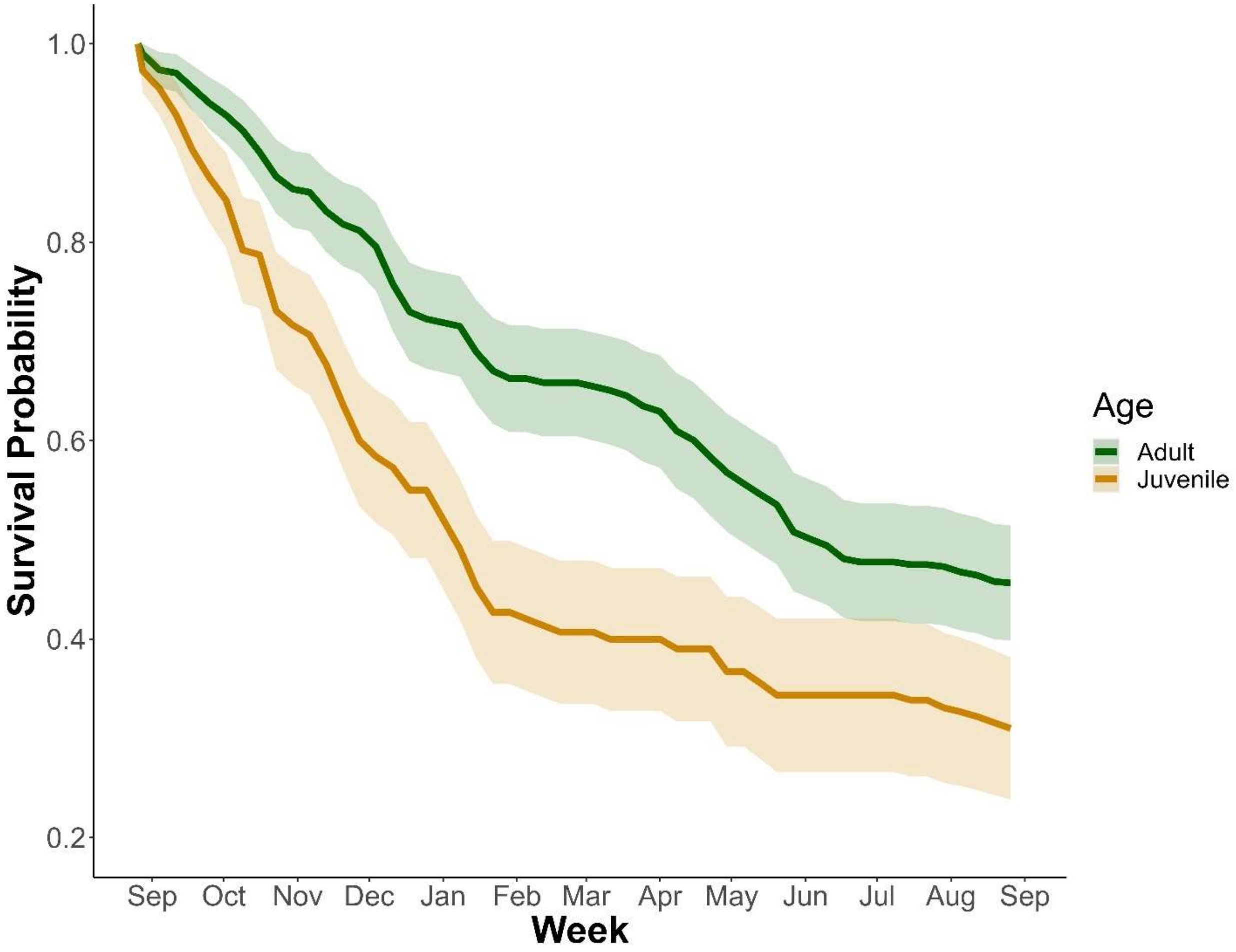

Figure 3.5. Kaplan-Meier survival curve (lines) and 95% confidence intervals (shaded regions) fit to the combined (2021–2024) weekly mortality data for adult (AHY; after hatching year) and juvenile (HY; hatching year and L; local) female mallards marked with GPS-GSM transmitters in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023.

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APPENDIX A: SURVIVAL MODELING SUPPORTING INFORMATION

Table A.1. Model selection table displaying loglikelihood (logLik), quasi-Akaike's Information Criteria adjusted for small sample size ($\mathrm{QAIC_c}$), difference in $\mathrm{QAIC_c}$ from the top model ($\Delta\mathrm{QAIC_c}$), model weight (ω), and number of parameters (K) for the top 10 models at each value of the variance inflation factor ($\hat{c}$) predicting survival of female mallards marked with GPS-GSM transmitter in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023.

Model	**logLik**	**$\mathrm{QAIC_c}$**	**$\Delta\mathrm{QAIC_c}$**	**ω**	**K**
$\hat{c} = 1$					
Age + p_urban + week	2846.67	2948.99	0.00	0.70	55
Age + p_urban + pwild + week	2846.36	2950.70	1.71	0.30	56
p_urban + week	2864.63	2964.94	15.96	0.00	54
Age + pwild + week	2872.66	2974.98	25.99	0.00	51
Age + p_urban	2981.56	2987.56	38.57	0.00	3
Age + pwild + p_urban	2981.26	2989.26	40.27	0.00	4
pwild + week	2891.01	2991.32	42.33	0.00	50
Age × pwild × p_urban	2977.06	2993.07	44.08	0.00	8
Age × week	844.03	2994.59	45.60	0.00	82
Age + week	910.53	2996.57	47.58	0.00	50
$\hat{c} = 1.25$					
Age + p_urban + week	2277.33	2387.71	0.00	0.60	55
Age + p_urban + pwild + week	2277.09	2389.48	1.77	0.25	56
Age + p_urban	2385.25	2391.25	3.54	0.10	3
Age + pwild + p_urban	2385.01	2393.01	5.30	0.04	4
Age × pwild × p_urban	2381.65	2397.65	9.95	0.00	8
p_urban + week	2291.71	2400.07	12.36	0.00	54
p_urban + Attachment	2396.51	2402.52	14.81	0.00	3
p_urban	2398.67	2402.67	14.96	0.00	2
pwild + p_urban	2397.67	2403.67	15.96	0.00	3
p_urban × Attachment	2396.38	2404.38	16.67	0.00	4
$\hat{c} = 1.5$					
Age + p_urban	1987.71	1993.71	0.00	0.68	3
Age + pwild + p_urban	1987.51	1995.51	1.80	0.28	4
Age × pwild × p_urban	1984.70	2000.71	7.00	0.02	8
p_urban	1998.89	2002.89	9.18	0.01	2
p_urban + Attachment	1997.10	2003.10	9.39	0.01	3
pwild + p_urban	1998.06	2004.06	10.35	0.00	3
p_urban × Attachment	1996.98	2004.98	11.27	0.00	4
pwild × p_urban	1997.50	2005.50	11.79	0.00	4
Age + p_urban + week	1897.78	2008.15	14.44	0.00	55
Age + p_urban + pwild + week	1897.58	2009.97	16.26	0.00	56

Table A.1 (cont’d).

$\hat{c} = 1.75$					
Age + p_urban	1703.75	1709.75	0.00	0.67	3
Age + pwild + p_urban	1703.58	1711.58	1.83	0.27	4
Age × pwild × p_urban	1701.18	1717.18	7.43	0.02	8
p_urban	1713.33	1717.33	7.58	0.02	2
p_urban + Attachment	1711.80	1717.80	8.05	0.01	3
pwild + p_urban	1712.62	1718.62	8.87	0.01	3
p_urban × Attachment	1711.70	1719.70	9.95	0.00	4
pwild × p_urban	1712.14	1720.15	10.40	0.00	4
Age + pwild	1718.66	1724.67	14.91	0.00	3
pwild	1728.92	1732.92	23.17	0.00	2
$\hat{c} = 2$					
Age + p_urban	1490.78	1496.78	0.00	0.65	3
Age + pwild + p_urban	1490.63	1498.63	1.85	0.26	4
p_urban	1499.17	1503.17	6.38	0.03	2
p_urban + Attachment	1497.82	1503.82	7.04	0.02	3
Age × pwild × p_urban	1488.53	1504.54	7.76	0.01	8
pwild + p_urban	1498.54	1504.54	7.76	0.01	3
p_urban × Attachment	1497.74	1505.74	8.96	0.01	4
pwild × p_urban	1498.13	1506.13	9.35	0.01	4
Age + pwild	1503.83	1509.83	13.05	0.00	3
pwild	1512.80	1516.80	20.02	0.00	2
$\hat{c} = 2.25$					
Age + p_urban	1325.14	1331.14	0.00	0.63	3
Age + pwild + p_urban	1325.00	1333.01	1.87	0.25	4
p_urban	1332.59	1336.59	5.45	0.04	2
p_urban + Attachment	1331.40	1337.40	6.26	0.03	3
pwild + p_urban	1332.04	1338.04	6.90	0.02	3
Age × pwild × p_urban	1323.14	1339.15	8.01	0.01	8
p_urban × Attachment	1331.32	1339.32	8.18	0.01	4
pwild × p_urban	1331.67	1339.67	8.53	0.01	4
Age + pwild	1336.74	1342.74	11.60	0.00	3
pwild	1344.71	1348.71	17.57	0.00	2
$\hat{c} = 2.5$					
Age + p_urban	1192.62	1198.63	0.00	0.60	3
Age + pwild + p_urban	1192.50	1200.51	1.88	0.24	4
p_urban	1199.33	1203.33	4.71	0.06	2
p_urban + Attachment	1198.26	1204.26	5.63	0.04	3
pwild + p_urban	1198.83	1204.84	6.21	0.03	3
p_urban × Attachment	1198.19	1206.19	7.57	0.01	4

Table A.1 (cont'd).

pwild × p_urban	1198.50	1206.50	7.88	0.01	4
Age × pwild × p_urban	1190.82	1206.83	8.21	0.01	8
Age + pwild	1203.06	1209.07	10.44	0.00	3
pwild	1210.24	1214.24	15.62	0.00	2
$\hat{c} = 2.75$					
Age + p_urban	1084.20	1090.21	0.00	0.58	3
Age + pwild + p_urban	1084.09	1092.10	1.89	0.22	4
p_urban	1090.30	1094.30	4.10	0.07	2
p_urban + Attachment	1089.32	1095.33	5.12	0.04	3
pwild + p_urban	1089.85	1095.85	5.65	0.03	3
p_urban × Attachment	1089.26	1097.26	7.06	0.02	4
pwild × p_urban	1089.55	1097.55	7.34	0.01	4
Age × pwild × p_urban	1082.57	1098.58	8.37	0.01	8
Age + pwild	1093.70	1099.70	9.49	0.01	3
pwild	1100.22	1104.22	14.02	0.00	2
$\hat{c} = 3$					
Age + p_urban	993.85	999.86	0.00	0.55	3
Age + pwild + p_urban	993.75	1001.76	1.90	0.21	4
p_urban	999.44	1003.44	3.59	0.09	2
p_urban + Attachment	998.55	1004.55	4.69	0.05	3
pwild + p_urban	999.03	1005.03	5.18	0.04	3
p_urban × Attachment	998.49	1006.49	6.64	0.02	4
pwild × p_urban	998.75	1006.75	6.90	0.02	4
Age × pwild × p_urban	992.35	1008.36	8.51	0.01	8
Age + pwild	1002.55	1008.56	8.70	0.01	3
pwild	1008.54	1012.54	12.68	0.00	2

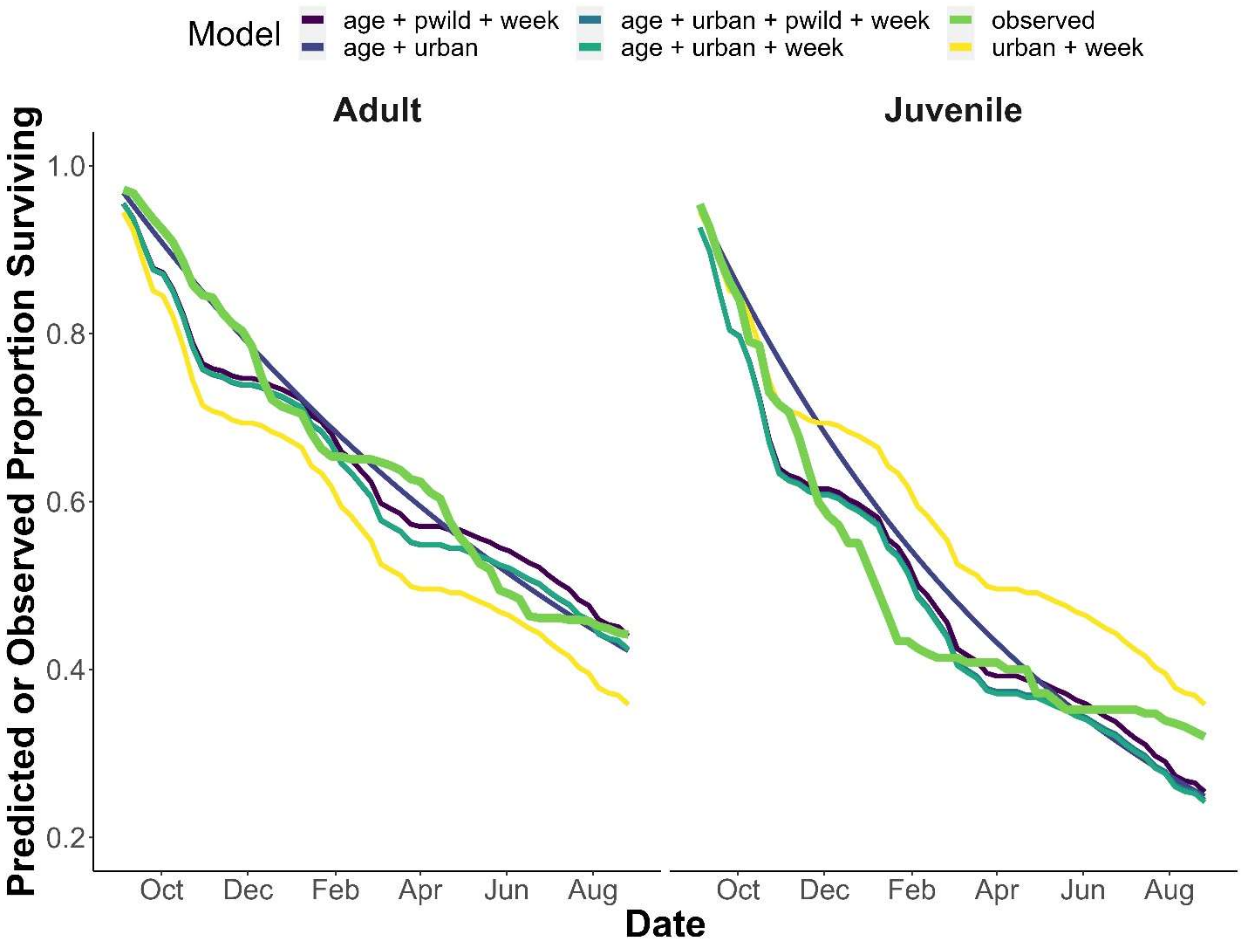

Figure A.1. Predicted survival probability (predicted proportion surviving) from the top five Known Fate survival models when the variance inflation factor ($\hat{c}$) was assumed to equal 1, and Kaplan-Meier survival curve fit to the observed mortality data (observed proportion surviving) for adult and juvenile female mallards marked with GPS-GSM transmitters in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023. Model covariates included age at capture (age; adult or juvenile), proportion wild genome (pwild), proportion of GPS locations in developed land cover (urban), and week (week of the year as a factor).

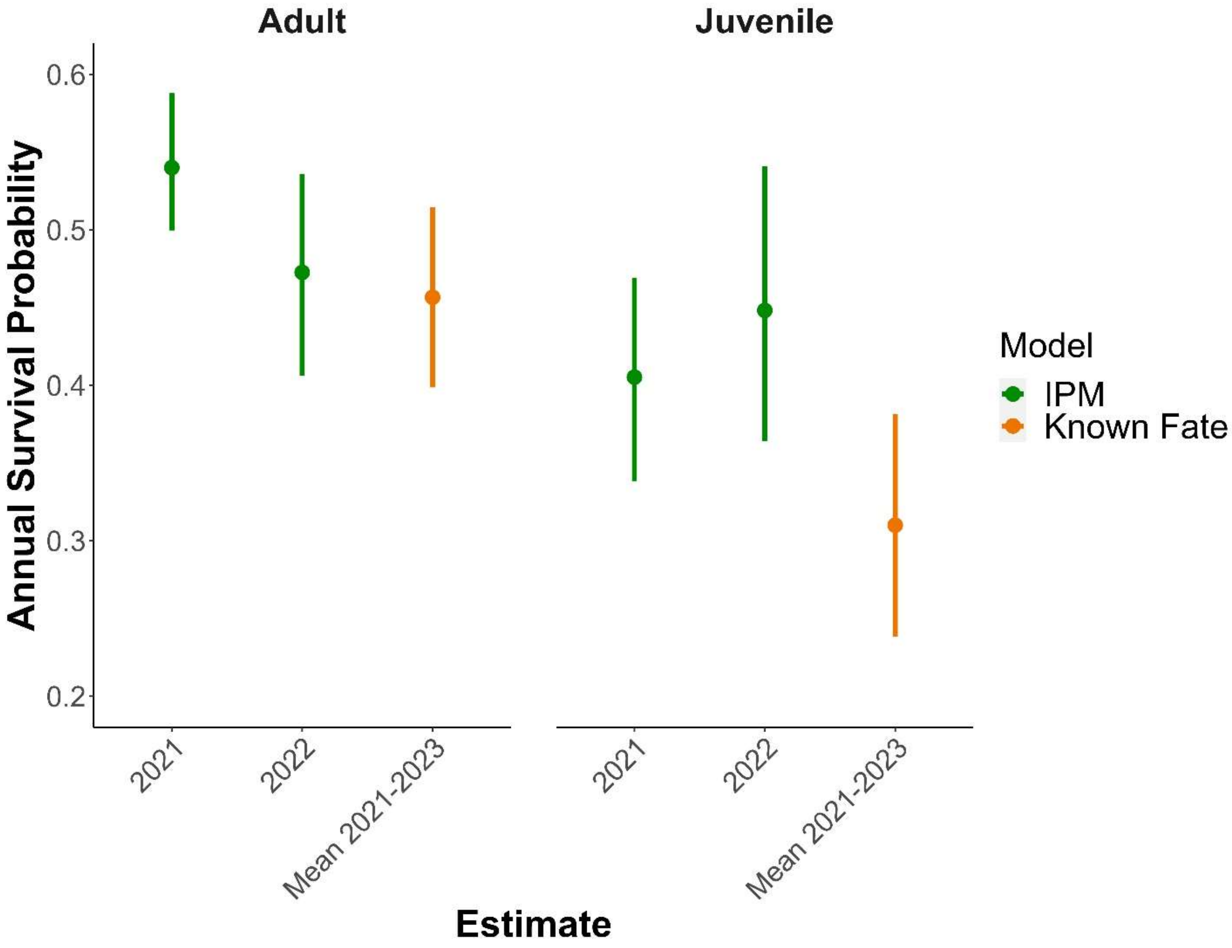

Figure A.2. Annual survival probability estimates (orange points) and 95% confidence intervals (orange error bars) from Known-Fate modeling for adult and juvenile female mallards marked with GPS-GSM transmitters in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023 and annual survival probability estimates (green points) and 95% credible intervals (green error bars) from an integrated population model (IPM) for adult and juvenile female mallards banded in Michigan and Wisconsin, 2021 and 2022 (Chapter 5).

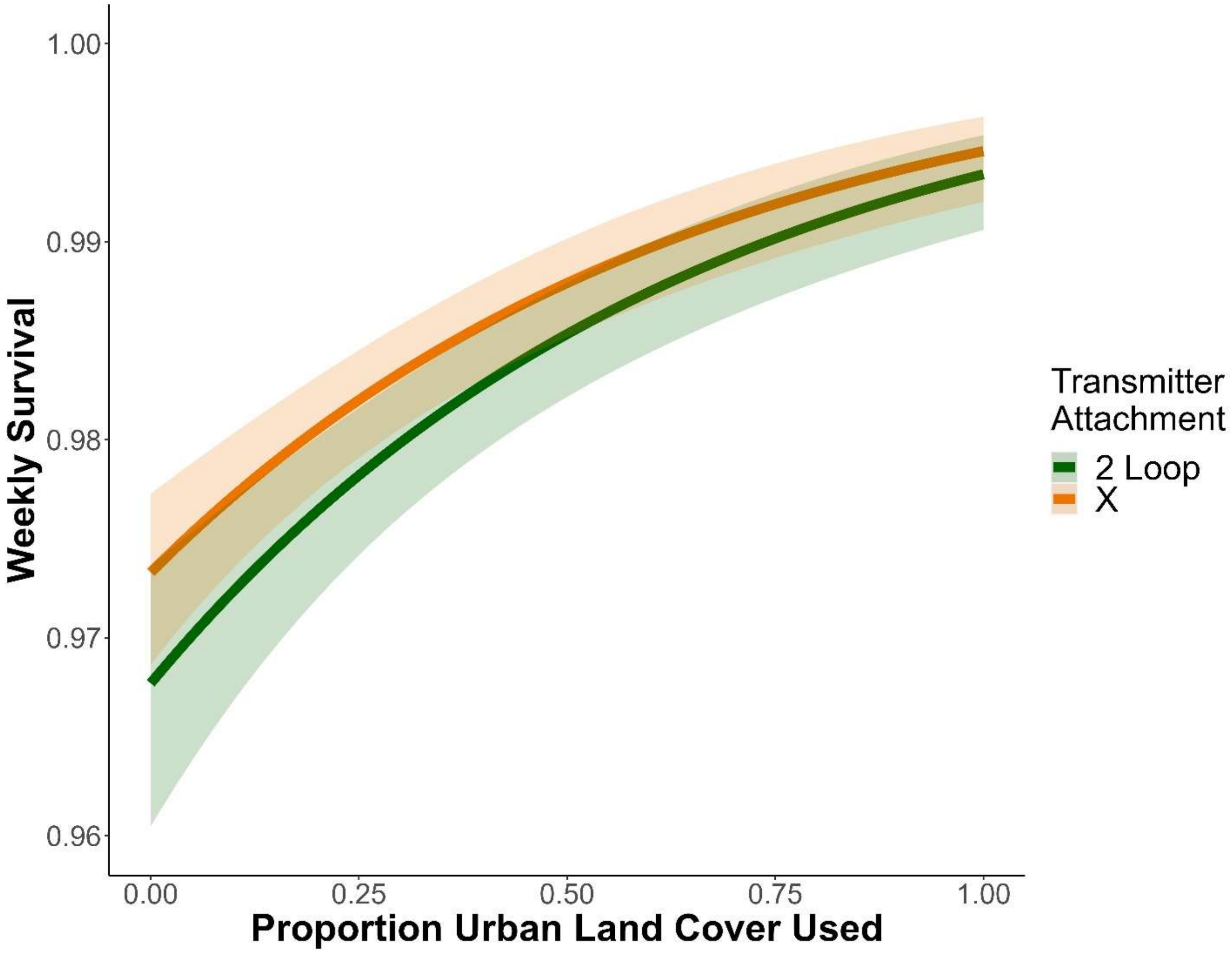

Figure A.3. Predicted weekly survival probability for female mallards marked with GPS-GSM transmitters in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023 in relation to transmitter attachment type (two separate loops [2 Loop] or a single loop in an "X" configuration [X]) using the model where survival is a function of proportion urban land cover used and transmitter attachment type (p_urban + attachment).

CHAPTER 4: GREAT LAKES MALLARD NESTING ECOLOGY AND FIDELITY

ABSTRACT

Dabbling duck population growth rates are often driven by female breeding survival and productivity, and management programs commonly aim to increase the quality or quantity of habitat types important for nesting and brood-rearing. Fidelity, or the proportion of a population returning to a breeding area, can also influence population dynamics, although fidelity is typically difficult to measure and has been less studied than survival and productivity in dabbling ducks. Breeding mallard (*Anas platyrhynchos*) abundance in the Great Lakes states of Michigan, Minnesota, and Wisconsin, USA steadily declined from 1.2 million in the year 2000 to 0.5 million in 2023. Two factors that could reduce productivity but have been largely unassessed are large-scale releases of domestic game-farm mallards and regional changes in habitat types used by female mallards during the breeding period. Our objectives were to assess the effects of mallard genotype, age class, nest site land cover, and nest initiation date on Great Lakes mallard incubation initiation and nest survival, and to estimate breeding period fidelity using GPS-GSM transmitter and isotope data collected from female mallards. We captured, obtained genetic and feather samples from, and marked 592 female mallards with GPS-GSM transmitters in Michigan, Wisconsin, Ohio, Indiana, and Illinois, USA from 2021–2023. We used ddRAD sequencing to identify genotypes and estimated probable areas of molting and hatching for GPS-marked mallards using stable hydrogen (δ^2H) isotopes. We used general linear models to estimate the probability of incubation initiation and nest success in relation to genotype and land cover covariates and estimated the proportion of the Great Lakes female mallard population that remained in or returned to the region during the breeding period. Our analysis identified 44% of GPS-marked mallards as genetically wild and 56% as wild x game-farm mallard hybrids. Early

generational hybrid mallards were less likely to initiate incubation than wild mallards and the amount of urban land cover around nesting locations was positively associated with hybrid and wild mallard nest success. Female Great Lakes mallards had high breeding fidelity, indicating emigration was low. Management actions that reduce hybridization between wild and domestic game-farm mallards, and that conserve breeding habitats at a regional scale are likely to increase Great Lakes mallard productivity.

INTRODUCTION

Estimating demographic parameters and their relationship to population growth rate is the foundation of modeling population dynamics. Across most bird species, as generation time increases, population growth rate is more influenced by adult survival than by fecundity (Sæther and Bakke 2000, Stahl and Oli 2006). However, in species with relatively long-lived life histories, annual adult survival may be relatively stable while fecundity varies in response to environmental conditions (Koons et al. 2014). Fecundity in upland nesting dabbling ducks is linked to temporally and spatially varying habitat and climatic conditions (Specht and Arnold 2018, Riecke et al. 2022). Nest success is a particularly important factor in dabbling duck fecundity (Greenwood et al. 1995, Devries et al. 2023) and conservation programs commonly aim to maintain or increase nest survival through restoration of quality nesting habitat (Soulliere et al. 2017, Prairie Habitat Joint Venture 2021), such as perennial grassland in proximity to emergent wetlands, and via predator management (Greenwood et al. 1995, Amundson and Arnold 2011, Amundson et al. 2013).

Although emigration and immigration can play important roles in population dynamics (Weegman et al. 2022), survival and fecundity are generally more studied in waterfowl, in part because of the difficulty in monitoring individuals over broad time periods or geographic areas.

Dabbling ducks can shift nesting distribution in response to resource conditions over space and time (Coulton et al. 2011, Devries et al. 2023). Breeding fidelity, or the probability an individual returns to a given area during the breeding period, is likely linked to demographic tradeoffs associated with dispersal (Greenwood and Harvey 1982, Coulton et al. 2011). Therefore, factors that affect nest survival and breeding fidelity are relevant to population and habitat management.

Sensitivity analyses of midcontinent and Great Lakes mallards (*Anas platyrhynchos*) previously suggested female breeding survival, nest success, and duckling survival explained the majority of variation in population growth rate in both populations, with the Great Lakes mallard population also sensitive to changes in female nonbreeding survival (Hoekman et al. 2002, Coluccy et al. 2008). Great Lakes mallard abundance historically followed the same trends as in the remainder of the midcontinent population. However, after a decade-long decline, prairie-nesting mallard abundance increased beginning in the mid-2000s while Great Lakes mallard abundance continued to decline. Breeding population size of Great Lakes mallards peaked near 1.2 million in 2000 based on state aerial surveys and steadily declined to around 0.5 million in 2023 (U. S. Fish and Wildlife Service 2023a). Declining Great Lakes mallard abundance is thus a concern for wildlife management agencies involved in hunting recreation as well as those implementing the North American Waterfowl Management Plan (Soulliere et al. 2017, NAWMP 2018). Hybridization with game-farm mallards is hypothesized to be a contributing factor to mallard decline in eastern North America (Lavretsky et al. 2020, Roberts et al. 2023). Game-farm mallard releases since the 1920s were estimated between >200,000 (U. S. Fish and Wildlife Service 2013) and >500,000 (Huesmann 1974) annually. Historically, game-farm mallards were released primarily in the Atlantic Flyway (Huesmann 1974, Hepp et al. 1988) and recent sampling revealed mallards in the U. S. portion of the Atlantic Flyway are a hybrid swarm comprised of approximately 90% wild x domestic game-farm mallard hybrids (Lavretsky et al. 2020).

Release of artificially selected animals can cause changes in morphology, behavior, and demography that negatively impact wild populations (Champagnon et al. 2012). Quantifying the population impact of hybridization between captive-bred and wild individuals can be difficult as the additive effects of introgression on fitness may be slow to develop (Tufto 2017). Large-scale, long-term releases of domestic mallards are predicted to negatively impact wild populations if gene flow transfers inheritable traits possessed by domestic ducks that are maladaptive in free-ranging wild populations (Söderquist et al. 2017, Lavretsky et al. 2020). Gene flow could have maladaptive consequences if domestic traits confer morphological or behavioral characteristics which reduce survival or reproductive capacity for admixed individuals. Domestic game-farm mallards had a longer egg laying period, higher egg production, and required longer incubation time to hatch eggs than did wild mallards (Prince et al. 1970, Cheng et al. 1980). These traits may be disadvantageous in the wild where individuals are exposed to predation during nesting, a significant component of annual mortality for hen mallards (Arnold et al. 2012). Finally, landscape changes potentially important to ground-nesting birds have occurred in the Great Lakes region concurrent with mallard population decline.

The Upper Mississippi/Great Lakes Joint Venture (UMGL JV) region lost an estimated 1.4 million ha of grassland and pasture from 2001 to 2016, while urban and agricultural land cover increased by 338,000 ha and 987,000 ha, respectively (Soulliere et al. 2020). Reduction in perennial upland cover could limit mallard nest success (Bortolotti et al. 2022, Devries et al. 2023) whereas agricultural practices such as insecticide use could reduce availability of invertebrate food resources (Hopwood et al. 2013, Morrissey et al. 2015, Soulliere et al. 2020).

Conversion to urban land cover could also limit productivity (Figley and VanDruff 1982, Dykstra et al. 2024, Chapter 5). More generally, agricultural intensification could reduce the amount or quality of both upland and wetland habitat types relevant to mallard productivity (Fowler et al. 2024). Thus, determining the influence of genetic and habitat factors on mallard nesting ecology and breeding fidelity are needed to inform management efforts.

Our objectives were to assess the effects of mallard genotype, age class, nest site land cover, nest initiation date, and latitude on Great Lakes mallard incubation initiation and nest survival, and to estimate breeding fidelity using GPS-GSM transmitter data collected from hen mallards. We captured and marked hen mallards with GPS-GSM transmitters from 2021 to 2023 in Michigan, Wisconsin, Ohio, Indiana, and Illinois, USA and monitored incubation initiation (probability of incubating a nest with eggs for ≥2 days), nest locations, and nest fates (hatch or fail). We hypothesized that breeding period fidelity to the Great Lakes region would be high for female mallards (Anderson et al. 1992, Arnold and Clark 1996, Doherty et al. 2002). We predicted that nesting effort and nest survival would be lower for hybrid than for wild mallards. We also predicted that nest survival would be inversely related to the amount of developed land cover and directly related to the amount of grassland cover around nest sites. We discuss the implications of our findings to population genetics and habitat management to conserve Great Lakes mallards.

STUDY AREA

We captured and marked female mallards with GPS-GSM (global positioning system-global system for mobile communications) transmitters in Bird Conservation Regions (BCRs; Bird Studies Canada and NABCI 2014) 12 (Boreal Hardwood Transition), 22 (Eastern Tallgrass Prairie), and 23 (Prairie Hardwood Transition) in the Great Lakes states of Michigan, Wisconsin, Ohio, Indiana, and Illinois, USA (hereafter, Great Lakes region; Figure 4.1). Bird Conservation Regions are landscape planning units comprised of similar ecosystems and bird communities and are relevant for landscape conservation planning in the Upper Mississippi/Great Lakes (UMGL) Joint Venture (JV) region (Soulliere and Al-Saffar 2021). The northern UMGL JV region is dominated by undeveloped natural communities with extensive upland and wetland forest and lakes (BCR 12) that transition to a mixed landscape of forests, lakes, and more herbaceous wetlands interspersed with agriculture and urban development (BCR 23). In the south (BCR 22) row crop agriculture and urban landscapes are prevalent, with a smaller proportion coverage in forest; about 90% of historic wetlands have been drained and most remaining wetlands in BCR 22 are associated with riverine systems (Soulliere et al. 2017). Regional temperatures and precipitation across much of the study area are influenced by the Great Lakes and generally consist of cold, snowy winters and hot, humid summers (Scott and Huff 1996). Moderating lake effects result in wetland conditions that are generally more stable and less seasonally dynamic than in the midcontinent Prairie Pothole Region (Euliss et al. 2004, Simpson et al. 2005). Mallards were the most abundant duck during the breeding period in the Great Lakes region (U. S. Fish and Wildlife Service 2023b) and spring densities were greatest in BCR 23 (Soulliere et al. 2017). We monitored movements of GPS-marked mallards within North America, which occurred in an area bounded by approximately 51.5ºN and 32ºN, and 75.2ºW, and 99.8ºW.

METHODS

Mallard Capture and Marking

We captured ducks using baited traps, rocket- and spring-propelled nets, handheld nets, and via night lighting from 4 March – 4 October, 2021–2023. We aged ducks as AHY (after hatch year; adult), HY (hatch year; juvenile capable of flight) or L (local; juvenile incapable of flight) and sexed birds via plumage characteristics (Carney 1992). We banded mallards with a size 7 United States Geological Survey (USGS) aluminum leg band. We attached 20 g Ornitela GPS-GSM transmitters (OrniTrack-E20 4GCT C48; Ornitela, Vilnius, Lithuania) dorsally to female mallards via 4.5 mm wide elastic straps. Transmitters were attached with two separate elastic loops in 2021 and via an X-shaped design consisting of a single piece of elastic in 2022 and 2023. Transmitters were distributed in approximate proportion to estimated breeding period mallard abundance by BCR (Soulliere et al. 2017). We classified transmitter deployment locations as urban if the proportion of developed land cover (low, medium, and high intensity developed, and developed open space from the 2021 National Land Cover Database [Dewitz 2023]) within a 7 km (mean of maximum daily net squared displacement) radius of the site was >0.5, or rural if ≤0.5. We weighed each hen mallard to the nearest 10 g and attached transmitters only to individuals >700 g so transmitters comprised <3% of body mass (mean = 1.9%). We measured total head, bill, total tarsus, and wing chord (Dzubin and Cooch 1992) of GPS-marked females. We drew approximately 0.1 ml of blood from the tarsal vein and clipped approximately 3 mm of the first secondary wing feather for genetic and isotope analyses, respectively. Ducks were released immediately after processing at capture locations. Transmitters were programmed to record a location every 30 minutes, 2 hours, or 4 hours when battery charge was >50%, <50% and >25%, or <25%, respectively, and uploaded data once every 24 hours when connected to cell networks. Transmitters recorded tri-axial accelerometer (ACC) readings at the time of each GPS location for two seconds at a frequency of 2 Hz when battery charge was ≥50% and recorded a single ACC reading at the time of each GPS location when battery charge was <50%. Approval to capture, band, sample, and attach transmitters was provided by Michigan State University institutional animal care and use committee (IACUC) permit PROTO202100046 and USGS Bird

Banding Laboratory (BBL) permit 03110.

Location data were forwarded to Movebank (Wikelski and Kays 2019) for storage. We performed data preparation and analyses in Program R (R Core Team 2023) and used the move package (Kranstauber et al. 2018) to retrieve GPS data from Movebank. We defined the nesting period as 1 March to 31 July based on the earliest and latest nesting attempts observed in hens monitored in this study. We censored GPS locations where a satellite fix was not obtained or only one satellite was successfully contacted, and/or locations with a horizontal dilution of precision (HDOP) <5 (D'Eon and Delparte 2005).

DNA Extraction, Sequencing, and Genetic Ancestry Analyses

We extracted genomic DNA from blood samples using a DNeasy Blood & Tissue kit following the manufacturer's protocols (Qiagen, Valencia, CA, USA). DNA quality was visually assessed on a 1% agarose gel to ensure high molecular weight bands. We followed ddRAD-seq (double-digest restriction site associated DNA sequencing) library protocols outlined in DaCosta and Sorenson (2014) and Lavretsky et al. (2015). In short, genomic DNA was enzymatically fragmented using *SbfI* and *EcoRI* restriction enzymes, and Illumina TruSeq compatible barcodes ligated for future de-multiplexing. The barcode-ligated fragments were then size selected using optimized double-sided bead selection protocols (Hernández et al. 2021). Libraries were then quantified with a Qubit 3 Flourometer (Invitrogen, Carlsbad, CA, USA) and pooled in equimolar amounts and sent to Novogenetics LTD (Sacramento, California, USA) for 150 base-pair, single-end chemistry sequencing on an Illumina HiSeq X. Raw Illumina reads were de-multiplexed using the *ddRADparser.py* script of the BU ddRAD-seq pipeline (DaCosta and Sorenson 2014) based on perfect barcode/index matches. Comparable sequences from previously published wild and domestic (game-farm and Khaki Campbell) mallards were included and served as respective references (Lavretsky et al. 2014a, b, 2019b, 2020). For each sample, we first trimmed or discarded sequences of poor quality using TRIMMOMATIC (Bolger et al. 2014), and then remaining quality reads aligned to a chromosomal-level reference wild mallard genome (Lavretsky et al. in press) using the BURROWS WHEELER ALIGNER v. 07.15 (Li and Durbin 2011). Samples were then sorted and indexed in SAMTOOLS v. 1.7 (Bolger et al. 2014) and combined using the *mpileup* function with the following parameters "-c –A -Q 30 -q 30." All steps through *mpileup* were automated using a custom Python script (Lavretsky et al. 2020). Next, we used VCFTOOLS v. 0.1.15 (Danecek et al. 2011) to filter variant call format (VCF) files for any base-pair missing >10% of samples that also included a minimum base-pair depth of 5X (i.e., 10X per genotype) and quality per base PHRED scores of ≥30.

All nuclear population structure was based on independent bi-allelic ddRAD-seq autosomal single nucleotide polymorphisms (SNPs), and without using *a priori* assignment of individuals to populations or species. The final dataset was obtained by using VCFTOOLS (Danecek et al. 2011) to first extract bi-allelic SNPs, and then PLINK v.1.9 (Purcell et al. 2007) to filter for singletons (minimum allele frequency: 0.0014), any SNP missing ≥10% of data across samples, as well as any SNPs found to be in linkage disequilibrium (LD). We randomly excluded all but one SNP for any positions found to be in significant LD ($r^2 > 0.5$). Population structure was first visualized using a principal components analysis (PCA) as implemented in PLINK v.1.9 (Purcell et al. 2007). Next, the program ADMIXTURE 1.3 (Alexander et al. 2013) was used to attain per sample maximum likelihood estimates of population assignments for each individual, with datasets formatted for the ADMIXTURE analyses using PLINK v.1.9 (Purcell et al. 2007), and following steps outlined in Alexander and Lange (2011). ADMIXTURE analyses were run for population models of *K* of 2 and 3 with a 10-fold cross validation, incorporating a quasi-Newton algorithm to accelerate convergence (Zhou et al. 2011). Each analysis used a block relaxation algorithm for point estimation and terminated once the change in the log-likelihood of the point estimations increased by <0.0001. Finally, standard deviations around each point estimate were calculated based on 1,000 bootstrap replicates. Ancestry assignments and their standard deviation were used to recategorize samples as feral game-farm, wild mallard, and to filial classes of hybrids (Schummer et al. 2023) under expected genotypes in generational backcrosses and uncertainty on assignment probabilities. Thus, we classified individuals with ≥ 0.92 wild assignment probability as wild and all others as hybrids. Assignment probabilities are also interpretable as an estimate of the proportion of an individual's genes that are of wild ancestry, and we considered proportion wild genome as a continuous covariate in nesting analyses.

Stable Isotope Analyses and Breeding Fidelity

Deuterium (δ^2H), a stable isotope of hydrogen, is found within local food webs and is incorporated in animal tissue during metabolic growth. In the case of feathers, δ^2H values become fixed after growth is complete (Inger and Bearhop 2008). A predictable pattern of δ^2H values in precipitation occurs across a latitudinal gradient in North America (Bowen et al. 2005), facilitating estimation of origins for migratory wildlife (Szymanski et al. 2007, Hobson and Norris 2008, Kusack et al. 2022, 2023). Comparison of δ^2H within mallard remiges to geographical variation of δ^2H in surface water thus serves as an intrinsic marker that can be used to estimate molting origins for adult and natal origins for juvenile ducks.

Mallard feather (1st secondary flight feather) samples were processed at the Cornell Stable Isotope Laboratory (COIL; Ithaca, NY, USA) for δ^2H. First, samples were cleaned using a 2:1 chloroform:methanol solvent rinse, then the distal section was clipped, weighed (mean =

0.422 μg; SD = 0.05 μg), and packed in sliver capsules. Pyrolytic combustion occurred at ~1,350°C on glassy carbon chips under helium flow. δ^2H was measured using a Thermo Delta V isotope ratio mass spectrometer interfaced to a Temperature Conversion Elemental Analyzer. Isotope values were corrected via the comparative equilibration technique (Wassenaar and Hobson 2003) using two standard keratin hydrogen isotope reference materials (caribou hoof standard [CBS], $\delta^2H = -197‰$; kudu horn standard [KHS], $\delta^2H = -54.1‰$). δ^2H results are reported in units of per mil (‰) and normalized on the Vienna Standard Mean Ocean Water (VSMOW) scale. The measurement error was estimated to be ≤2.9‰ using n = 8 within-run keratin reference materials.

We converted the amount-weighted growing season precipitation isoscape ($\delta^2\mathrm{H_p}$; Bowen et al. 2005) into a feather isoscape ($\delta^2\mathrm{H_f}$) using the calibration equation recommended for the dabbling duck guild by Kusack et al. (2023):

$$\delta^2\mathrm{H_f} = -69.9 + 0.7 \times \delta^2\mathrm{H_p}$$

We determined likely natal or molt regions of individual ducks using a likelihood-based assignment method described by Kusack et al. (2022). We used a normal probability distribution function to develop individual probability rasters where raster cell values represented the probability that an individual originated from that area, and where standard deviation included isoscape model (Bowen et al. 2005) and residual error from the calibration relationship (17.7‰; Kusack et al. 2023). We then created a binary surface of likely origin for each individual at a 2:1 odds ratio by assigning cells with values ≥0.66 a value of 1 and summing rasters for all individuals. We then used a cluster analysis to group geographically similar individuals into spatial regions of likely origin using the isocat package (Campbell et al. 2020). To do this, we computed a similarity matrix using Schoener's D-metric and used hierarchical clustering by correlation distance (Suzuki and Shimodaira 2013). We arbitrarily cut the dendrogram tree at a height of 0.25 because this threshold produced four areas of probable origin across our assignment range and provided the opportunity to delineate between the Great Lakes region and areas further north. We then determined the discrete category of origin for each individual to determine whether adults likely molted or juveniles likely hatched within the Great Lakes region. Finally, we visualized the general spatial range most associated with each identified cluster to depict the regions of highest relative association within the aggregated origins of groups of individuals (Campbell et al. 2020).

To obtain an estimate of fidelity, we calculated the proportion of GPS-marked hens from the Great Lakes region (i.e., likely molted in or hatched in the Great Lakes region in the previous year based on cluster assignment) that returned to the Great Lakes region each year after marking, conditional on survival. For hens classified as having Great Lakes region origin from the clustering analysis and which provided data on or after April 1 in the year following capture (those that survived and had functional transmitters), we calculated the proportion of locations from 1 March to 31 July that were within the Great Lakes region. We classified emigrants as hens that had >50% of locations outside of the Great Lakes region and/or initiated incubation of a nest outside the Great Lakes region. Therefore, fidelity is an estimate of the proportion of the Great Lakes female mallard breeding population that returned to the Great Lakes region each year.

Incubation and Nest Survival

We trained a machine learning algorithm to identify days when hen mallards were incubating using GPS and ACC data from individuals known to either be incubating a nest or not engaged in incubation. A subset of marked hens was located between 1 March and 31 July when data indicated repeat visits to a single location for ≥7–10 consecutive days. We searched for and recorded the presence or absence, location, and incubation status of nests. Incubation status (incubated nest or non-incubated nest) was determined by observation of the female mallard actively incubating, or by candling eggs (Weller 1956). We considered nests to be in the incubation stage (advanced past the egg laying stage) when at least two eggs displayed evidence of development such as a darkly defined yolk or vitelline veins (Hanson 1954). We visited nests at least twice to confirm incubation status and subsequent fate (hatch or fail). We assumed hens incubated known nests when ≥85% of daily locations (Afton and Paulus 1988) were within a 50 m radius (mean GPS transmitter accuracy = 24.6 m; standard error [SE] = 1.1 m) of the nest site. Observed individuals for which no nesting attempt was detected were classified as non-nesting. We used data from n = 50 GPS-marked hens that were directly observed during the incubation period to create a dataset where the daily incubation status of each individual was known. We extracted data collected from 1 March to 31 July from 2021 to 2023 and calculated GPS and ACC summary statistics (Appendix B) characterizing geographic and physical movement of GPS-marked hens. GPS and ACC statistics were adapted from previous work to predict animal behavior from GPS and ACC data (Resheff et al. 2014, Weegman et al. 2017, Askren 2021, Schreven et al. 2021). Known incubation status data were randomly split into 80% and 20% to form training and test datasets, respectively. We used the gradient boosted decision tree capability within the xgboost package (Chen et al. 2023) to predict a binary classification of incubation or no incubation for each hen mallard within each 24-hour period. We ran 1000 iterations with a binary:logistic objective using the training dataset to develop a model predicting incubation status. Next, we applied the model to the test dataset and designated days as incubating when the algorithm-predicted incubation probability was >0.5. The trained algorithm accuracy was 93.98% (i.e., the percentage of days where the predicted incubation status matched the known incubation status). We then applied the trained algorithm to predict daily incubation status for all other GPS-marked hens whose incubation status was unobserved.

Start and end dates of incubation attempts were identified as the first and last dates classified as incubating when ≥2 consecutive days were classified as incubating. We assumed unobserved nests were successful (at least one egg hatched) when the difference between the incubation end and start dates were 25–29 days, as this was the range in observed successful nests. For nesting attempts identified by the incubation algorithm, we determined nest coordinates by calculating the average latitude and longitude in decimal degrees across all days predicted as incubating. We modeled the probability of incubation initiation, defined as ≥2 consecutive days classified as incubating, using general linear models in the lme4 package (Bates et al. 2015). Candidate model variables included proportion wild genome of individual mallards, the proportion of GPS locations in developed urban land cover during the breeding period, and hen mallard age (SY = second year, AHY = after hatch year). We estimated daily nest survival probability using the nest survival model (Dinsmore et al. 2002) implemented in MARK (White and Burnham 1999) via package RMark (Laake and Rexstad 2018). Nest survival model covariates included nest initiation date (days since 1 March), individual proportion wild genome, and proportion urban (low, medium, and high intensity developed, and developed open space), forest (upland deciduous, evergreen, and mixed forest), wetland (emergent herbaceous and forested wetland), and grassland (grassland/herbaceous and pasture/hay) land cover within 10.4 km^2 (1.82 km radius) and 41.1 km^2 (3.63 km radius) areas (Reynolds et al. 2001, Stephens et al. 2005) surrounding nests. Land cover covariates were identified using the 2021 National Land Cover Database (Dewitz 2023) and 2020 Land Cover of Canada Database (Latifovic 2022).

Although we expected hens in their second or subsequent nesting season to have higher nest success (Coluccy et al. 2008), we did not include hen age as a nest survival covariate because there were only seven hens we knew to be SY (first nesting season), while the remainder were a combination of AHY and ASY (after second year). Nests from hens that were aged as AHY comprised 63% of the nest sample, and these birds could have been in their first nesting season (aged SY) or their second or later nesting season (aged ASY). Individual mallards with <45 days of monitoring data between 1 March and 31 July were excluded from nest survival analysis. We examined covariates for multicollinearity prior to modeling. Each pair of land cover covariates (proportion urban, forest, wetland, and grassland) were correlated between the 10.4 km^2 and 41.1 km^2 scales, thus we only retained the 10.4 km^2 scale land cover covariates. Nest success probability was estimated as the 26-day survival interval by exponentiating daily nest survival probabilities and calculating standard errors via the Delta method. We note that our nest success estimates omit the probability a nest survives the egg laying stage as nests were monitored from the start of incubation to hatch or failure, and daily nest survival probability may differ between the egg laying and incubation stages (Dinsmore and Dinsmore 2007) as hens increase nest attendance as egg laying progresses (Afton and Paulus 1988, Loos and Rohwer 2004). We ranked models using Akaike's Information Criteria (AIC; Burnham and Anderson 2002) in the MuMIn package (Barton 2019). While nest survival models lack a formal goodness-of-fit test (Dinsmore and Dinsmore 2007), model assumptions were likely met because nest age was determined only in relation to days since incubation initiation rather than by estimating days of embryonic development in eggs which may lead to subjective classification error, survival of nests identified and monitored remotely using GPS and ACC metrics was not influenced by field observations of the actual nest, and nest fates were likely to be independent. Although the incubation algorithm may lead to incorrect assignment of nest fate for nests that fail immediately before or during hatching (on the last days of incubation), the probability of a nest failure on the day before hatch should be no more probable than failure on any single preceding day (assuming equal daily survival probability throughout incubation), and any misclassification of nest fate is likely to be random with respect to model covariates.

RESULTS

We attached GPS transmitters to 592 hen mallards in 2021 (n = 194), 2022 (n = 241), and 2023 (n = 157). Mallards were captured using baited traps (n = 331), rocket- and spring-propelled nets (n = 166), hand-held nets (n = 55), and via night-lighting (n = 40). The marked sample included 74 mallards that were captured during nest incubation. Transmitters were deployed across all five states, three BCRs, and three mallard age classes (Table 4.1). After GPS data quality control, transmitters provided 118,389 locations from 75 mallards, 395,119 locations from 151 mallards, and 593,324 locations from 176 mallards from 1 March to 31 July in 2021, 2022, and 2023, respectively.

Genetic Ancestry

A total of 590 (of 592) samples provided usable genomic material and a total of 33,216 (of 34,230) independent bi-allelic ddRAD-seq SNPs were retained for nuclear population structure analyses. The first two principal components (Figure 4.2) explained a total of 26.8% of the variance, and clearly separated reference wild mallards, game-farm mallards, and Khaki Campbells, with samples from this study distributed between the wild mallard and game-farm mallard reference sets (Figure 4.2). Given no evident clustering with Khaki Campbells, we attained assignment probabilities by analyzing a dataset excluding them. Plotting ADMIXTURE assignment probabilities under a *K* population of two distinguished between wild and game-farm mallards, while samples from this study possessed assignment probabilities to either the wild mallard genetic cluster only or had interspecific assignments to both clusters (Figure 4.2). In total, we identified 44% of GPS-marked mallards as genetically wild, whereas 56% were classified as wild x game-farm mallard hybrids. The proportion of wild mallards captured in each state ranged from 8.1% in Indiana to 63.9% in Wisconsin. Generally, fewer hybrids were captured in the northern and western portions of the study area. Of mallards captured at rural sites (n = 353), 58.4% were wild and 41.6% were hybrids. Mallards captured at urban sites (n = 237) were comprised of 21.9% wild and 78.1% hybrid individuals.

Mallard Origins and Breeding Fidelity

Feathers were collected from 586 of 592 GPS-marked mallards and submitted for analysis. Four individuals were adults marked during flightless molt and thus flight feather samples were not possible, and two individuals were released without acquiring feather samples. The cluster analysis defined four regions of likely origin (Figure 4.3). Cluster 1 was the southern-most region, which included the southern Great Lakes states and BCR 22. Clusters 2 and 3 primarily included BCR 23 and BCR 12 at the latitudes within Michigan and Wisconsin. Cluster 4, the northern-most region, primarily covered the boreal and Hudson plain, and the northern U. S. and Canadian prairies. We classified individuals with predicted natal or molting origins in clusters 1, 2, and 3 as having origins from Great Lakes region because these clusters primarily corresponded to the study area and no marked individuals were located south of the Great Lakes region in Cluster 1 during the primary nesting and molting period from peak incubation initiation (7 May) to 31 July. We classified individuals with predicted origins in Cluster 4 as having hatched or molted outside (i.e., north) of the Great Lakes region. This resulted in 84% (95% CI: 77, 91), 77% (70, 83), and 72 % (63, 81) of adults predicted to have molted within the Great

Lakes region in 2021, 2022, and 2023, respectively. The percentages of juveniles predicted to have hatched within the Great Lakes region were 70% (95% CI: 59, 80), 77% (70, 85), and 59% (45, 72) in 2021, 2022, and 2023, respectively. The proportion of mallards with Great Lakes region origin were relatively similar for birds captured during preseason (1 July–4 October) banding (82% [77, 87]) and during spring (1 March–30 June) banding (71% [63, 79]). Fidelity, or the proportion of female mallards with Great Lakes region isotope signatures that remained in or returned to the Great Lakes region was 98% (95, 100) in 2022 and 98% (95, 100) in 2023. Only two incubation attempts were detected (via the incubation algorithm) outside of the Great Lakes states among hen mallards monitored in the study. Nest locations generally aligned with the spatial areas where the greatest number of marked mallards had 2:1 odds of assignment (Figure 4.4).

Incubation Initiation

Field observations revealed 46 incubation attempts from n = 50 observed mallards, while four were non-nesting. The incubation algorithm predicted 91 incubation attempts lasting ≥2 consecutive days among 214 mallard-year combinations (one individual mallard monitored in 1 year = 1 mallard-year). Thus, field observation and remote monitoring revealed a combined total of 137 incubation attempts among 264 mallard-years. Models predicting probability of incubation initiation are ranked in Table 4.2. The most-supported model held 85.5% of the model weight and included a quadratic effect of proportion wild genome, with additive effects of proportion urban land cover use and age. Top-model predictions indicated the probability of initiating incubation declined rapidly with declining proportion of wild ancestry for individuals with ≤50% wild genomes (Figure 4.5). The probability of incubation was positively related to the proportion of GPS locations in developed land cover (Figure 4.5), and AHY hens were more likely to incubate than SY hens ($\beta_{\text{age}} = -1.2; 95\% \text{ CI} = [-2.1, -0.3]$).

Nest Survival

We obtained sufficient data for 114 nests, comprised of 15, 40, and 59 nests in 2021, 2022, and 2023, respectively. The top-ranked nest survival model indicated an interaction of proportion wild genome and the proportion of urban developed land cover in a 10.4 km^2 area around the nest best predicted daily nest survival probability of the covariates examined. The top three models collectively comprised 94% of the model weight and all included proportion wild genome as a predictor (Table 4.3). The amount of developed land cover generally had a positive effect for late generation (second [F2; 0.72–0.82 wild ancestry] and third [F3; 0.86–0.92 wild ancestry] generation) hybrids and wild mallard hens, and a negative effect on early generation (first generation [F1; 0.43–0.63 wild ancestry]) hybrid nest survival (Figure 4.6). However, there were only five nests resulting from hens with <50% wild ancestry, so we caution interpretation of early generational hybrid nest survival estimates and covariate relationships due to low sample size. Wild mallard nests were surrounded by an average of 26.1% developed land cover, and nest survival to 26 days was 0.186 (0.097, 0.275). Nests of first generation hybrids had an average of 69.9% developed land cover in the surrounding area and predicted nest success was 0.481 (0.258, 0.678). However, in highly developed land cover (95% developed), wild hen nest success was 0.365 (0.159, 0.570) and similar to F1 hybrid nest success of 0.345 (0.011, 0.678).

DISCUSSION

Genetic Ancestry

Over half of hen mallards captured and marked with transmitters in the Great Lakes states were wild x game-farm mallard hybrids, suggesting that large scale releases of game-farm mallards (Huesmann 1974, U. S. Fish and Wildlife Service 2013) in the eastern North America over the last 100 years resulted in flow of domestic genes into wild mallard populations (Lavretsky et al. 2019a). The proportion of hybrids in our sample of Great Lakes mallards was intermediate between the U. S. portion of the Atlantic Flyway where previous research suggested about 90% of mallards were wild x game-farm hybrids (Lavretsky et al. 2019a) and the Central Flyway where mallards were almost entirely wild (Lavretsky et al. 2023). Our findings support the limited available data suggesting past releases of game-farm mallards occurred in eastern North America and primarily in the Atlantic Flyway. Our results contrast with genetic sampling of hunter-harvested mallards in the lower Mississippi Flyway where only 4% were hybrids (Davis et al. 2022). The lower Mississippi alluvial valley is a major wintering area for Mississippi and Central Flyway mallards (Bellrose 1976), however, Great Lakes mallards comprise only about 10% of the midcontinent population (U. S. Fish and Wildlife Service 2023b), thus prairie-breeding mallards are likely to far outnumber Great Lakes-breeding mallards in this wintering region. Additionally, there was an inverse relationship between the proportion of wild ancestry and the probability of migration by hen mallards in this study (Chapter 2), which may contribute to few hybrid mallards from the Great Lakes region migrating to the southern Mississippi Flyway.

More hybrid mallards were captured and marked at urban than rural sites in the Great Lakes region, a pattern that may have several contributing factors. First, the use and relative strength of selection for developed land cover was positively related to the proportion of domestic ancestry (Chapter 2), resulting in hybrid mallards, and particularly early generational hybrids, primarily selecting and using urban areas. Second, because early generational hybrids were rarely captured in or used rural locations (Chapter 2), it is unclear how well early generational hybrids can survive in traditional mallard habitat such as rural emergent wetlands.

Mallards with more domestic ancestry may rely on semi-domestic characteristics of urban areas such as fewer predators and supplemental feeding at urban parks to survive (Chapter 3). Correspondingly, early generational hybrids nested in areas dominated by urban development, while wild mallards nested in more undeveloped areas, but demonstrated greater variance in urban developed land cover composition surrounding nests. Further genetic sampling and improved documentation of the spatial extent and quantity of domestic game-farm mallard releases would advance our knowledge of primary sources of domestic mallard genetics.

Mallard Origins and Breeding Fidelity

The cluster analysis of isotope values within sampled flight feathers identified four discrete areas of origin for adult and juvenile female mallards in our sample. Clusters 1–3 aligned with latitudes of the Great Lakes region, whereas cluster 4 covered an area north of the Great Lakes. Most adult and juvenile females sampled in the study likely molted or were hatched in the Great Lakes region based on isotope analysis. Female mallards that did not have origins from the Great Lakes region likely molted or hatched north of the Great Lakes in the boreal forest, Hudson Bay lowlands (Cadman et al. 2007), or Canadian prairies. These results mostly support the assumption that preseason banding operations primarily captured female mallards from the Great Lakes mallard population (D. Avers, Michigan Department of Natural Resources, personal communication). However, our results suggested about 18% of preseason banded female mallards could have hatched or molted north of the Great Lakes. Further, there was greater annual variation in the proportion of juveniles originating from the Great Lakes region, suggesting in one year of this study (2023), as many as 41% of juvenile females banded in the Great Lakes region could have hatched north of the Great Lakes. The subarctic is a remote area where waterfowl banding is logistically difficult and expensive (Brook et al. 2021). Traditional harvest derivations relying on banding data could therefore underestimate the contribution of mallards from areas where few or no mallards are banded (Palumbo et al. 2019, Kucia et al. 2023), and isotopes represent a valuable emerging tool to identify origins of birds from remote areas in both banded and harvested samples.

Combined inferences from isotopes and monitoring of female mallard locations using GPS transmitters suggested that female Great Lakes mallards had high breeding period fidelity to the Great Lakes region. Nearly all females identified as having likely molted or hatched in the Great Lakes region remained in or returned to the region in the following year to nest or molt. With the exception of two incubation attempts, the few individuals that left the region appeared to primarily be making molt migrations to the Prairie Pothole Region. These results suggest that emigration was likely a negligible contributor to decline in the Great Lakes mallard population during 2021–2023. Although this study was not designed to estimate the rate of immigration of mallards into the Great Lakes population, our results suggest that a portion of female mallards banded in the Great Lakes region could have molted or hatched north of the region, which could include birds from either the midcontinent or eastern population survey areas, or regions that are not included in the Waterfowl Breeding Population and Habitat Survey (U. S. Fish and Wildlife Service 2023b).

Incubation Initiation

The probability of initiating incubation was positively related to the proportion of wild ancestry in hen mallards, supporting our hypothesis that individuals with greater game-farm ancestry would have lower nesting investment. In captivity, domestic game-farm mallards had longer egg laying periods and laid more eggs than wild hens (Prince et al. 1970, Cheng et al. 1980). Although egg-laying in captivity was greater for domestic than for wild hens, large-scale or commercial game farms would likely rely on artificial incubators to efficiently hatch domestic mallard eggs and maximize production of young. Traits present in wild animals can be lost or modified in captivity (Geffroy et al. 2020), so artificial incubation of game-farm mallard eggs and artificial selection for hens that laid more but did not necessarily incubate eggs could explain why hybrids with more domestic ancestry were less likely to incubate in wild settings.

Alternatively, lack of incubation behavior could be related to energetics. Egg laying and incubation are extremely energetically demanding on female mallards (Alisauskas and Ankney 1992), and individuals with inadequate nutrient reserves may forego nesting (Devries et al. 2008a). A study of captive game-farm and wild mallards suggested that female game-farm mallards had lower feeding efficiency than did wild female mallards (Halligan 2022). If feeding efficiency is lower for early generational hybrids than for wild hens, hybrids may be unable to obtain the necessary energy to enable incubation behavior. Further, habitat selection has been shown to result in carry-over effects on reproductive performance in waterfowl (Fowler et al. 2020). Because hybrids with more domestic ancestry were more likely to select, use (Chapter 2), and nest in urban areas, they may lack access to high quality forage, reducing body condition and limiting their ability to spend time incubating.

Early generational hybrid hens are likely to produce fewer ducklings than wild hens due to their lessened probability of incubating a nest. However, the incidence of nest parasitism of early generational hybrids on wild mallards is unknown and an opportunity for further research. Early generational hybrids that did not incubate eggs could have parented young if they laid eggs in the nests of other mallards. However, the overall evidence from this study suggests lower productivity by early generational hybrid mallards. Use and selection of urban areas (Chapter 2) and low incubation incidence by early generational hybrids corresponds to lower productivity indices at urban banding sites in the southern Great Lakes region identified using age ratios at banding (Chapter 5). Productivity, or the average number of juvenile female mallards per adult female mallard was lower at sites where hybrid female mallards were most prevalent. Therefore, continued release of game-farm mallards and subsequent hybridization with wild mallards may contribute to declining productivity in Great Lakes mallards (Chapter 5). However, later generational hybrids and especially 3rd generation (F3) hybrids, had similar probabilities of initiating incubation as those of wild hens, suggesting that several generations of backcrossing hybrid with wild mallards results in incubation behavior similar to that observed in wild mallards. Wild hens were more likely to initiate incubation when they spent more time in developed areas during the breeding period. This may be related to predation pressure during nesting. Incubation is a hazardous activity and mortality during the nesting period can drive annual mortality in hen mallards (Arnold et al. 2012, Riecke et al. 2022). Mallards nesting outside of developed areas in grassland or wetlands likely encounter more nest predators and therefore may be more likely to lose nests during the egg laying period, and we suggest this primarily explains the pattern observed in this study.

There is potential for marker effects when transmitters are used to monitor wildlife, and radio transmitters have been shown to bias hen mallard nesting effort and timing in the wild (Pietz et al. 1993, Rotella et al. 1993). However, we were unable to equivalently monitor incubation for hen mallards without transmitters and thus we were unable to assess if transmitter effects are present in this study. Transmitter effects could bias model results if the effect was related to hen mallard genotype, land cover use, or age. If transmitter bias was unrelated to model parameters, relative comparisons of incubation probability across covariate values would be unbiased. The range of incubation probabilities predicted in this study (0.54–0.84) were comparable to a nesting propensity estimate of 44–86% reported in Losito et al. (1995) and 73–97% in Devries et al. (2008) but slightly lower than the 80–89% reported for Great Lakes mallards (Coluccy et al. 2008). Breeding propensity is usually defined as the probability of a female mallard initiating at least one nest (Hoekman et al. 2002), including nests in the egg laying stage (Devries et al. 2008a). Our estimates of incubation probability do not include egg laying because of inability to distinguish this behavior via GPS and ACC data, thus an unknown proportion of individuals in our study that failed to incubate likely initiated a nest that never progressed past the egg laying stage. A conservative interpretation of our incubation probability estimates would be to consider probabilities as minimum estimates of the proportion of females reaching the incubation stage.

Nest Survival

Nest survival models suggested mallard genotype and the amount of developed land cover within a 1.82 km radius of nests best predicted daily nest survival probability of the covariates examined. Contrary to our hypothesis, the proportion of grassland was not an influential predictor of daily nest survival probability. Whereas some research identified a positive relationship between amount of grassland cover and nest survival for upland nesting dabbling ducks (Greenwood et al. 1995, Stephens et al. 2005), other studies did not identify a significant relationship (Howerter 2003). Quantifying landscape effects on avian nest success is complicated by measurement scale, covariance between amount and configuration of habitat, and difficultly studying a range of habitat amounts and configurations (Stephenson 2022) in observational studies. Additionally, the strength and direction of relationships between nest survival and habitat covariates can vary spatially (Devries et al. 2023). Our study was limited by a relatively modest sample of nests (n = 114) and the proportion of grassland varied only between 0–0.32, with 74% of nests surrounded by <5% grassland, which may explain why grassland amount was not predictive of nest survival. Additionally, mallards may respond to land cover type composition more broadly during the breeding period because they are a habitat generalist, potentially limiting the predictive ability of a single land cover covariate such as grassland (Fowler et al. 2024).

The proportion of developed land cover within a 1.82 km radius of nests was positively associated with F3 hybrid and wild hen mallard nest survival, but negatively associated with F2 and early generational hybrid nest survival. There were only five nests resulting from hens <50% wild, of which two were successful, resulting in high uncertainty regarding early generational hybrid nest survival. The leading cause of mallard nest failure was typically predation (Sargeant and Raveling 1992, Sovada et al. 2001, Emery et al. 2005, Pieron and Rohwer 2010, Amundson and Arnold 2011), thus the positive effect of urban land cover may be related to predator abundance and species diversity. The relationship between developed land cover and generalist mammalian or avian predator abundance is variable (Prange and Gehrt 2004, Klug et al. 2009, Graser et al. 2012), but lower predator abundance or altered predator forage sources could reduce predation pressure on birds nesting in developed areas (Rodewald et al. 2011). Mallards nesting in more highly developed areas probably encounter fewer nest predators (Figley and VanDruff 1982).

Wild hen mallard nest survival (26-day interval) in this study (0.186 [0.097, 0.275]) was similar to the Great Lakes mallard nest survival range of 0.1–0.19 reported by Coluccy et al. (2008) but lower than the 35-day interval survival estimate of 0.326 reported by Kaminski et al. (2013). Our wild mallard nest success estimates were within ranges reported for mallards nesting in the Canadian Prairie Pothole Region (0.06–0.36; Devries et al. 2023), and similar to nest success in the Prairie-Parkland Region (0.22–0.33; Devries et al. 2008b). Nest survival estimates were substantially higher for wild and hybrid mallards that nested in urban areas. This trend was similar to the proportion of successful nests observed in housing developments (73%) compared to nests in rural marsh impoundments (17%) and salt marsh (21%) in New Jersey (Figley and VanDruff 1982). However, these authors also noted that insufficient escape cover from avian predation, lack of invertebrate food sources, and anthropogenic hazards contributed to duckling mortality exceeding 70% in developed areas (Figley and VanDruff 1982). Others have similarly found mallard nest survival can be high in urban areas, but duckling survival was low (Dykstra et al. 2024). In our study, five hen mallards with <50% wild ancestry nested but none were observed with broods in the three weeks post-nesting. Our results suggested that a small proportion of early generational hybrids incubated a nest, and those that did nested in areas dominated by urban development.

Hybridization between wild and domestic game-farm mallards is likely a contributing factor to declining productivity in Great Lakes mallards (Chapter 5) due to lack of incubation behavior and limitation of nest site selection to urban developed areas by early generational hybrids. Release of domestic mallards has long been questioned as a viable management option (Lincoln 1934), and the results of this study add to previous evidence that domestic or captive-reared mallards had lower nesting incidence (Yerkes and Bluhm 1998) and lacked secretive behavior in selecting nest sites compared to wild mallards (Hunt et al. 1958), which limits their contribution to population productivity. Additional research to estimate nest and brood survival for early generational hybrids nesting in rural areas is warranted. As long-term game-farm mallard releases have presumably increased the proportion of the Great Lakes mallard population comprised of hybrids (Lavretsky et al. 2023), the component of the population benefitting from rural emergent wetland and grassland conservation has declined, reducing population response to traditional habitat management. Managing water features of existing or new urban developments to enhance mallard brood survival (Dykstra et al. 2024) in eastern North America may be incompatible with population management objectives considering female mallards using urban areas in the Great Lakes region and U. S. portion of the Atlantic Flyway could primarily be wild x game-farm mallard hybrids (Lavretsky et al. 2020). However, the effectiveness of rural habitat management actions aimed at increasing nest and brood survival could be enhanced by simultaneously addressing genetic and habitat components. The Great Lakes region lost an estimated 1.4 million ha of grassland and pasture from 2001 to 2016 while agriculture became more intensive (Soulliere et al. 2020). Sensitivity analyses have suggested brood survival was more important than nest success for breeding Great Lakes mallards (Coluccy et al. 2008), but this relationship could be reexamined given the substantial loss of regional grasslands. Reducing hybridization between wild and game-farm mallards is likely to improve the effectiveness of rural grassland and wetland habitat conservation for the Great Lakes mallard population and provide the greatest potential for increasing productivity.

MANAGEMENT IMPLICATIONS

Female mallards had high breeding fidelity to the Great Lakes region, suggesting emigration is a negligible contributor to population change and management efforts that focus on productivity and or breeding survival would likely be more effective in addressing the Great Lakes mallard population decline. Moreover, early generational hybrid mallards were less likely to initiate incubation than were wild mallards, suggesting release of game-farm mallards and subsequent hybridization with wild mallards contributes to reduced productivity in the Great Lakes mallard population. Developed urban areas may provide a semi-domestic setting where early generational hybrid mallards can be successful in establishing nests, but low incubation incidence limits their contribution to production relative to that of wild mallards. The positive effect of urban land cover on wild mallard nest success could create selective pressure for wild mallards to nest in urban areas where contact with hybrid mallards is more likely. Large-scale habitat changes likely play a role in relatively low success for mallards nesting in rural areas. Waterfowl and wetland management agencies with objectives to increase Great Lakes mallard productivity may prioritize regulation of domestic game-farm mallard releases and conservation of nesting and brood-rearing habitats at a regional scale.

TABLES

Table 4.1. Number of hen mallards marked with GPS-GSM transmitters by Bird Conservation Region (BCR), state, and age (AHY = after hatch year; HY = hatch year; L = local) in the Great Lakes region from 2021–2023.

	Michigan			**Wisconsin**			**Ohio**			**Indiana**			**Illinois**			
	AHY	**HY**	**L**	**AHY**	**HY**	**L**	**AHY**	**HY**	**L**	**AHY**	**HY**	**L**	**AHY**	**HY**	**L**	**Total**
BCR 23	127	49	3	80	51	10	61	30	0	12	11	2	0	2	0	438
BCR 22	-	-	-	-	-	-	2	2	0	28	9	0	26	10	0	77
BCR 12	12	36	1	7	18	3	-	-	-	-	-	-	-	-	-	77
Total	139	85	4	87	69	13	63	32	0	40	20	2	26	12	0	592

Table 4.2. Candidate models predicting probability of incubation for hen mallards marked with GPS-GSM transmitters in the Great Lakes region from 2021–2023. Models are ranked by Akaike's Information Criterion adjusted for small sample size (AIC_c) and the table includes the log-likelihood (logLik), difference in AIC_c relative to the top model (ΔAIC_c), model weight (ω), and number of parameters (K). Model covariates include proportion wild genome of individuals (pwild), proportion of GPS locations in urban (developed) land cover during the nesting period (purban), and age (after hatch year [AHY] or second year [SY]).

Model	**logLik**	**AIC_c**	**ΔAIC_c**	**ω**	**K**
pwild^2 + pwild + purban + age	-126.95	264.19	0.00	0.86	5
pwild^2 + pwild + age	-130.56	269.32	5.13	0.07	4
pwild^2 + pwild + purban	-130.59	269.37	5.18	0.06	4
pwild^2 + pwild	-133.86	273.84	9.65	0.01	3
purban	-136.19	276.43	12.24	0.00	2
age	-137.22	278.49	14.30	0.00	2
pwild	-140.92	285.89	21.70	0.00	2

Table 4.3. Candidate models predicting daily nest survival probability for hen mallards marked with GPS-GSM transmitters in the Great Lakes region from 2021–2023. Models are ranked by Akaike's Information Criterion adjusted for small sample size (AIC_c) and the table includes the log-likelihood (logLik), difference in AIC_c relative to the top model (ΔAIC_c), model weight (ω), and number of parameters (K). Model covariates include proportion wild genome of individuals (pwild), proportion of developed (urban), grassland (grass), forest, and wetland land cover in a 1.82 km radius around nests, and nest initiation date (initdate; days since 1 March).

Model	**logLik**	**AIC_c**	**ΔAIC_c**	**ω**	**K**
pwild × urban	531.49	539.52	0.00	0.56	4
pwild	538.13	542.14	2.62	0.15	2
pwild × grass	534.96	542.99	3.47	0.10	4
pwild × grass × initdate	528.98	545.08	5.56	0.03	8
pwild × initdate	537.18	545.20	5.69	0.03	4
pwild × forest	537.78	545.81	6.29	0.02	4
pwild × wetland × initdate	529.83	545.93	6.41	0.02	8
pwild × urban × initdate	530.30	546.40	6.88	0.02	8
urban	542.42	546.43	6.91	0.02	2
pwild × forest × initdate	532.03	548.13	8.62	0.01	8
grass × initdate	540.53	548.55	9.04	0.01	4
grass	545.23	549.23	9.72	0.00	2
urban × initdate	541.39	549.41	9.90	0.00	4
Null	548.12	550.13	10.61	0.00	1
wetland × initdate	542.10	550.13	10.61	0.00	4
initdate	546.93	550.94	11.42	0.00	2
forest	548.01	552.01	12.50	0.00	2
forest × initdate	544.11	552.14	12.62	0.00	4

FIGURES

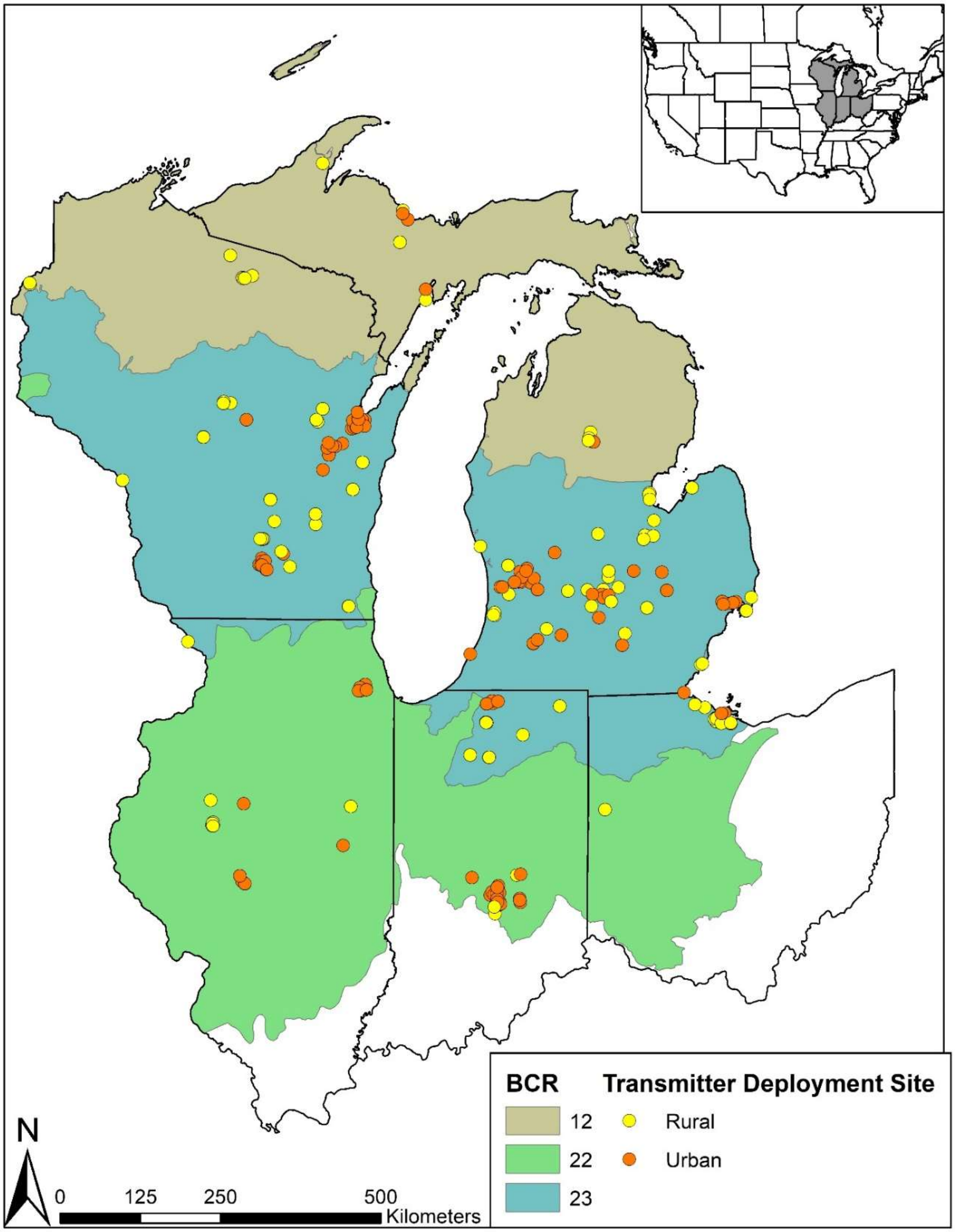

Figure 4.1. Capture and GPS-GSM transmitter deployment locations for female mallards captured in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023 in relation to banding site type (urban or rural) and Bird Conservation Regions (BCR) 12, 22, and 23.

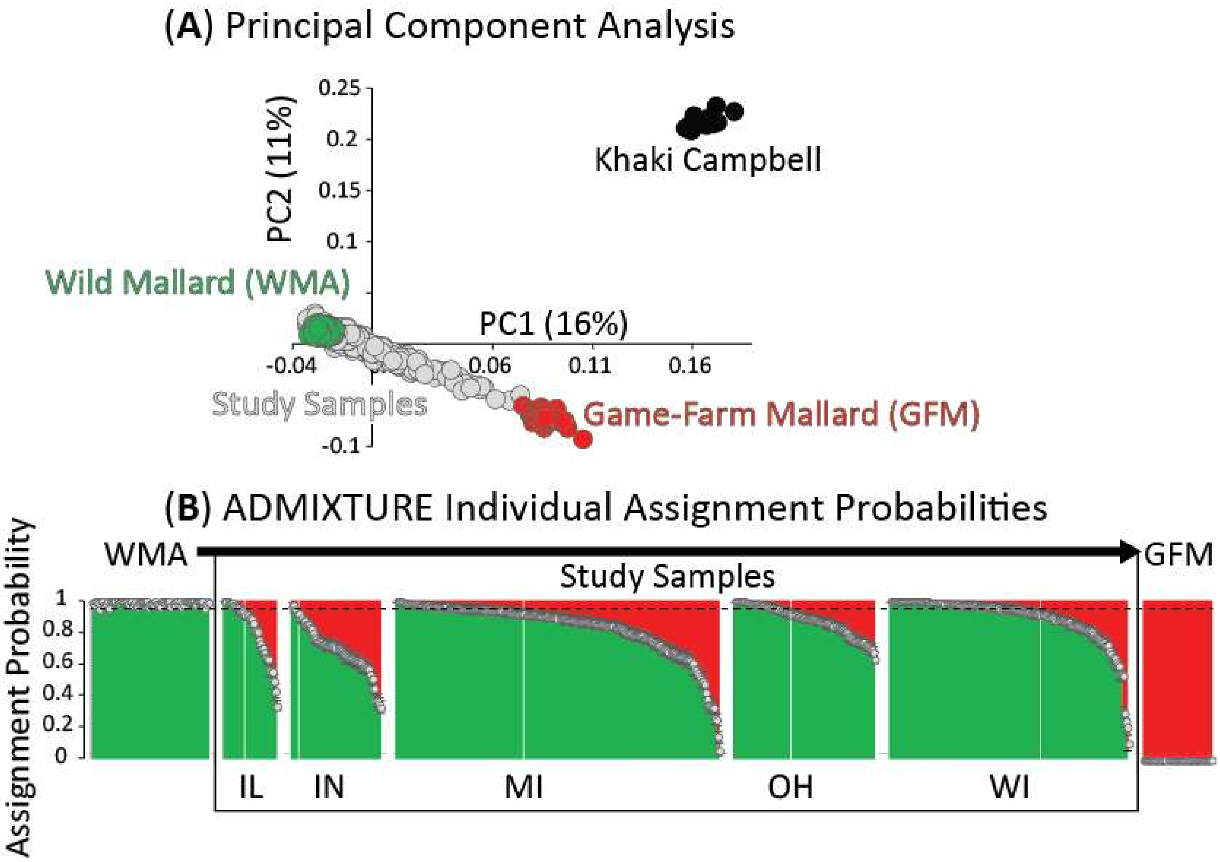

Figure 4.2. Principal component plot (A) of the first 2 principal components explaining variation in nuclear ddRAD sequencing results for reference wild (WMA; green circles), domestic game-farm mallard (GFM; red circles), and Khaki Campbell (black circles) samples and genetic samples collected from female mallards marked with GPS-GSM transmitters in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023 (Study Samples; grey circles). ADMIXTURE assignment probabilities (B) for individual Great Lakes mallard study samples by capture state, and wild and game-farm mallard reference samples.

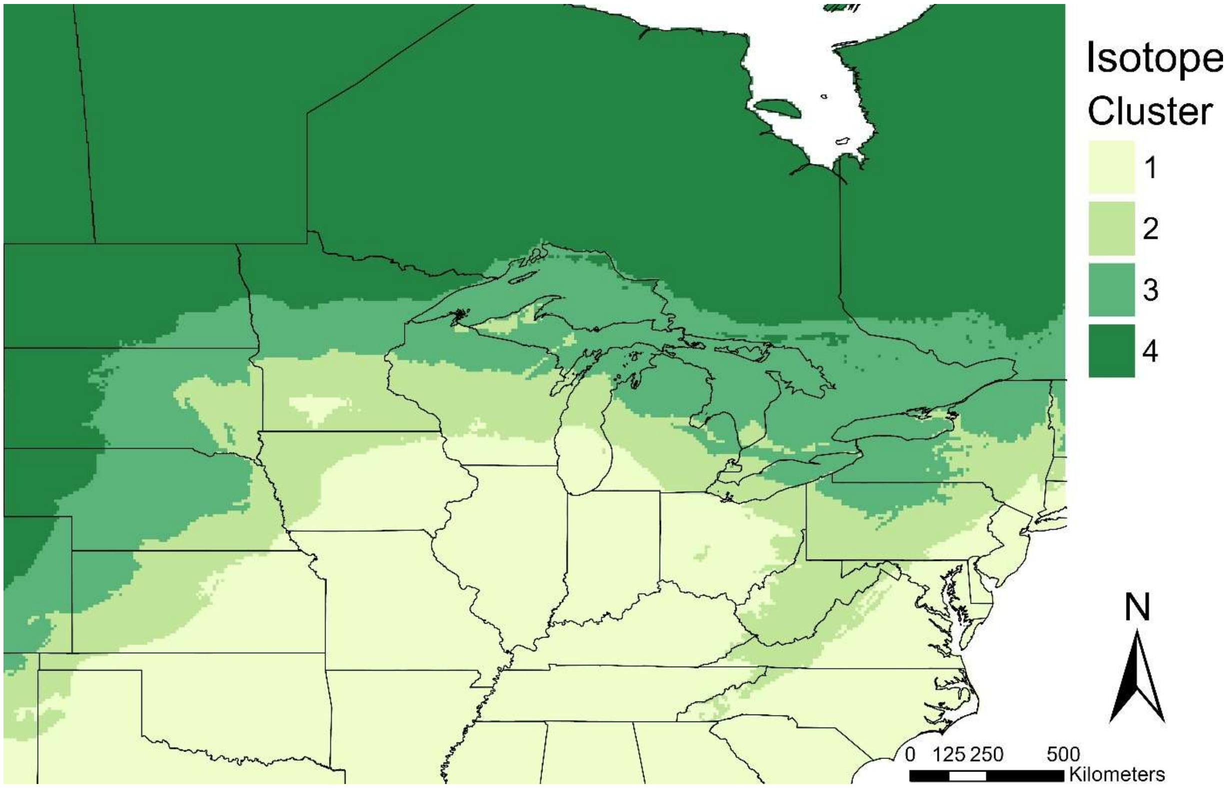

Figure 4.3. Summarized areas of origin (clusters) inferred from spatially explicit likelihood-based assignment of δ^2H analyzed in adult and juvenile hen mallard flight feathers. All sampled individuals were marked with GPS-GSM transmitters in the Great Lakes region from 2021–2023.

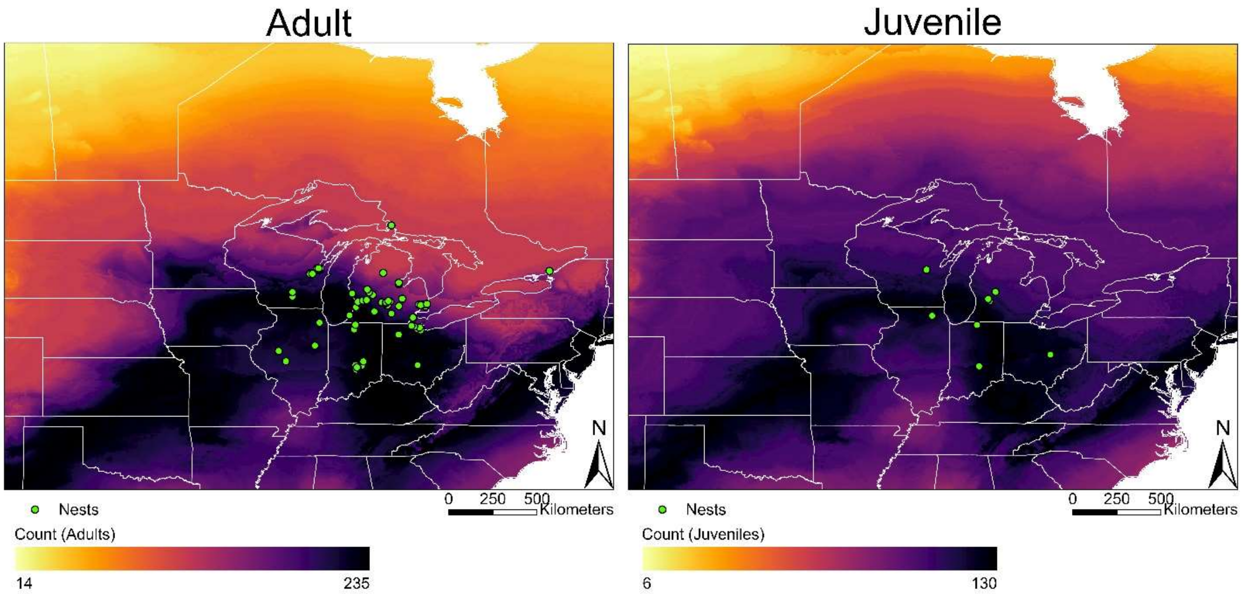

Figure 4.4. Estimated adult molting (left) and juvenile natal (right) origins (rasters) and nest locations (points) of female mallards marked with GPS-GSM transmitters in Michigan, Wisconsin, Illinois, Indiana, and Ohio, 2021–2023. Cell counts designate the number of individuals with likely origins from the cell assigned at 2:1 odds.

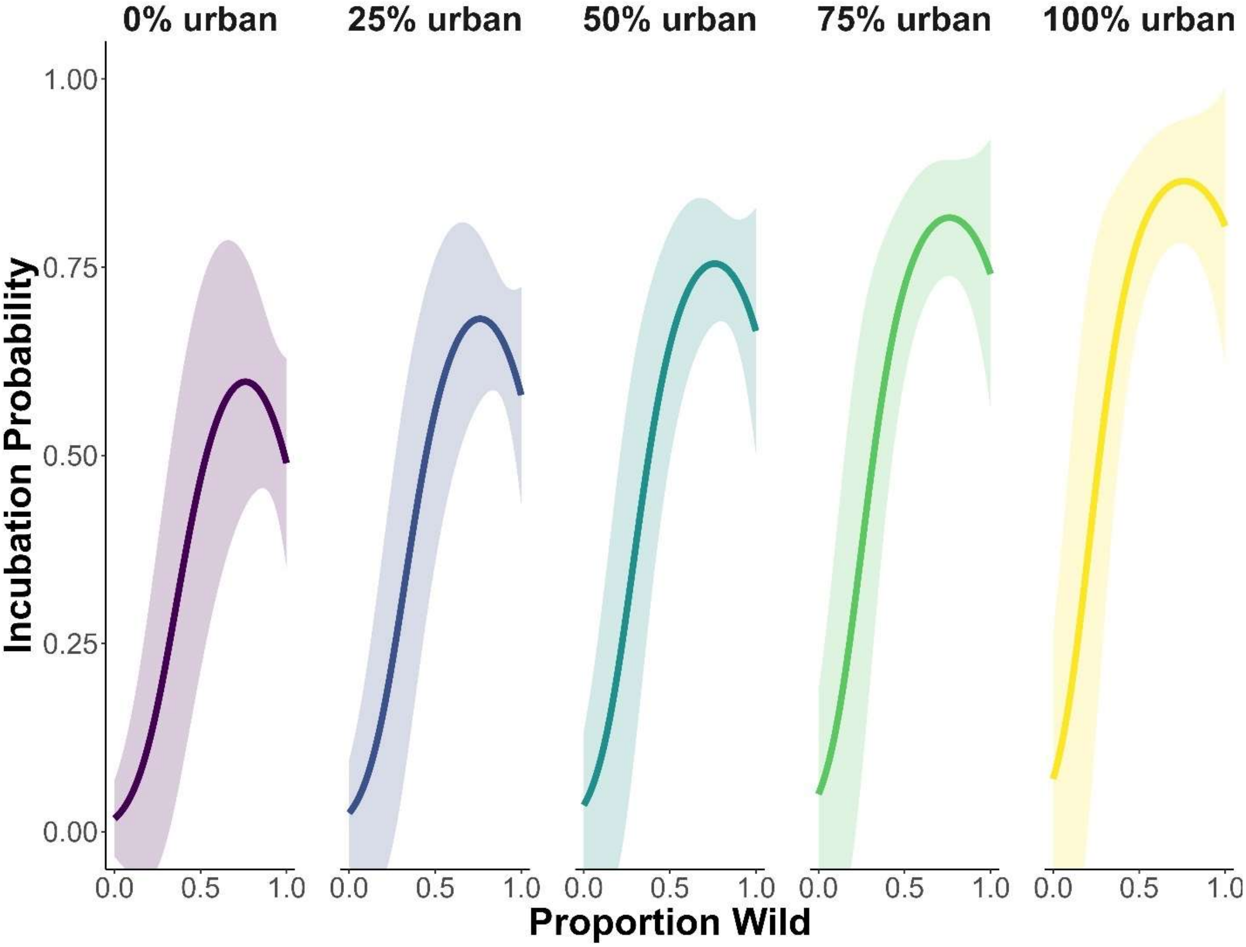

Figure 4.5. Predicted probability of initiating incubation (≥2 consecutive days incubating; lines) and 95% confidence intervals (shaded region) from the most-supported model predicting incubation probability for hen mallards marked with GPS-GSM transmitters in the Great Lakes region from 2021–2023. The model indicated incubation probability was a function of the interaction of a quadratic effect of proportion wild genome, the proportion of GPS locations in developed land cover (panels), and hen mallard age (adult or juvenile; predictions are averaged across ages).

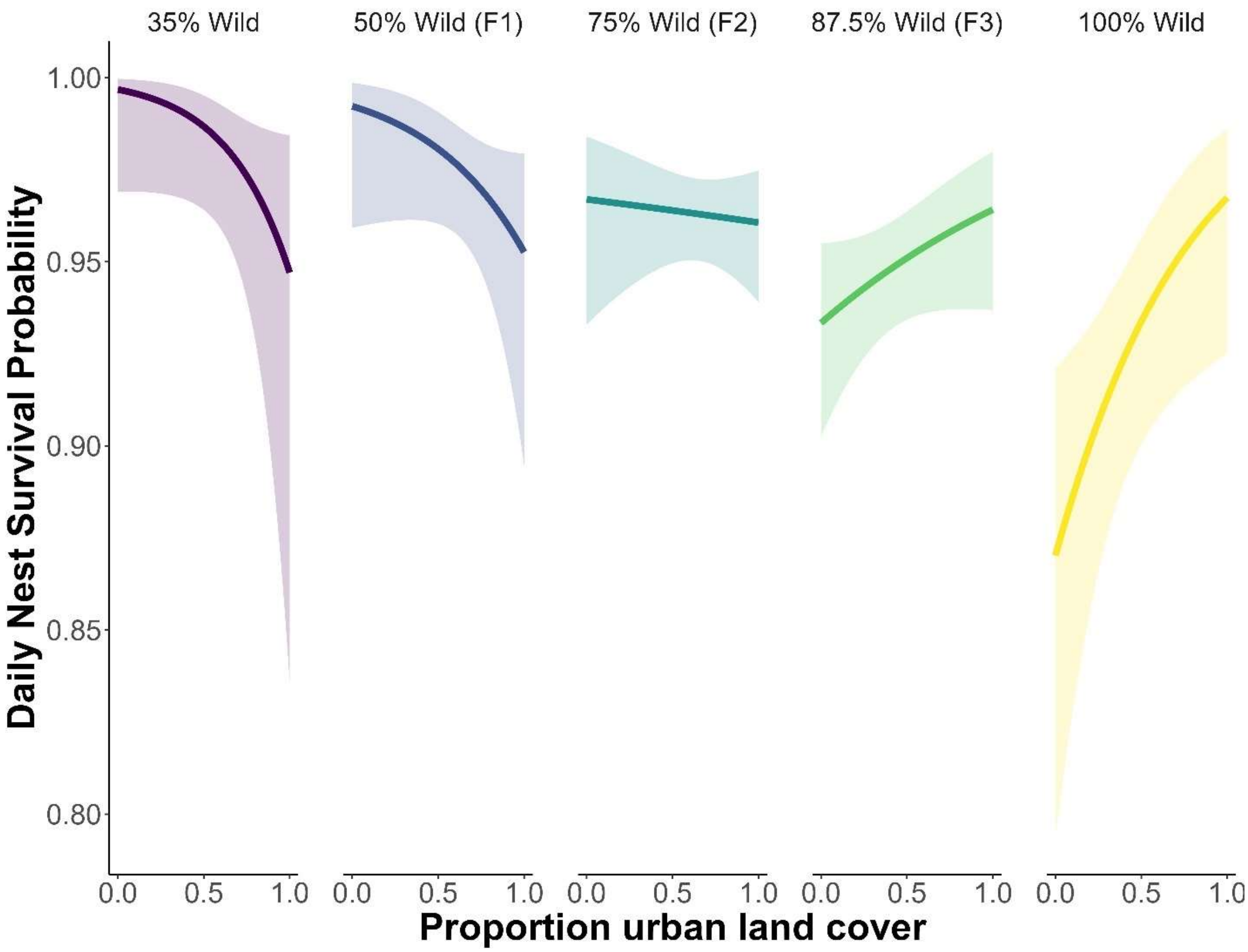

Figure 4.6. Predicted daily nest survival probability (lines) and 95% confidence intervals (shaded regions) in relation to proportion wild genome of individuals (panels) and proportion of a circular 10.4 km^2 area around the nest comprised of urban land cover for hen mallards marked with GPS-GSM transmitters in the Great Lakes region from 2021–2023. Nest sample sizes were 4, 20, 10, 15, and 31 for the feral (~35% wild), F1, F2, F3, and wild categories, respectively.

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APPENDIX B: GLOBAL POSITIONING SYSTEM AND ACCELEROMETER SUMMARY STATISTICS

Definitions and abbreviations:

- **Accelerometer (ACC):** device that measures acceleration in the x, y, and z dimensions in millivolts (Ornitela transmitters). ACC readings are collected at each GPS location and are denoted by ACCX, ACCY, and ACCZ for the x, y, and z dimension values, respectively.
- **Static acceleration (SA):** mean of ACC values in each dimension during each 24-hour period.
- **Dynamic acceleration (DA):** the absolute value of the difference between each ACC value and the static acceleration (SA) value.
- **Overall dynamic body acceleration (OBDA):** sum of all dynamic acceleration values for all 3 dimensions.
- **Net-squared displacement (NSD):** the squared Euclidean distance in kilometers between a given GPS location and the first GPS location in the trajectory.
- **NSD.day:** NSD with the first location in each 24-hour period used as the reference location.
- **NSD.total:** NSD with the first location from the first day of monitoring used as the reference location.

The following summary statistics were calculated using ACC values and latitude and longitude (in decimal degrees) recorded during each day (24-hour period), resulting in a single value of each statistic for each individual mallard in each 24-hour period, and were then used as input data to train a machine learning algorithm to predict mallard incubation status (incubation or no incubation) during each 24-hour period. The overall dynamic body acceleration statistic was derived from Schreven et al. 2021. Skewness and kurtosis were calculated using the R package moments (Komsta and Novomestky, 2022). Net-squared displacement was calculated using the R package amt (Signer et al. 2011).

Statistic	Calculation
Mean ACC	mean(ACCX) mean(ACCY) mean(ACCZ)
Standard Deviation ACC	sd(ACCX) sd(ACCY) sd(ACCZ)
Overall Dynamic Body Acceleration (ODBA)	DA(ACCX) + DA(ACCY) + DA(ACCZ)
Skewness ACC	skewness(ACCX) skewness(ACCY) skewness(ACCZ)
Kurtosis ACC	kurtosis(ACCX) kurtosis(ACCY) kurtosis(ACCZ)

Covariance ACC	cov(ACCX, ACCY) cov(ACCX, ACCZ) cov(ACCY, ACCZ)
Correlation ACC	cor(ACCX, ACCY) cor(ACCX, ACCZ) cor(ACCY, ACCZ)
Mean ACC Axis Difference	mean(ACCX - ACCY) mean(ACCX - ACCZ) mean(ACCY - ACCZ)
SD ACC Axis Difference	sd(ACCX - ACCY) sd(ACCX - ACCZ) sd(ACCY - ACCZ)
SD Latitude (Decimal Degrees)	sd(latitude)
SD Longitude (Decimal Degrees)	sd(longitude)
Mean Net-squared Displacement (NSD)	mean(NSD.day) mean(NSD.total)
Standard Deviation NSD	sd(NSD.day) sd(NSD.total)
Minimum NSD.total	min(NSD.total)
Maximum NSD	max(NSD.day) max(NSD.total)

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CHAPTER 5: POPULATION DYNAMICS OF GREAT LAKES MALLARDS

ABSTRACT

Abundance data collected during spring aerial surveys suggested breeding mallard (*Anas platyrhynchos)* populations in the Great Lakes region (Michigan, Minnesota, and Wisconsin, USA) declined by >30% between 2000–2022. Mallards are an important waterfowl species in this region, where an estimated 60-80% of the mallard harvest is comprised of locally produced birds. Extensive population monitoring datasets were available for mallards, presenting an opportunity to reduce uncertainty in addressing complex questions such as estimating productivity at large spatial and temporal scales, identifying the effects of harvest on demographic rates, quantifying mechanisms for harvest compensation, and integrating multiple datasets to quantify the demographic drivers of population change. Our objective was to simultaneously examine factors affecting demographic parameters and their relative contribution to Great Lakes mallard population dynamics. We used 32 years of banding, band recovery, and aerial survey data collected for mallards from Michigan and Wisconsin, USA to develop an integrated population model (IPM). We used age ratios at banding to estimate productivity, band recoveries from hunter-harvested birds to estimate survival and cause-specific mortality (i.e., harvest or natural), and modeled abundance using aerial survey and demographic parameter estimates from 1991–2022. IPM results suggested decline in Great Lakes mallard abundance was caused by increased natural (non-hunting) mortality and a decline in productivity since 2000. Productivity varied spatially but declined with loss of Conservation Reserve Program (CRP) area. Moreover, our productivity assessment provided evidence of density dependence in reproduction. Natural mortality was 3.5–6.7 times and 1.3–4.2 times greater than harvest mortality for adult and juvenile female mallards, respectively, suggesting environmental factors

during spring and summer, not harvest, drove annual mortality for female mallards. Our IPM reduced uncertainty in the factors affecting Great Lakes mallard population dynamics and suggested management actions that address natural mortality and productivity would be most effective in increasing Great Lakes mallard abundance.

INTRODUCTION

The first goal of the North American Waterfowl Management Plan is to maintain abundant and resilient waterfowl populations to support hunting and other uses (NAWMP 2018). Researchers and managers have long invested in waterfowl population monitoring and data analysis, with North American waterfowl being some of the most intensively monitored species in the world (Arnold et al. 2018). At a continental scale, annual waterfowl monitoring includes aerial surveys to estimate abundance (U. S. Fish and Wildlife Service 2023*b*), banding and systematic recording of band recoveries (Celis-Murillo et al. 2022), and waterfowl hunter surveys to estimate quantity and composition of annual harvest (Raftovich et al. 2022). This wealth of data allows scientists to explore challenging questions, such as predicting the effects of management actions on population dynamics (Cowardin and Johnson 1979), estimating productivity at large spatial and temporal scales (Specht and Arnold 2018), identifying the effects of harvest on demographic rates (Burnham and Anderson 1984, Rexstad 1992), quantifying mechanisms for harvest compensation (Riecke et al. 2022*b*), and integrating multiple datasets to quantify the demographic drivers of population change (Koons et al. 2017). Integrated population models (IPMs) are particularly well suited to applied population research when multiple datasets are available to estimate one or more population parameters.

The application of IPMs in waterfowl research has become more common (Arnold et al. 2018), providing a framework to jointly analyze ≥2 datasets that inform population size or structure (Besbeas et al. 2002, Schaub and Abadi 2011). Benefits from IPMs can include reduced parameter uncertainty, ability to estimate unmonitored parameters, accurate error propagation in population projection, and increased understanding of relationships between demographic parameters and abundance (Schaub and Abadi 2011, Arnold et al. 2018, Zipkin and Saunders 2018, Riecke et al. 2022*a*). Therefore, the ability to provide insight into complex questions is increasing for well monitored wildlife species such as the mallard (*Anas platyrhynchos*; Wiegers et al. 2022, Roberts et al. 2023).

In North America, mallards have been delineated into three populations for harvest management, which are defined by breeding geography and administrative flyway, including eastern, midcontinent, and western mallards (U. S. Fish and Wildlife Service 2023*a*). The midcontinent mallard population is the largest and comprises mallards nesting from the Northwest Territories in Canada to the Great Lakes region in the U. S. The Waterfowl Breeding Population and Habitat Survey (WBPHS) and Great Lakes state (Michigan, Minnesota, and Wisconsin) breeding waterfowl surveys are conducted annually to estimate breeding abundance of midcontinent mallards (U. S. Fish and Wildlife Service 2022). Great Lakes mallard abundance historically followed the same trend as the remainder of the midcontinent population (U. S. Fish and Wildlife Service 2023*b*). However, prairie-nesting mallard abundance increased following a decline in the early 2000s while Great Lakes mallard abundance continued to decline. Great Lakes mallard abundance peaked near 1.2 million in 2000 based on state aerial surveys and declined to around 0.5 million in 2023 (U. S. Fish and Wildlife Service 2023*a*). Regionally produced mallards are particularly important to hunters in the Great Lakes region as an estimated 58-83% of their mallard harvest is derived from mallards produced within the region (Arnold and De Sobrino 2010). Declining Great Lakes mallard abundance is thus a concern for wildlife management agencies involved in waterfowl harvest management as well as those implementing the North American Waterfowl Management Plan (Soulliere et al. 2017).

Although the causes of Great Lakes mallard population decline are unknown, several factors are of concern and interest to waterfowl managers, such as the relationship between harvest and abundance. During the early 1990s, duck hunting regulations were liberalized, reflecting increased duck abundance across North America. Season lengths increased in the Mississippi Flyway from 30 to 60 days, and in 2011, 2014, and 2020, the hen mallard daily harvest limit increased from one to two in Minnesota, Michigan, and Wisconsin, respectively. Some stakeholders voiced concern that liberalization of female mallard harvest was contributing to population decline in the Great Lakes region (B. Avers, Michigan Department of Natural Resources, personal communication), although some research suggests harvest is a relatively small component of total mortality in female midcontinent mallards (Riecke et al. 2022*b*) and harvest rates were not consider unsustainable for Great Lakes mallards (Singer 2014).

There have been substantial changes in landscapes used for nesting habitat by Great Lakes mallards and other grassland-nesting birds. Between 2001 and 2016, the area of developed land, classified as low, medium, and high intensity developed in the National Land Cover Database (NLCD; Yang et al. 2018), expanded by 338,000 ha and the area of cultivated cropland increased by 987,000 ha in the Upper Mississippi / Great Lakes Joint Venture (UMGLJV) region. In contrast, the area of land cover categorized as grassland/herbaceous and hay/pasture declined by 1.4 million ha (Soulliere et al. 2020). The loss of grassland is expected to reduce the quantity and quality of upland nesting habitat for mallards. Further, expansion and intensification of agriculture, including increasing use of systemic pesticides (i.e., neonicotinoid insecticides) potentially reduce availability of invertebrate food resources and reproductive capacity in mallards (Hopwood et al. 2013, Morrissey et al. 2015, Soulliere et al. 2020). Further, long-term, large-scale releases of game-farm mallards since the 1920s, annually estimated between >200,000 (U. S. Fish and Wildlife Service 2013) and >500,000 (Huesmann 1974), are hypothesized to be a contributing factor to mallard population declines in eastern North America (Lavretsky et al. 2020, 2023, Roberts et al. 2023). Intensive Great Lakes mallard monitoring through aerial population surveys and annual banding provide an opportunity to reduce uncertainty regarding complex and potentially confounding factors contributing to population decline.

We developed an integrated population model to identify how ecological and anthropogenic factors affect Great Lakes mallard abundance. Our objectives were to examine factors affecting demographic parameters and the relative contribution of demographic parameters to Great Lakes mallard population growth rate. We used abundance estimates derived from spring aerial surveys, estimated productivity from age ratios at banding (Specht and Arnold 2018), and estimated survival, harvest mortality, and natural mortality probabilities (Riecke et al. 2022*b*) for female mallards surveyed and banded in Michigan and Wisconsin from 1991–2022. We hypothesized that productivity and adult female survival would be the parameters most strongly linked to population growth rate, but expected productivity to be more annually variable than adult survival (Koons et al. 2014). We predicted harvest would be a small component of mortality relative to non-hunting mortality (Riecke et al. 2022*b*). The results of this study reduce uncertainty around the sources of Great Lakes mallard population decline and reinforce the value of integrated population modeling approaches in waterfowl management.

STUDY AREA

Aerial breeding waterfowl surveys and annual pre-season mallard banding in Michigan, Minnesota, and Wisconsin support monitoring of the Great Lakes component of the midcontinent mallard population (U. S. Fish and Wildlife Service 2023*b*) and contribute to Adaptive Harvest Management (AHM) models (U. S. Fish and Wildlife Service 2023*a*). However, 27% of Minnesota is within the Prairie Pothole Region (PPR; Bird Studies Canada and NABCI 2014), where land cover and mallard population dynamics differ from the Great Lakes region (Coluccy et al. 2008), and aerial surveys for breeding waterfowl cover only about 40% of the state (Cordts 2023). Further, a vital assumption of IPMs is that all data sources are derived from the same population (Schaub and Abadi 2011, Arnold et al. 2018). To achieve spatial congruence, we used data from mallards surveyed and banded in Michigan and Wisconsin only and assumed that population demography for this sample was representative of mallards nesting within Great Lakes states Bird Conservation Regions (BCRs) 12, 22, and 23. Therefore, we consider mallards nesting in Michigan and Wisconsin representative of the Great Lakes mallard component of the midcontinent mallard population.

Aerial surveys and mallard banding were conducted within the Michigan and Wisconsin study area and band recoveries occurred throughout North America (Figure 5.1). Michigan and Wisconsin are primarily comprised of BCRs 23 (Prairie Hardwood Transition) and 12 (Boreal Hardwood Transition; Bird Studies Canada and NABCI 2014). These BCRs are dominated by extensive upland and wetland forests and lakes in the north (BCR 12) that transition to a landscape of forests, lakes, and herbaceous wetlands mixed with human-modified land covers (agricultural and developed) in the south (BCR 23; Soulliere et al. 2017). Regional temperatures and precipitation are influenced by the Great Lakes and generally consist of cold, snowy winters and hot, humid summers (Scott and Huff 1996). Moderating lake effects result in wetland conditions that are generally more stable and less seasonally dynamic than in the midcontinent prairies and parklands (Euliss et al. 2004, Simpson et al. 2005). Mallards were the most abundant nesting duck in the Great Lakes region (U. S. Fish and Wildlife Service 2023*b*) and nesting densities were estimated to be greatest in BCR 23 (Soulliere et al. 2017). Michigan and Wisconsin are within the Mississippi Flyway, where mallards historically migrated to and wintered primarily in the Mississippi alluvial valley (Bellrose 1976).

METHODS

We developed an IPM to examine factors affecting annual survival and productivity and the influence of these demographic parameters on Great Lakes mallard population growth rate. Additionally, we estimated annual harvest mortality and natural (non-hunting) mortality probabilities to determine the relative contribution of cause–specific mortality to annual survival (Riecke et al. 2022*b*). Annual productivity indices were derived from female age ratios at banding (Specht and Arnold 2018). Great Lakes mallard abundance was estimated as a function of annual survival and productivity and informed by aerial survey abundance estimates. We assumed that emigration and immigration were negligible at the spatial scale of this analysis (Chapter 4).

Banding, Recovery, Population and Habitat Survey Data

During April and May, stratified random transects were flown with fixed wing aircraft in Michigan and Wisconsin and trained observers recorded waterfowl and wetland counts according to the North American Waterfowl Breeding Population and Habitat Survey (WBPHS) protocol (U.S. Fish and Wildlife Service 1987). Visibility correction factors (VCFs) were employed in each survey to account for imperfect detection from the fixed wing aircraft using a modified ground count method in Wisconsin (March et al. 1973) and via helicopter surveys in Michigan (Soulliere and Chadwick 2003). These surveys provide estimates of total abundance of waterfowl species (Smith 1995), and total wetlands on a statewide scale. We modeled true wetland (pond) abundance ($\mathrm{P_t}$) in year *t* in a state-space framework where the sum of observed wetland counts in Michigan and Wisconsin ($\mathrm{v_t}$) was normally distributed with observation variance ($\sigma^2_{\mathrm{P,\,obs}}$) and true wetland abundance in the next year was a function of current wetland abundance and process variance (σ^2_{P}):

$$\mathrm{v_t} \sim \mathrm{Normal}(\mathrm{P_t},\ \sigma^2_{\mathrm{P,obs}})$$

$$\mathrm{P_{t+1}} \sim \mathrm{Normal}(\mathrm{P_t},\ \sigma^2_{\mathrm{P}})$$

$$\sigma_{\mathrm{P}} \sim \mathrm{Uniform}(0,\ 5)$$

$$\sigma_{\mathrm{P,\,obs}} \sim \mathrm{Uniform}(0,\ 10)$$

We obtained banding and recovery data for mallards marked in Michigan and Wisconsin during 1991–2022 from the United States Geological Survey (USGS) Bird Banding Laboratory (BBL) Gamebirds database (Celis-Murillo et al. 2022).

Mallards were captured from 1 July to 30 September using baited traps, rocket nets, night-lighting, and by hand. Birds were aged and sexed using plumage characteristics (Carney 1992) and banded with a size 7 USGS aluminum leg band. We included female mallards released in the same 10-minute block (standard spatial areas used by USGS BBL that are 10 minutes of latitude by 10 minutes of longitude) as captured (BBL status code = 003) and marked with standard aluminum or control bands (i.e., standard bands paired with reward bands in studies to estimate band reporting probability) in analyses. We retained only hunter-harvested band recoveries (BBL how obtained code = 01) to enable estimation of cause specific mortality hazard rates (Riecke et al. 2022*b*). Mallard capture and banding was permitted by the USGS BBL and this study followed ethical guidelines provided by the Michigan State University institutional animal care and use committee (IACUC) permit PROTO202100046.

Survival and Mortality Models

We first modeled time-specific harvest ($h_{\kappa,t}$) and natural ($h_{\eta,t}$) mortality hazard rates for each age class (a; adult=AHY [after hatching year], juvenile=HY [hatching year]). Hazard rates are the instantaneous intensity of lethal events that individuals are exposed to in continuous time and are measured on a ratio scale. Hazard rates are particularly useful when modeling competing sources of mortality (e.g., harvest vs natural) and when modeling the effects of covariates on mortality (Ergon et al. 2018). We partitioned mortality sources by assuming the majority of hen mallard natural mortality occurred outside of the hunting season, primarily during the nesting and brood rearing periods (Hoekman et al. 2002, Arnold et al. 2012). Any mortality occurring during the hunting season would be attributed to harvest, thus estimates of natural mortality are conservative in this analysis framework. We expected that natural mortality hazard rate would be affected by annual wetland abundance (Devries et al. 2003) and mallard abundance (N_t; Riecke et al. 2022*b*), where η_a subscripts denoted β parameter estimates correspond to natural mortality hazard rate and are age (a) specific, and ε_{η_a} represented random error:

$$\log\left(h_{\eta,t_a}\right) = \beta_{\eta_a 1} + \beta_{\eta_a 2} \times P_t + \beta_{\eta_a 3} \times N_t + \varepsilon_{\eta_a}$$

We were also interested in determining the effects of the total number of duck hunters in Michigan and Wisconsin (H_t), an index of harvest regulations (R_t), and mallard abundance on hen mallard harvest mortality hazard rate, where κ_a subscripts denoted age-specific β parameter estimates for harvest mortality hazard rate, and ε_{κ_a} represented random error:

$$\log\left(h_{\kappa,t_a}\right) = \beta_{\kappa_a 1} + \beta_{\kappa_a 2} \times H_t + \beta_{\kappa_a 3} \times N_t + \beta_{\kappa_a 4} \times R_t + \varepsilon_{\kappa_a}$$

We retrieved annual estimates of duck hunter abundance provided by the Harvest Information Program (HIP) in Michigan and Wisconsin (Raftovich et al. 2022). To characterize female mallard harvest regulations, we developed a harvest regulation index as the duck hunting season length in days multiplied by the hen mallard daily harvest limit in each state (Luukkonen et al. 2021), then summed the values for Michigan and Wisconsin. Thus, higher values of the harvest regulation index indicated more liberal hen mallard harvest regulations (longer seasons and higher daily limits). We z-standardized all mortality hazard rate covariates. We used the following priors for regression parameters in the natural and harvest mortality hazard rate models so likely β parameter means were between -6.2 and 6.2 on the log scale (Lemoine 2019):

$$\beta \sim \mathrm{Normal}(0,\ 100)$$

$$\sigma_{\beta} \sim \mathrm{Uniform}(0,\ 2)$$

$$\varepsilon \sim \mathrm{Normal}(0,\ \sigma_{\varepsilon})$$

$$\sigma_{\varepsilon} \sim \mathrm{Uniform}(0,\ 2)$$

We then estimated annual survival probability (S; the probability that an individual alive at banding in year *i* is alive at banding in year *i+1*) for each age class (a) using the Brownie dead recovery parameterization, with banding and recovery data in an m-array format with cell probabilities a function of survival and recovery probabilities (Brownie et al. 1978). First, we converted harvest mortality hazard rate to annual harvest mortality probability (κ_{t_a}; the probability an individual alive in year *t* is shot and killed by a hunter during the duck hunting season in year *t*):

$$\kappa_{t_a} = 1 - e^{-h_{\kappa,t_a}}$$

We calculated natural mortality probability (η_{t_a}) conditional on surviving harvest (Riecke et al. 2022*b*):

$$\eta_{t_a} = \left(1 - \kappa_{t_a}\right) \times \left(1 - e^{h_{\eta,t_a}}\right)$$

We estimated annual band recovery probability (f_{t_a}), or Brownie dead recovery probability (Brownie et al. 1978), as the probability a banded individual alive in year *t* is shot, retrieved $(1 - c)$, and the band is reported (ρ_t) to the BBL:

$$f_{t_a} = \kappa_{t_a}(1 - c)\rho_t$$

We assumed a time-constant wounding loss for unretrieved hunter-shot birds of $c = 0.2$ (Anderson and Burnham 1976, Ellis et al. 2022, U. S. Fish and Wildlife Service 2023*a*), used estimates of mallard band reporting probability (ρ) from 1991-2016 from Arnold et al. (2020), and used $\rho_{2017} = 0.833$ (SD $= 0.03$), $\rho_{2018} = 0.84\ (0.03)$, $\rho_{2019} = 0.849\ (0.03)$, $\rho_{2020} = 0.898\ (0.03)$, $\rho_{2021} = 0.906\ (0.03)$, and $\rho_{2022} = 0.906\ (0.03)$ from a recent reward band analysis (P. Garrettson and S. Boomer, USFWS, unpublished). Finally, we used natural and harvest mortality hazard rates to calculate annual survival probability:

$$S_{t_a} = e^{-(h_{\kappa,t_a} + h_{\eta,t_a})}$$

Productivity Model

We defined mallard productivity (γ_t) as the ratio of juvenile females to adult females captured and banded (Specht and Arnold 2018, Riecke et al. 2022*b*) during pre-season banding (1 July – 30 September). However, we modeled the proportion of juvenile females captured and banded (J) because this parameterization was bounded between 0 and 1 and allowed J at a given banding site to be modeled as a binomial random variable weighted by the total number of mallards banded annually at a given site, thus accounting for spatial and temporal variation in banding effort (Specht and Arnold 2018).

$$J = \frac{\text{Juvenile Females}}{\text{Juvenile Females} + \text{Adult Females}}$$

J can be converted to the traditional productivity estimate of juvenile females per adult female (γ):

$$\gamma = \frac{J}{1 - J}$$

If capture probability is equal for juvenile and adult females, we obtain a direct estimate of productivity. If capture probability varies by age, for example if juveniles were more susceptible to capture, γ is an unbiased index of fecundity as long as capture probability varies randomly across years and sites, and independently of covariates (Specht and Arnold 2018). We assumed γ was an unbiased index of productivity and thus accounted for spatial and temporal variation in captures using fixed and random effects. We modeled J with a mixed-effects logistic regression model.

We predicted that z-standardized annual mallard and wetland abundance could influence productivity and considered two banding site level (b) covariates. We included z-standardized banding site latitude (L_b) to account for potential latitudinal variation in productivity. Michigan and Wisconsin account for the northern 30% of the UMRGL JV region, where periodic landscape change and bird habitat assessments have been completed. A recent JV evaluation documented loss of an estimated 1.4 million ha of grassland and hay/pasture between 2001-2016 (Soulliere et al. 2020). In order to annualize change in potential production habitat, we included the z-standardized area (G_t) in Michigan and Wisconsin enrolled in the United States Department of Agriculture's (USDA) Conservation Reserve Program (CRP) as an index of regional grassland abundance (Reynolds et al. 2001) to assess if productivity was related to loss of grassland nesting habitat (U. S. Department of Agriculture 2024). We hypothesized that mallards using urban areas would have lower productivity (Chapter 4). Thus, we used the proportion of developed land cover (U_b), classified as developed open space, or low, medium, and high intensity developed in the 2021 NLCD database (Dewitz 2023) in a 7 km radius (GPS-marked mallard daily movement distance; Chapter 2) of each banding site as a site covariate:

$$\mathrm{logit}(J_{t,b}) = \beta_{\gamma 1} + \beta_{\gamma 2} \times U_b + \beta_{\gamma 3} \times L_b + \beta_{\gamma 4} \times N_t + \beta_{\gamma 5} \times P_t + \beta_{\gamma 6} \times G_t + \varepsilon_{t,b}$$

All productivity coefficients were modeled as normal random variables with priors of $\mu = 0$ and $\sigma = 2$, resulting in likely β parameter means between -3.9 and 3.9 on the logit scale. Priors on coefficient standard deviations were uniform from 0 to 5. The residual random effect of banding site and year ($\varepsilon_{t,b}$) was considered normal:

$$\varepsilon_{t,b} \sim \mathrm{Normal}(0, \sigma_b^2)$$

$$\sigma_{t,b} \sim \mathrm{Uniform}(0, 5)$$

Use of age ratios to estimate fecundity assumes that banding captures do not target specific age mallards. While we were unaware of any age specific banding operations, we excluded any combination of banding site and year where only adults or only juvenile female mallards were banded (Specht and Arnold 2018), which totaled 163 site-year combinations, or 1.3% of banded female mallards.

Abundance Model

We modeled an index of annual mallard abundance in Michigan and Wisconsin where the mallard abundance index in the next year equals the number of adult (after hatching year; AHY) hens alive in the current year that survive to the next year, plus the number of juvenile (hatching year; HY) hens that are produced and survive to the next year:

$$N_{t+1} = N_t(1 - \kappa_{AHY_t} - \eta_{AHY_t}) + (N_t \times \gamma_t)(1 - \kappa_{HY_t} - \eta_{HY_t})$$

We considered the sum of estimated mallard abundance in Michigan and Wisconsin from spring breeding aerial surveys (y_t) to be normally distributed around a mean of true mallard abundance with observation variance ($\sigma^2_{y,\,obs}$):

$$y_t \sim \mathrm{Normal}(N_t,\ \sigma^2_{y,\,obs})$$

$$\sigma_{y,\,obs} \sim \mathrm{Uniform}(0,\ 2)$$

We did not separately estimate abundance by sex or the proportion of the female population comprised of adult and of juvenile hen mallards. We expected females in their second or subsequent nesting season to have higher productivity (Coluccy et al. 2008, Devries et al. 2008*b*), although productivity estimates using the ratio of juvenile to adult females provide an aggregate index of productivity across all hen ages. Further, aerial survey observations do not distinguish between juvenile and adult hens. Therefore, our population model provided annual indices of total abundance of adult and juvenile hens combined. Aerial survey abundance estimates included male mallards (paired and unpaired; Smith 1995), but we assumed males outnumbered females (Alisauskas et al. 2014) and were non-limiting, and that population abundance estimates provided an index of total female mallard abundance (Riecke et al. 2022*b*, *a*). Finally, we estimated annual population growth rate (λ_t) as a derived parameter:

$$\lambda_t = \frac{N_{t+1}}{N_t}$$

Model Implementation

All models were fit using Bayesian Markov chain Monte Carlo (MCMC) in JAGS (Plummer 2003) through program R (R Core Team 2022) using package jagsUI (Kellner 2016). We sampled three chains for 500,000 iterations, including 250,000 burn-in iterations and retained every 25th iteration. We checked that all posterior distributions had $\widehat{R} < 1.01$ (Brooks and Gelman 1998) and inspected trace plots to assess convergence. We report medians of posterior distributions and 95% credible intervals unless otherwise indicated, and υ, the proportion of the posterior distribution on the same side of zero as the mean as an estimate of the probability a coefficient is greater than or less than zero.

RESULTS

There were 30,148 adult and 70,128 juvenile female mallards banded during the pre-season period in Michigan and Wisconsin from 1991–2022. The mean number of female mallards banded per year was 942 and 2,192 for adults and juveniles, respectively. Hen mallards were captured at 316 sites throughout the study area. Hunters harvested, recovered, and reported 3,752 adult and 12,167 juvenile female mallards with bands (Figure 5.1).

The area in Michigan and Wisconsin enrolled in CRP during 1991–2022 peaked in the 1990s and declined after the early 2000s (Figure 5.2). Pond counts during 1991–2022 spring breeding waterfowl surveys were variable but increased beginning around 2015 (Figure 5.2). The number of duck hunters during this period increased to a peak in the early 2000s then declined to lows comparable to the early 1990s (Figure 5.2). Duck hunting season lengths increased from 30 days in 1991 to the first 60-day season in both Michigan and Wisconsin in 1997, and remained 60 days through the rest of the study period. The hen mallard daily limit increased from one to two hens in Michigan in 2014 and in Wisconsin in 2020, representing a general liberalization of regulations from 1991–2022 (Figure 5.2). Spring mallard abundance estimates from aerial surveys were positively correlated with CRP area ($r = 0.758$) and hunter abundance ($r = 0.521$), and negatively correlated with pond abundance ($r = -0.315$) and the harvest regulation index ($r = -0.615$). Midcontinent mallard AHM provides more liberal hunting season frameworks when abundance is high (U. S. Fish and Wildlife Service 2023*a*), resulting in difficulty in determining the effects of harvest on abundance (Riecke et al. 2022*b*). The opposite trend has generally been true for Great Lakes mallards, where harvest regulations remained constant or became more liberal as the population declined.

Survival and Mortality

Adult hen mallard survival probability estimates steadily declined from 0.56 (0.52, 0.61) to 0.47 (0.41, 0.53) during 1991–2022, while juvenile hen mallard survival declined and then slightly increased during the study (Figure 5.3). Overall, juvenile female survival declined from 0.52 (0.45, 0.59) to 0.45 (0.36, 0.54) during the study. Adult hen mallard harvest mortality probability estimates remained relatively constant (range: 0.09–0.13), while natural mortality probability steadily increased from 0.32 (0.27, 0.36) to 0.43 (0.37, 0.50). Juvenile hen mallard harvest (range: 0.15–0.27) and natural mortality (range: 0.24–0.44) increased initially, but harvest mortality declined beginning in 2010 while natural mortality continued to increase (Figure 5.4).

Adult female natural mortality was inversely related to mallard abundance ($\beta_{\eta,\mathrm{AHY},2} = -0.08\ [-0.13, -0.03]$) and directly to pond abundance ($\beta_{\eta,\mathrm{AHY},3} = 0.04\ [-0.02, 0.10]$). Juvenile female natural mortality was inversely related to mallard abundance ($\beta_{\eta,\mathrm{HY},2} = -0.16\ [-0.26, -0.06]$) and was relatively unrelated to pond abundance ($\beta_{\eta,\mathrm{HY},3} = -0.07\ [-0.07, 0.03]$). Adult female harvest mortality was not clearly related to hunter abundance ($\beta_{\kappa,\mathrm{AHY},2} = 0.01\ [-0.05, 0.08]$), mallard abundance ($\beta_{\kappa,\mathrm{AHY},3} = -0.02\ [-0.09, 0.06]$), or duck hunting regulations ($\beta_{\kappa,\mathrm{AHY},4} = -0.05\ [-0.12, 0.03]$). Juvenile female harvest mortality was most strongly related to hunter abundance ($\beta_{\kappa,\mathrm{HY},2} = 0.13\ [0.05, 0.21]$), negatively related to mallard abundance ($\beta_{\kappa,\mathrm{HY},3} = -0.06\ [-0.15, 0.04]$), and was unrelated to harvest regulations ($\beta_{\kappa,\mathrm{HY},4} = -0.05\ [-0.12, 0.03]$; Table 5.1). Changes in the number of duck hunters and increases in duck hunting season lengths and hen mallard daily harvest limits did not result in changes to adult female harvest mortality. The increase in duck hunters corresponded to an increase in juvenile female harvest mortality, although harvest mortality then declined with hunter numbers and did not substantially change with the increase from a one to two hen mallard daily limit in Michigan and Wisconsin (Figure 5.5). Natural mortality probabilities were on average 4.4 (range: 3.5–6.6) times greater and 2.6 (range: 1.3–4.2) times greater than harvest mortality probabilities for adult and juvenile female mallards, respectively. Further, the ratio of natural to harvest mortality increased over time (Figure 5.6), suggesting natural mortality became an increasingly larger component of total annual mortality.

Productivity

Productivity estimates varied with temporal and spatial factors during the study (Table 5.1, Figure 5.7). Annual productivity indices increased from 1991 into the early 2000s, then generally declined (Figure 5.8). Productivity increased with latitude ($\beta_{\gamma,3} = 0.25\ [0.15, 0.35]$) and was higher in years when more area was enrolled in CRP ($\beta_{\gamma,6} = 0.25\ [-0.31, 0.70]$), though most CRP enrolment was likely in the southern portion of the study area where cultivated cropland is a dominate landcover (U. S. Department of Agriculture 2024). Productivity declined with an increasing proportion of developed land cover within a 7 km radius of banding sites ($\beta_{\gamma,2} = -1.02\ [-1.50, -0.55]$), increasing mallard abundance ($\beta_{\gamma,4} = -0.14\ [-0.26, -0.02]$), and increasing pond abundance ($\beta_{\gamma,5} = -0.38\ [-0.69, -0.31]$). Thus, for the average annual mallard abundance, pond abundance and CRP area, per capita productivity was estimated to be lowest at developed sites in the southern Great Lakes region (Figure 5.9).

Abundance

Model indices of mallard abundance tracked estimates from spring breeding aerial surveys and showed a consistent decline in abundance since the early 2000s (Figure 5.10). Abundance generally increased from 1991 to 2000 due to increased productivity, despite declines in adult and juvenile survival during that time. Population declines since 2000 occurred with declines in survival and productivity. Population growth rate was positively correlated with adult and juvenile female survival probability and productivity, and negatively correlated with adult and juvenile natural and harvest mortality probability (Figure 5.11). Population growth rate was more strongly correlated with adult natural mortality (r = -0.45) and juvenile natural mortality (r = -0.44) than with adult harvest mortality (r = -0.14) or juvenile harvest mortality (r = -0.27). Further, population growth rate had higher correlation with adult survival (r = 0.51) and juvenile survival (r = 0.53) than with productivity (r = 0.12).

DISCUSSION

We analyzed 32 years of banding, band recovery, and population abundance data to identify factors affecting natural mortality, harvest mortality, and productivity, and the subsequent influence of these parameters on Great Lakes mallard population dynamics. Great Lakes mallard population growth from 1991 to 2000 was driven by a three-fold increase in productivity and relatively high adult and juvenile female survival. Mallard abundance in Michigan and Wisconsin peaked near 750,000 in the year 2000. Both declining productivity and adult and juvenile survival contributed to a steady decrease in abundance from 2000 to 2022. Cause-specific mortality probability estimates revealed that declines in survival were primarily driven by increases in natural (non-hunting) mortality. Further, adult and juvenile natural mortality probabilities were the parameters most highly correlated with population growth rate. Given our modeling assumption that natural mortality is conditional on surviving harvest, and that natural mortality primarily occurs outside of the duck hunting season for female mallards, processes acting in the spring and summer portion of the annual cycle have most affected population size. This corresponds to previous work suggesting duckling production and mortality during the breeding period drive upland-nesting dabbling duck population dynamics (Cowardin and Johnson 1979, Hoekman et al. 2002, Arnold et al. 2012, Riecke et al. 2022*a*, *b*, Roberts et al.

2023). Decreasing natural mortality and or increasing productivity would positively influence Great Lakes mallard abundance.

Natural mortality of adult and juvenile hen mallards was negatively related to mallard abundance, suggesting that as abundance increases, the risk of natural mortality declines. Under density dependence in natural mortality, we expect natural mortality risk to increase with increasing population size, a relationship observed for adult but not for juvenile midcontinent mallards (Riecke et al. 2022*b*). Increasing pond abundance was related to increased natural mortality for adult females, but to decreased natural mortality for juvenile females. Adult females make a larger investment in reproduction than juvenile females through higher probability of nesting (Devries et al. 2008*a*) and re-nesting (Arnold et al. 2010). If adult females increased reproductive effort when wetlands were more abundant, the tradeoff between exposure to mortality during incubation in terrestrial environments and nesting effort (Arnold et al. 2012) may explain increased adult natural mortality in years with wetter conditions. Alternately, the "pond count" parameter was simply a weak reflection of breeding habitat abundance in the Great Lakes region. Compared to the PPR, where the pond count typically reflects natural wetland basins (potholes) suitable for duck reproduction, surveys completed in the far more heterogenous Great Lakes states included a variety of wet areas recorded as "ponds" but likely unsuitable for mallard production (G. J. Soulliere, U.S. Fish and Wildlife Service, personal communication), reducing the value of these data as a habitat indicator.

Female Great Lakes mallard breeding period survival was negatively related to the amount of forest cover in home ranges, with predation considered the leading cause of mortality (Boyer et al. 2018). Forest cover in proximity to nesting and brood rearing habitats likely supports a greater abundance and/or diversity of predator species, especially perching avian predators (e.g., red-tailed hawks [*Buteo jamaicensis*] and great horned owls [*Bubo virginianus*]) which prey on mallards (Devries et al. 2003). However, the proportion of forest cover in the Great Lakes region has remained relatively constant (Oswalt et al. 2019, Soulliere et al. 2020). The expansion of agriculture and loss of grassland (Soulliere et al. 2020) could have direct and indirect (Murphy 2003, Stanton et al. 2018) effects on non-hunting mortality through reduction in the quantity and quality of nesting habitat, leading to increased predation risk, or to reduction in invertebrate prey (Nebel et al. 2010, Hallmann et al. 2014) required to meet energetic demands of reproduction (Alisauskas and Ankney 1992). Further, raptor and mammalian meso-predator abundances have likely remained stable or increased since the early 1990s (Gehrt et al. 2006, Crimmins et al. 2016, Rosenberg et al. 2019, Bauder et al. 2020), suggesting another potential mechanism for increased natural mortality. Hybridization of wild with domestic game-farm mallards (Lavretsky et al. 2020) could additionally be a factor contributing to increased natural mortality (Schladweiler and Tester 1972) as domestic mallards suffered high predation rates and had low survival (Smith 1999, Osborne et al. 2010, Söderquist et al. 2013) in free-ranging environments. Recent work demonstrating a large component of the Great Lakes mallard population is comprised of wild x game-farm mallard hybrids (Chapter 2) warrants further investigation in the demographic consequences of hybridization. The interaction between nesting and brood-rearing habitat quantity and quality, predation pressure, and anthropogenic factors such as agricultural intensification and urban development is likely complex and additional work is needed to understand mechanisms for increased natural mortality.

Adult female harvest mortality was remarkably constant from 1991–2022 despite changes in the number of duck hunters and liberalization of harvest regulations. There was limited evidence of a negative relationship of adult and juvenile female harvest mortality with spring mallard abundance, suggesting that harvest risk declines when the population is larger, a trend also detected in wood ducks banded in the UMGLJV (Greenawalt 2023). Juvenile hen mallard harvest mortality increased with the number of duck hunters, but was not tied to harvest regulations. Harvest was a small component of total annual mortality for adult and juvenile hens, consistent with findings that dabbling duck population growth rates are primarily influenced by environmental factors rather than harvest (Sedinger et al. 2019, Riecke et al. 2022*b*, *a*). While harvest regulations were not closely tied to Great Lakes hen mallard survival, determining the effects of the number of hunters, regulations, and ultimately harvest on population dynamics requires accounting for potentially confounding effects of environmental factors and population density (Riecke et al. 2022*a*). Although Great Lakes mallard abundance has declined since harvest regulations were liberalized, harvest mortality is a fraction of natural mortality and declines in survival were primarily related to increasing non-hunting mortality. Further, harvest is likely partially compensated by natural mortality, as adult females were approximately 3.5 to 6.5 times more likely to die from non-hunting causes than from harvest. Therefore, restricting harvest regulations, especially given recently declining waterfowl hunter abundance, is unlikely to increase female survival or Great Lakes mallard abundance. However, the proportion of the adult component of the midcontinent mallard population comprised of male mallards has increased since 1961, with recent estimates suggesting 3–4 adult males for every 1 adult female (Alisauskas et al. 2014). Excess adult male mallards could incur increased costs on female mallards through their use of food resources or energetic costs from pursuit flights during the breeding period; the effect of a changing sex ratio on demographic parameters remains uncertain. Liberalizing male mallard harvest regulations could reduce this uncertainty and improve learning capacity of adaptive harvest management models that are currently employed for midcontinent mallards (Koons et al. 2022).

The survival and mortality models rely on the assumptions that natural mortality occurs outside of the hunting season, band reporting probability estimates are unbiased, banded female mallards have the same probability of being reported as male mallards, and that wounding loss remained constant at 20% during the study. Although unavailable for this study, post-season or winter banding can provide additional data required to fit seasonal survival models. Joint analysis of pre- and post-season banding allows estimation of seasonal survival (e.g., hunting season vs non-hunting season) without the assumption that non-hunting mortality occurs only outside of the hunting season. Seasonal survival models present an opportunity to further learn about mortality processes occurring throughout the annual cycle and their contribution to population dynamics (Roberts et al. 2023).

Productivity varied substantially during the study in relation to environmental and anthropogenic factors. Temporal productivity trends identified in this study were similar to trend and magnitude of mallard age ratios in the prairie potholes and prairie parklands (Specht and Arnold 2018) and to long-term average Great Lakes mallard productivity derived from Lincoln estimates (Singer et al. 2016). Productivity indices were lowest in southern Michigan and southern Wisconsin where urbanization and row crop agriculture covered a far greater proportion of the landscape. Hybridization of wild with domestic game-farm mallards likely contributes to lower incubation incidence in hybrids with predominantly domestic genes (Chapter 4), and movement data collected from GPS transmitters suggests hybrid mallards select for urban areas and are more prevalent in the southern Great Lakes (Chapter 2). These findings are consistent with lower female age ratios at developed and southern locations and raises concern regarding the impact of game-farm mallard releases on Great Lakes mallard productivity.

Productivity was also related to habitat conditions and was higher during years when more hectares were enrolled in CRP. Because habitat types provided by CRP have been linked to increased nest success and production in upland-nesting ducks (Reynolds et al. 2001), we surmised the total area of CRP could provide a reasonable annual index of regional upland nesting cover abundance. Indeed, we found mallard productivity was higher during years when more of the study area was enrolled in CRP. The estimated loss of 1.4 million ha of grassland and pasture in the UMGL JV region since 2001 corresponds to the decline in CRP and subsequently mallard productivity. Loss of upland nesting cover and agricultural intensification are likely inversely related. Because we did not include agricultural intensity as a covariate in our models, it is unclear whether declining productivity is primarily related to loss of upland nesting habitat, increase of cropland area or pesticide use, or an interaction of these factors, which is an area for further research. There is a well-established link between wetland counts and mallard abundance in the PPR (U. S. Fish and Wildlife Service 2023b)., Likewise, Michigan breeding mallard abundance was historically (1991–2007) correlated ($\mathrm{R}^2 = 0.679$) with wetland hydrology measured using the deviation from average water level in Lake Michigan and Lake Huron in the previous year. However, this relationship in Michigan disappeared ($\mathrm{R}^2 = 0.038$) in more recent years (2008–2018), suggesting a disconnect between wetland conditions and productivity for mallards nesting in Michigan (D. R. Luukkonen; Michigan Department of Natural Resources, unpublished data). While area enrolled in CRP declined, wetland counts during aerial surveys were variable annually with an increase in the last several years of this study. The lack of response in productivity to increased wetland abundance could be influenced by lack of upland nesting cover relative to landscape conditions in the early 2000s, with nesting cover becoming more limiting than brood rearing wetlands. Additionally, wetlands with relatively constant hydrology may proceed to late successional stages where wetland area is dominated by emergent vegetation, reducing value to breeding mallards (Fowler et al. 2024). The relationship between wetlands and productivity for Great Lakes mallards warrants further research, especially the influence of hybridization, use of urban areas for nesting (Chapters 2 and 4), and the consequences of intensive agricultural practices on brood-rearing wetlands.

Productivity was lower in years when mallard abundance was high, suggesting the potential for density dependence in productivity. This is consistent with the hypothesis that resources such as quality nest sites, brood rearing habitat, or food become more limiting when the number of breeding mallards increases relative to the supply of these resources, and therefore nest success is lower or fewer ducklings survive until fledging at high population density. Identification of density dependence varies among studies and likely depends on the scale at which density is measured (Singer et al. 2016, Specht and Arnold 2018, Riecke et al. 2022*b*, Devries et al. 2023). Detecting density dependence is also complicated by the need to measure density in relation to resource (e.g., suitable wetlands, nesting cover) abundance, or per capita resource availability (Black et al. 2007). Density dependence in productivity would provide another mechanism for harvest compensation, in addition to compensation through increased natural mortality.

Our model suggests the Great Lakes mallard population is primarily limited by natural (non-hunting) mortality and productivity, resulting from environmental and anthropogenic factors, while female mallard harvest has not been a factor in the population decline. Integrated analysis of multiple datasets will continue to be valuable to inform management actions and predict population dynamics under changing environmental conditions (Zhao et al. 2019, Weegman et al. 2022). While IPMs provide valuable insight at a population level over large temporal and spatial scales, additional research will be required to more fully understand the effects of habitat change and release of domestic game-farm mallards on natural mortality and productivity of Great Lakes mallards.

MANAGEMENT RECOMMENDATIONS

This analysis used banding and aerial survey data to determine that the Great Lakes mallard population decline was due to increasing natural mortality of female mallards and declining productivity. We encourage maintaining or increasing investment in banding and population survey programs as these datasets will continue to be invaluable for monitoring the effects of ecological and anthropogenic factors on waterfowl population dynamics. Management actions that reduce female mallard mortality during spring and summer, and that increase productivity at large scales are most likely to positively influence Great Lakes mallard abundance. Programs that increase the quantity and quality of upland nesting habitat (i.e., grassland) and brood rearing wetlands in the southern (BCR 23) portion of the Great Lakes region would likely be most effective. Restricting Great Lakes hen mallard harvest regulations is unlikely to increase female mallard abundance. Additional research focused on identifying the primary causes of increasing natural mortality and declining productivity would greatly inform future management actions given the uncertainty in the relative influences of environmental, habitat, and anthropogenic factors on decline in Great Lakes mallards.

TABLES

Table 5.1. Regression coefficient (β) medians, 95% credible intervals (CRI), and the proportion of the posterior distribution on the same side of zero as the mean (υ) for models estimating Great Lakes adult (AHY) and juvenile (HY) female mallard natural mortality hazard rate (h_{η}; log-link), harvest mortality hazard rate (h_{κ}; log-link), and age ratio (J; proportion juveniles; logit-link). Covariates include z-standardized mallard abundance (N), wetland abundance (P), waterfowl hunter abundance (H), duck hunting regulation index (R), proportion urban landcover at banding sites (U), banding site latitude (L), and annual Michigan and Wisconsin Conservation Reserve Program hectares (G).

β	**Response**	**Predictor**	**Median**	**Lower 95% CRI**	**Upper 95% CRI**	**υ**
$\beta_{\eta,AHY,1}$	$h_{\eta,\, t_{AHY}}$	Intercept	-0.71	-0.77	-0.67	-
$\beta_{\eta,AHY,2}$	$h_{\eta,\, t_{AHY}}$	N	-0.08	-0.13	-0.03	1.00
$\beta_{\eta,AHY,3}$	$h_{\eta,\, t_{AHY}}$	P	0.04	-0.02	0.10	0.91
$\beta_{\eta,HY,1}$	$h_{\eta,\, t_{HY}}$	Intercept	-0.51	-0.62	-0.41	-
$\beta_{\eta,HY,2}$	$h_{\eta,\, t_{HY}}$	N	-0.16	-0.26	-0.06	1.00
$\beta_{\eta,HY,3}$	$h_{\eta,\, t_{HY}}$	P	-0.07	-0.16	0.03	0.92
$\beta_{\kappa,AHY,1}$	$h_{\kappa,\, t_{AHY}}$	Intercept	-2.18	-2.30	-2.04	-
$\beta_{\kappa,AHY,2}$	$h_{\kappa,\, t_{AHY}}$	H	0.01	-0.05	0.08	0.66
$\beta_{\kappa,AHY,3}$	$h_{\kappa,\, t_{AHY}}$	N	-0.02	-0.09	0.06	0.66
$\beta_{\kappa,AHY,4}$	$h_{\kappa,\, t_{AHY}}$	R	-0.05	-0.12	0.03	0.90
$\beta_{\kappa,HY,1}$	$h_{\kappa,\, t_{HY}}$	Intercept	-1.45	-1.57	-1.29	-
$\beta_{\kappa,HY,2}$	$h_{\kappa,\, t_{HY}}$	H	0.13	0.05	0.21	1.00
$\beta_{\kappa,HY,3}$	$h_{\kappa,\, t_{HY}}$	N	-0.06	-0.15	0.04	0.89
$\beta_{\kappa,HY,4}$	$h_{\kappa,\, t_{HY}}$	R	-0.01	-0.09	0.08	0.56
$\beta_{\gamma,1}$	$J_{t,b}$	Intercept	0.92	0.77	1.07	-
$\beta_{\gamma,2}$	$J_{t,b}$	U	-1.02	-1.50	-0.55	1.00
$\beta_{\gamma,3}$	$J_{t,b}$	L	0.25	0.15	0.35	1.00
$\beta_{\gamma,4}$	$J_{t,b}$	N	-0.14	-0.26	-0.02	0.99
$\beta_{\gamma,5}$	$J_{t,b}$	P	-0.38	-0.69	-0.31	1.00
$\beta_{\gamma,6}$	$J_{t,b}$	G	0.25	-0.31	0.70	0.81

FIGURES

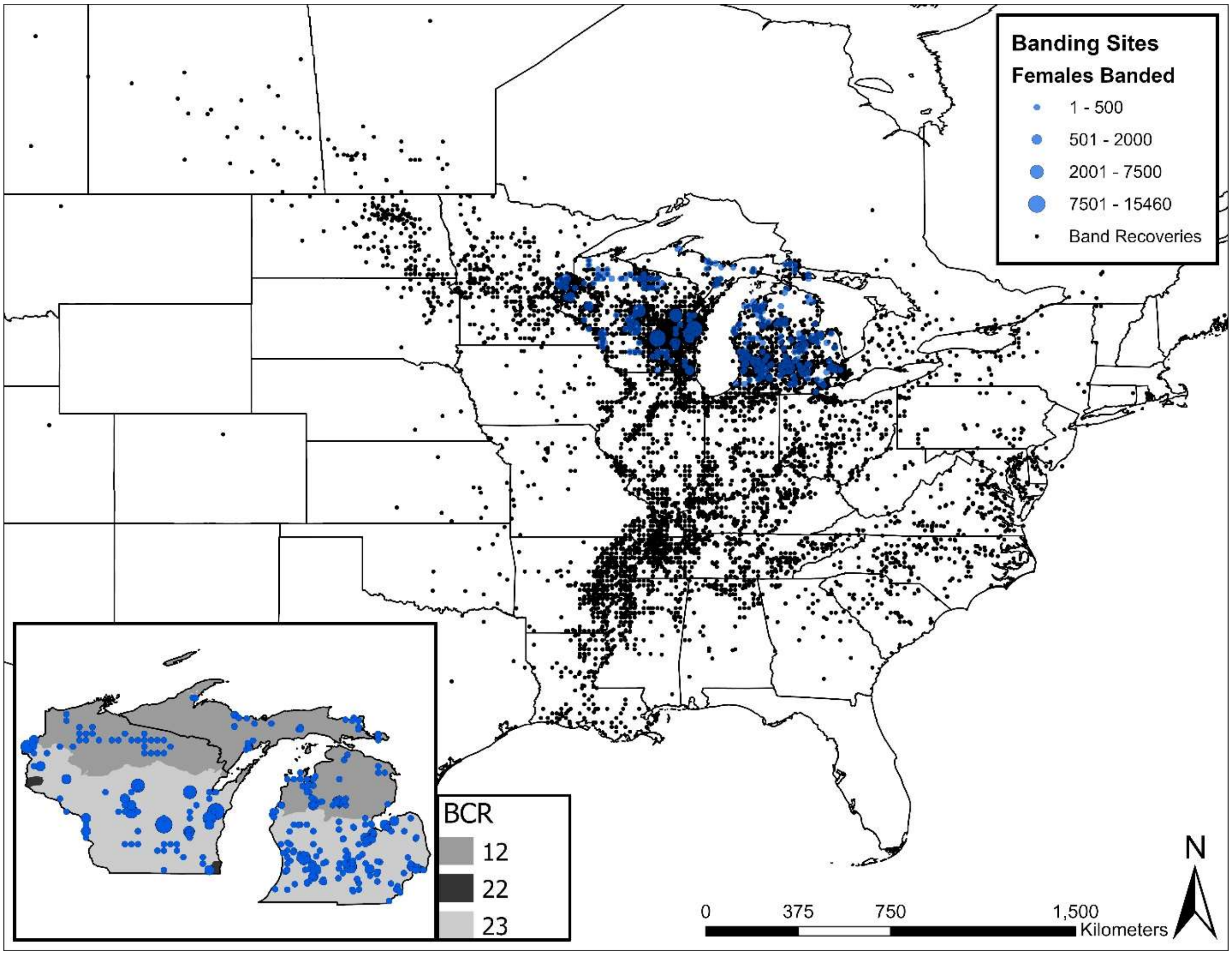

Figure 5.1. Female mallard banding locations and effort (total female mallards banded) in Michigan and Wisconsin Bird Conservation Regions (BCRs), and resulting harvest locations of banded mallards, 1991–2022.

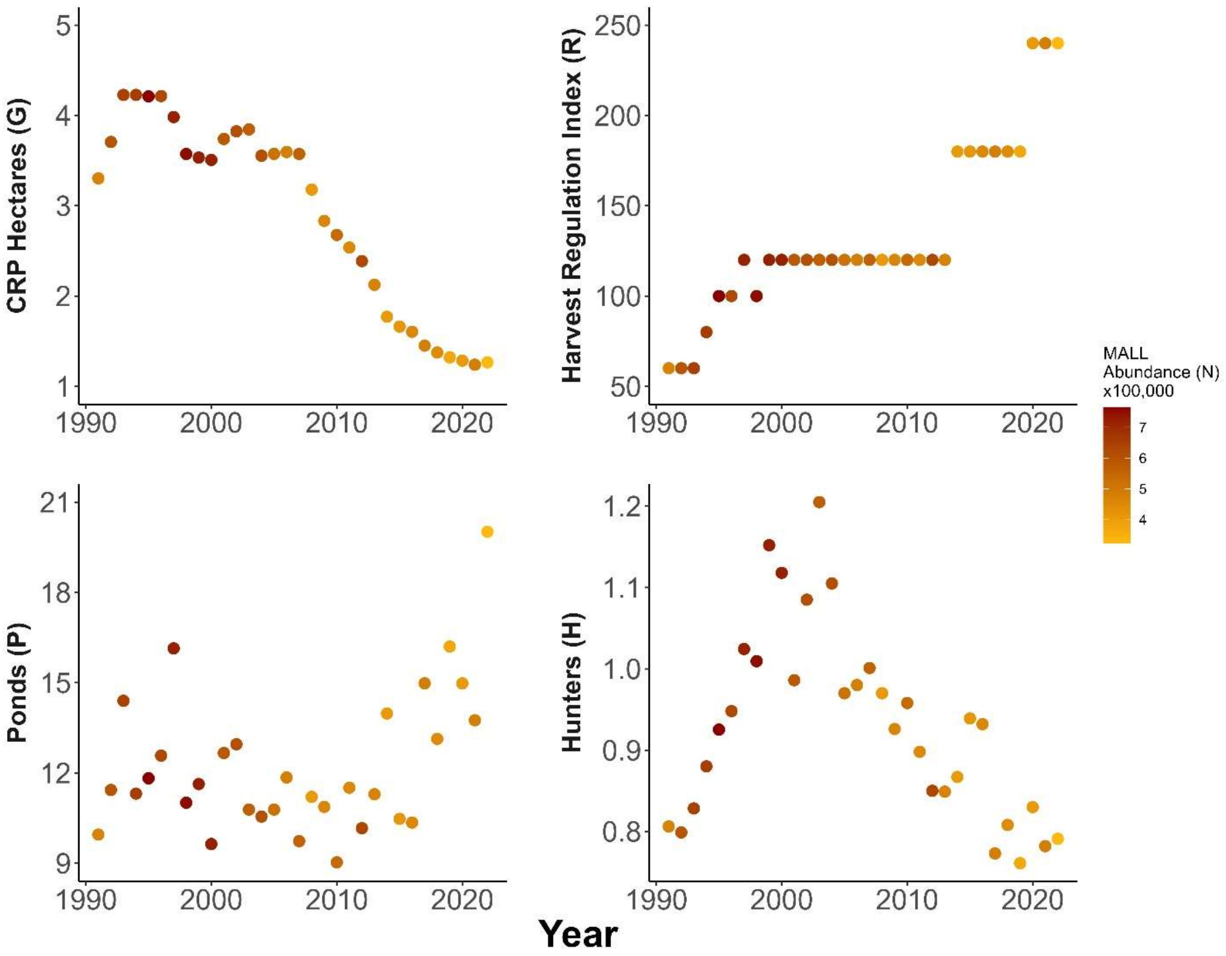

Figure 5.2. Annual Conservation Reserve Program (CRP) hectares in Michigan and Wisconsin, duck hunting regulation indices (season length × hen mallard daily bag limit in Michigan + Wisconsin), pond (wetland) counts from spring breeding waterfowl aerial surveys, and total licensed duck hunters in Michigan and Wisconsin, 1991–2022. Point color represents total estimated mallard abundance in Michigan and Wisconsin from the spring breeding waterfowl surveys. CRP hectares, ponds, duck hunters, and mallard abundance scales are in 100,000s.

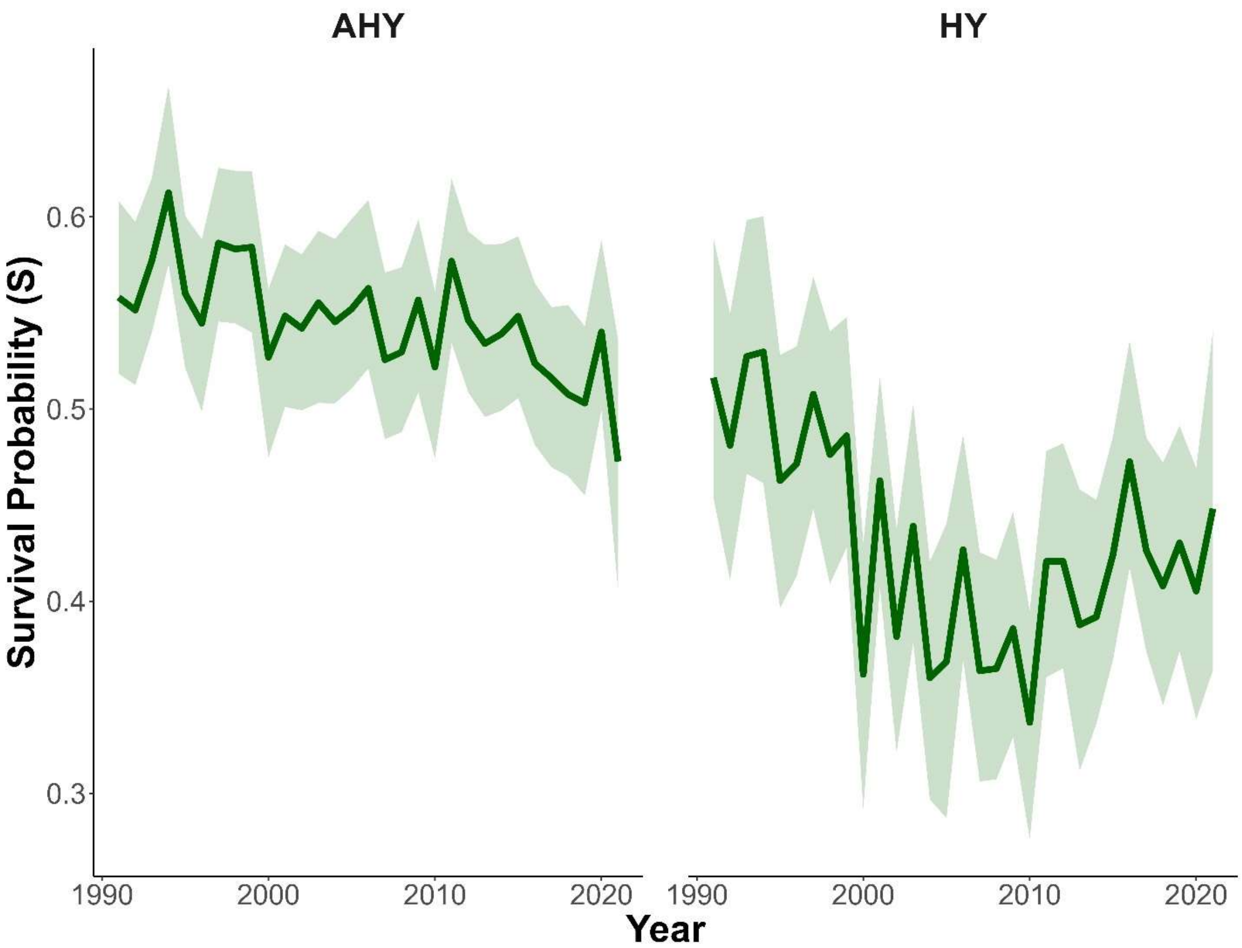

Figure 5.3. Posterior medians (lines) and 95% Credible Intervals (CRI; shaded regions) of annual survival probability (S) for adult (AHY) and juvenile (HY) female mallards banded in Michigan and Wisconsin, 1991–2022.

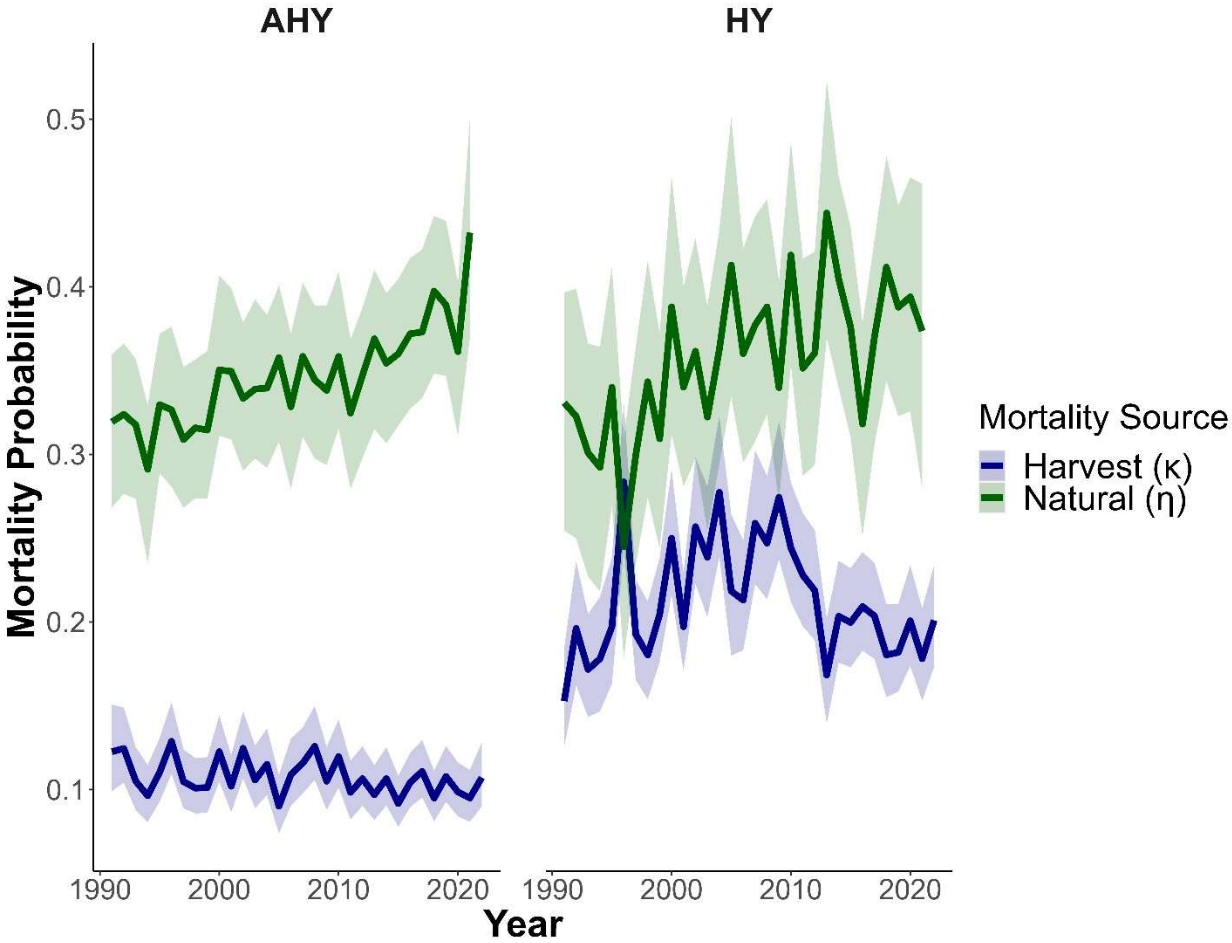

Figure 5.4. Posterior medians (lines) and 95% Credible Intervals (CRI; shaded regions) of annual natural (η; non-hunting) mortality probability (green) and harvest (κ; hunting) mortality probability (blue) for adult (AHY) and juvenile (HY) hen mallards banded in Michigan and Wisconsin, 1991–2022.

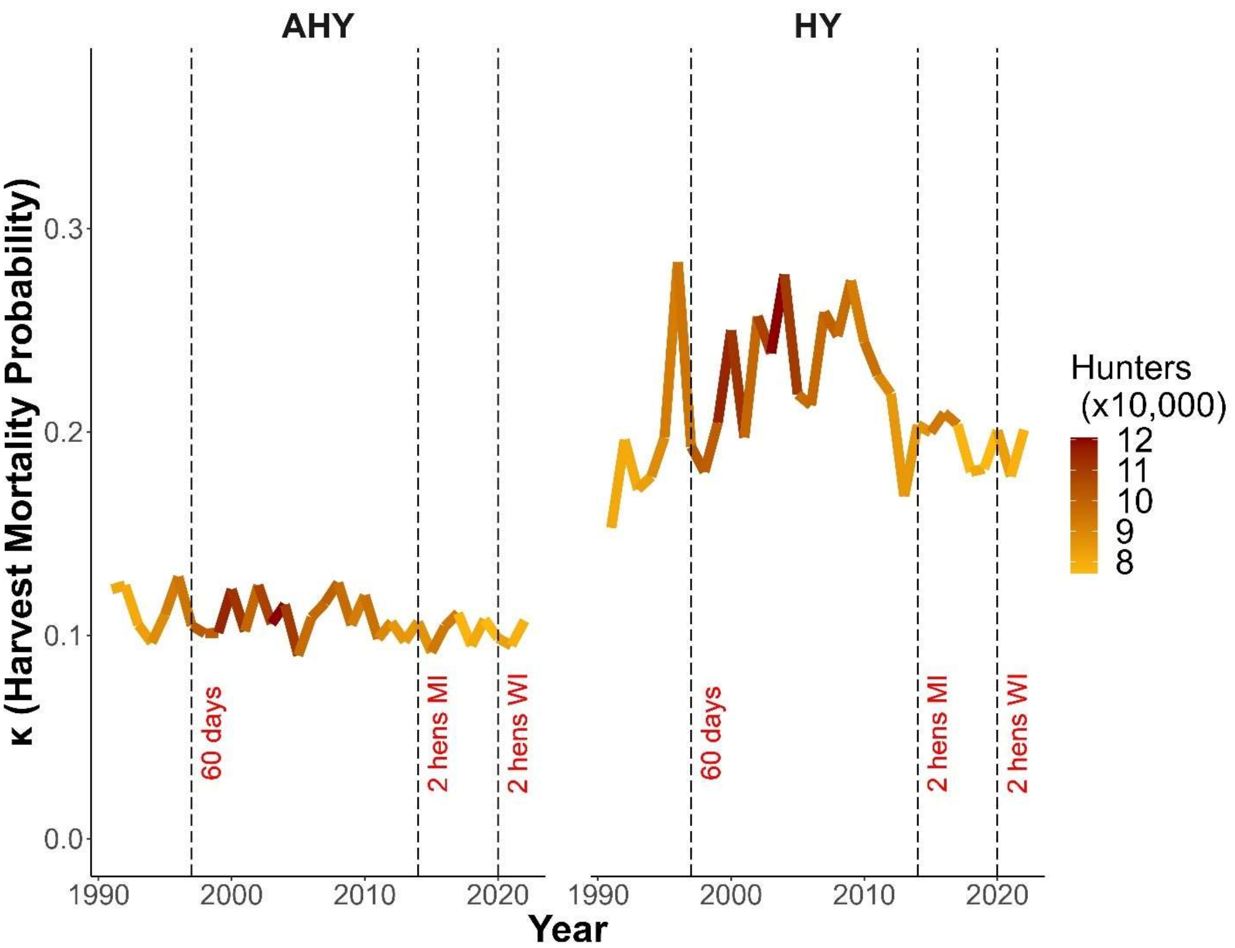

Figure 5.5. Posterior medians (lines) of harvest mortality probability (κ) for adult (AHY) and juvenile (HY) female mallards banded in Michigan and Wisconsin, 1991–2022. Line color corresponds to the annual number of licensed duck hunters in Michigan and Wisconsin, and vertical dashed lines denote the first 60-day duck season (concurrent in Michigan and Wisconsin) and the years when the daily hen mallard harvest limit was increased from 1 to 2 hens in Michigan (MI) and Wisconsin (WI).

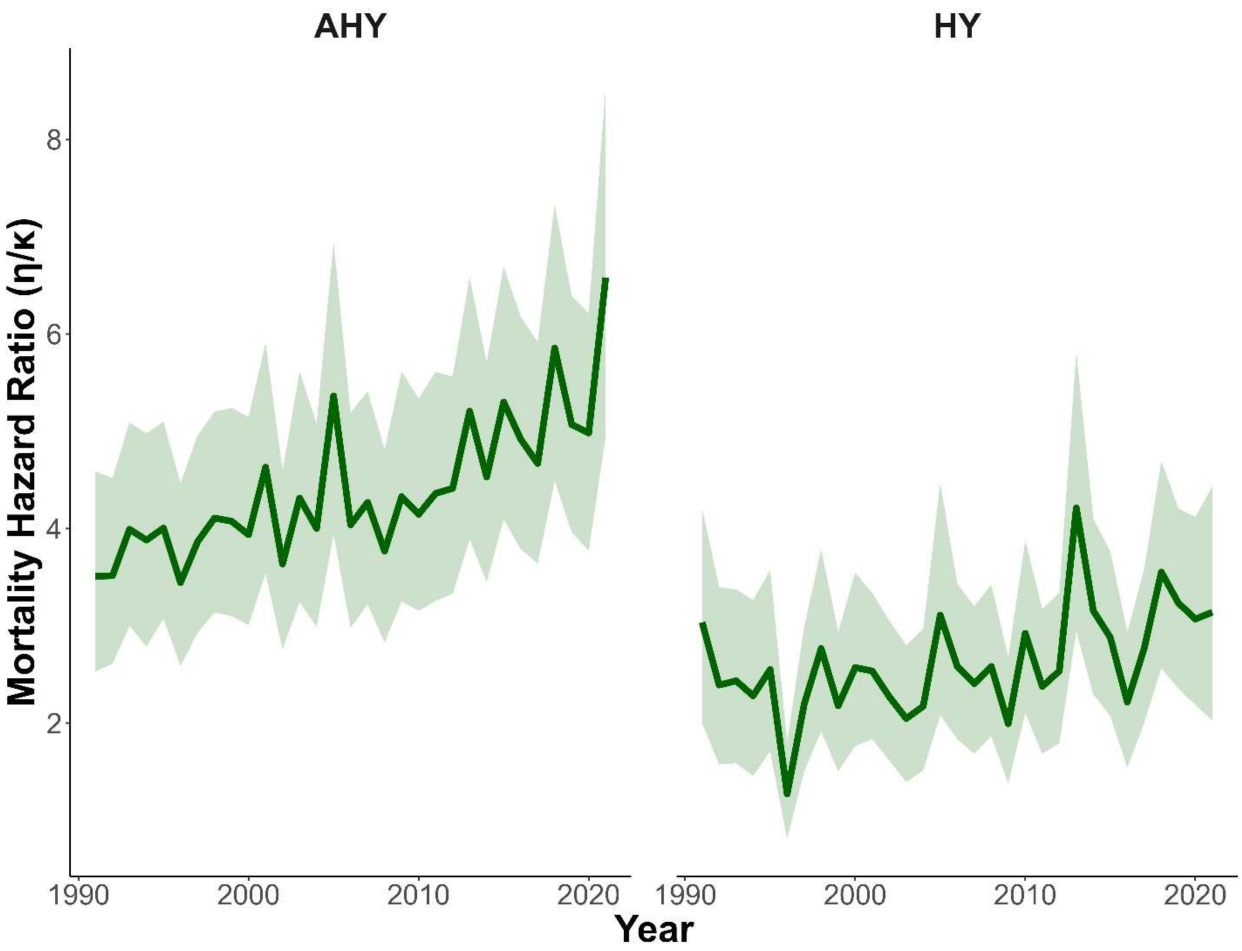

Figure 5.6. Posterior medians (lines) and 95% Credible Intervals (CRI; shaded regions) of the ratio of natural to harvest mortality probability (natural mortality probability / harvest mortality probability) for adult (AHY) and juvenile (HY) female mallards banded in Michigan and Wisconsin, 1991–2022.

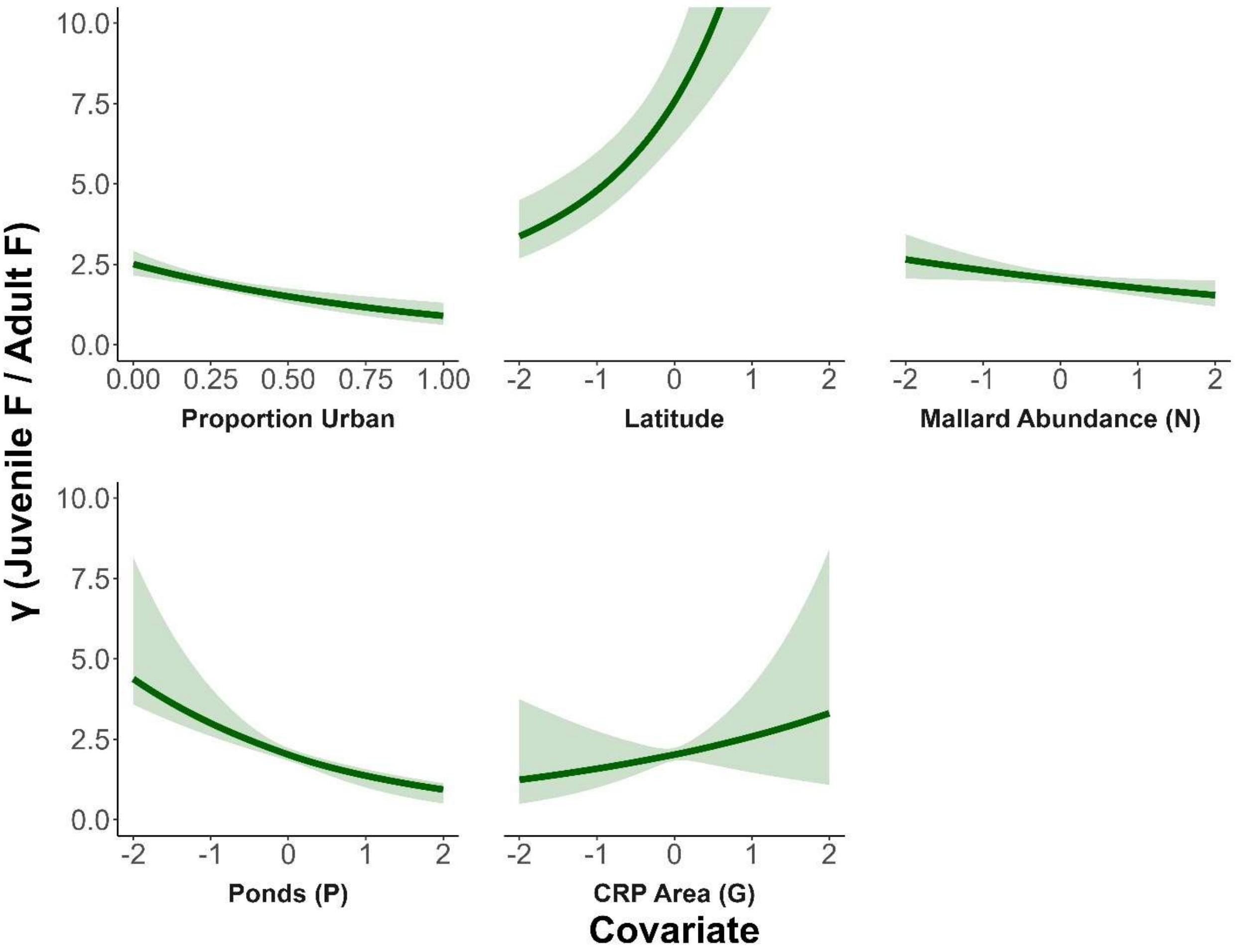

Figure 5.7. Spatial and temporal covariate relationships (lines) and 95% Credible Intervals (CRI; shaded regions) with productivity (γ; juvenile females per adult female) for mallards banded in Michigan and Wisconsin, 1991–2022. All covariates except the proportion urban landcover in a 7 km radius of banding sites (proportion urban) are presented on the standardized scale.

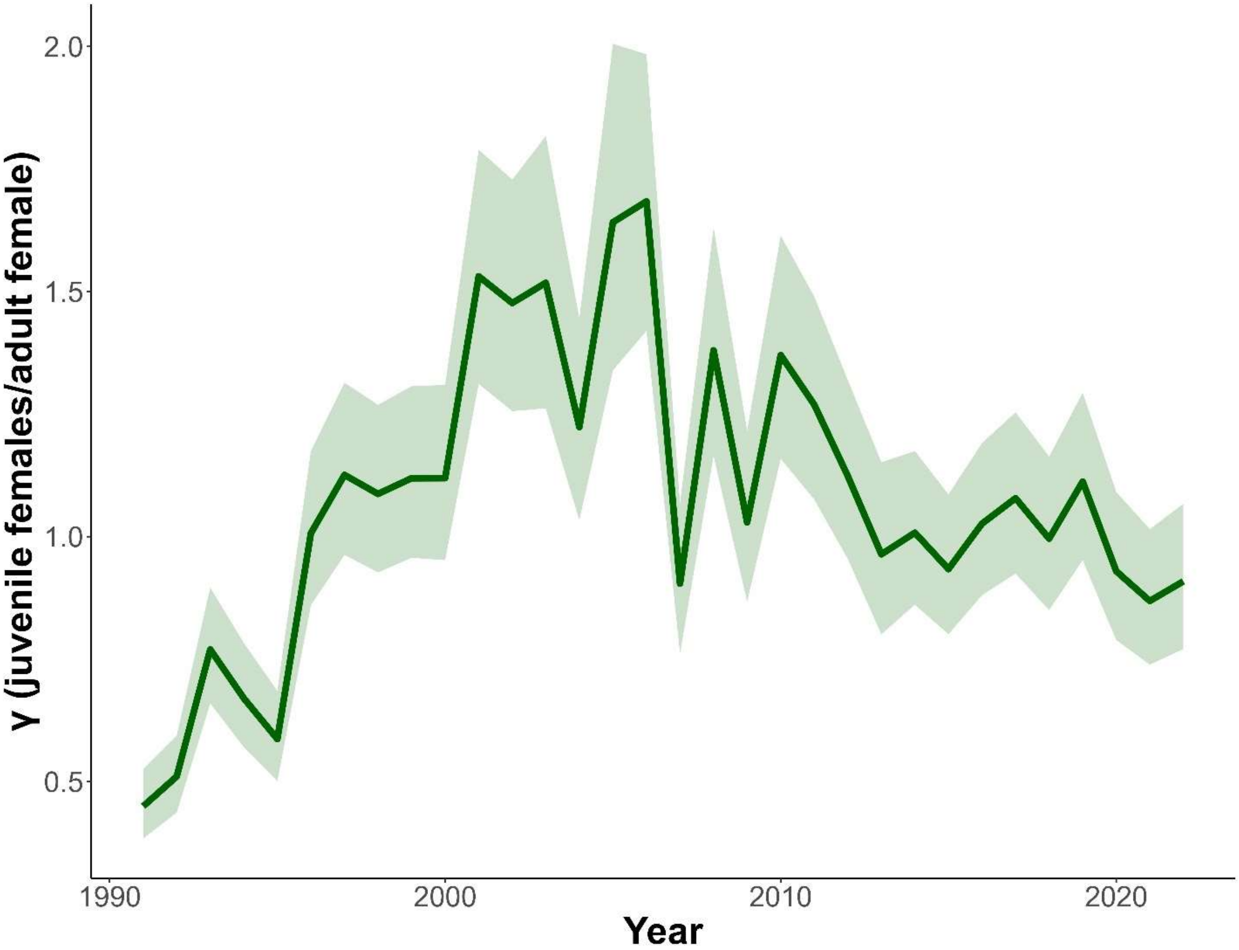

Figure 5.8. Posterior medians (line) and 95% Credible Intervals (CRI; shaded regions) of annual productivity (γ; juvenile females per adult female mallard) for mallards banded in Michigan and Wisconsin, 1991–2022.

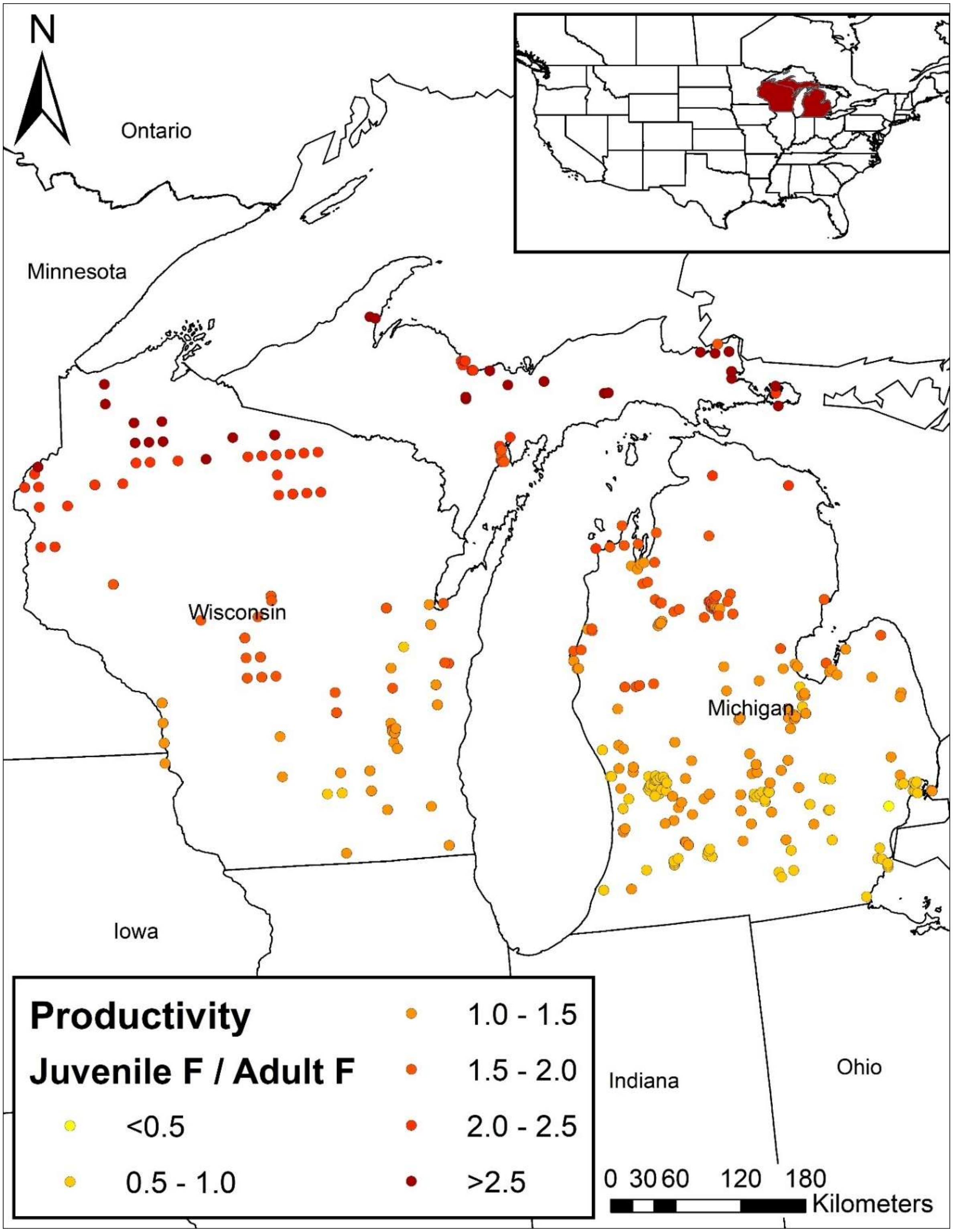

Figure 5.9. Model predicted productivity indices (juvenile females per adult female) at mallard banding sites in Michigan and Wisconsin, USA from 1991–2022. Predictions are for the mean observed values of mallard abundance, pond abundance, and Conservation Reserve Program hectares during 1991–2022.

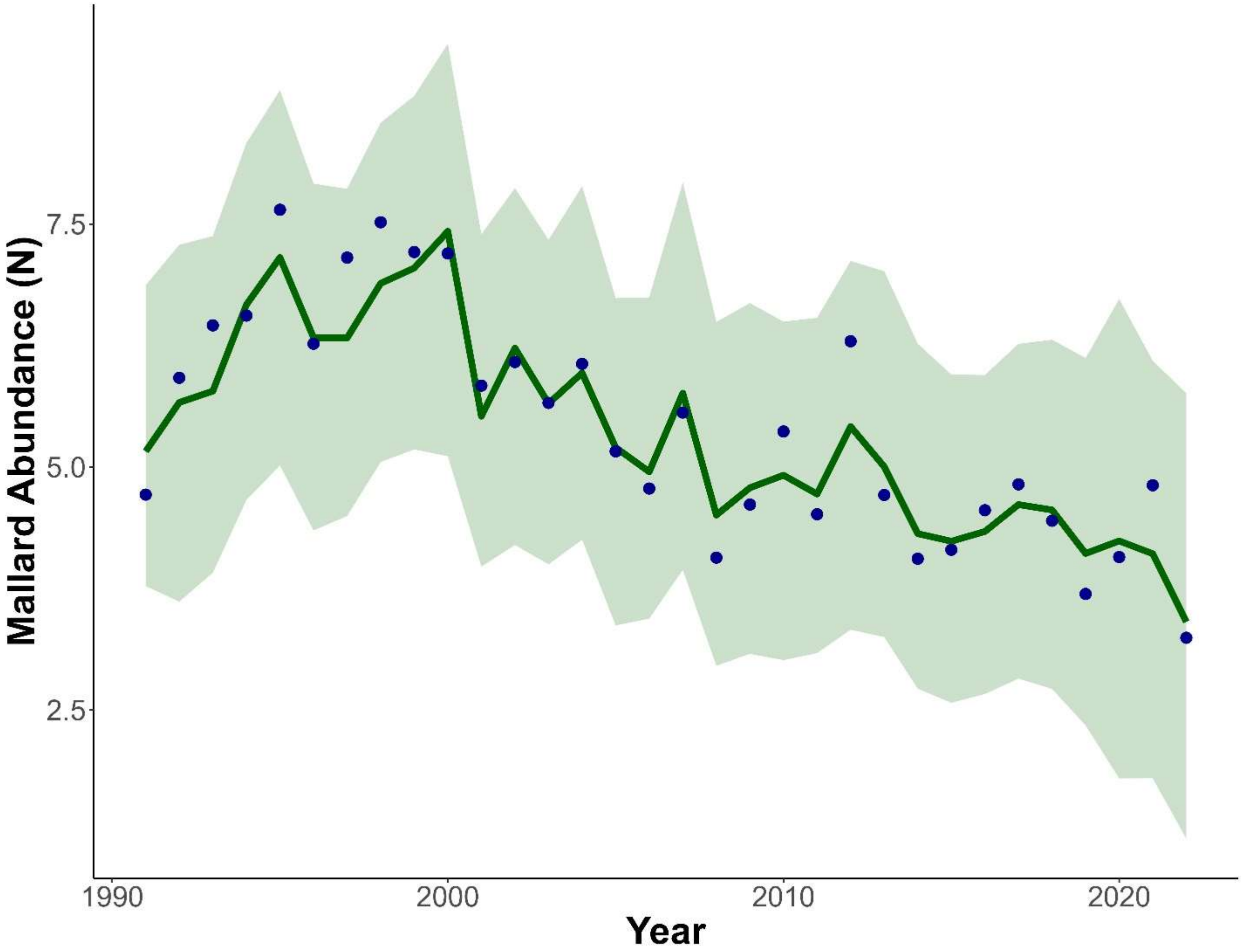

Figure 5.10. Posterior medians (line), 95% Credible Intervals (CRI; shaded region) of mallard abundance (N), and estimated mallard abundance (in 100,000s) from the Michigan and Wisconsin spring breeding aerial waterfowl surveys (points), 1991–2022.

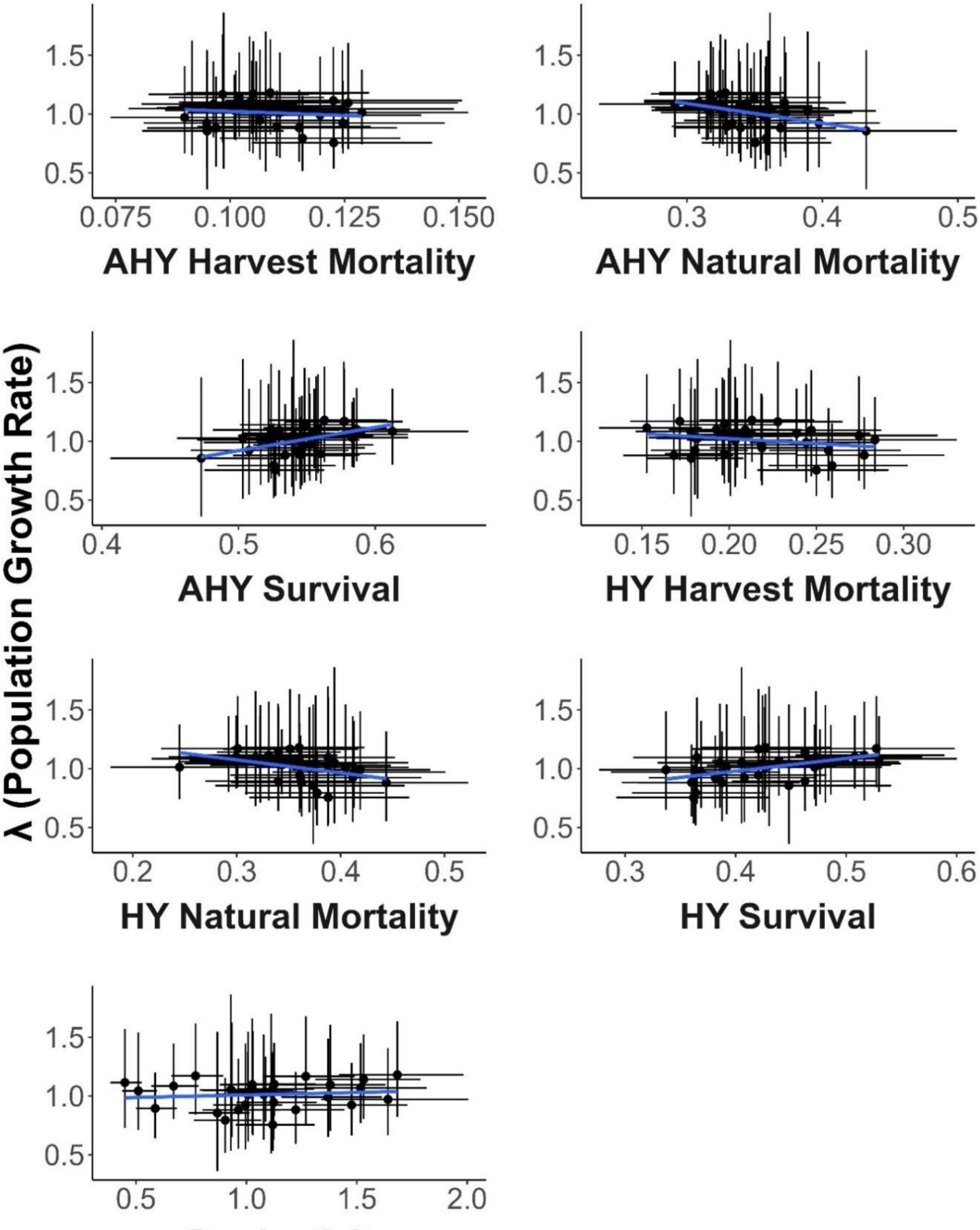

Figure 5.11. Correlation between population growth rate (λ) and adult (AHY) and juvenile (HY) harvest mortality probability, natural mortality probability, survival, and productivity. Points are medians, error bars denote 95% Credible Intervals, and blue lines show the linear trend fit to the estimates.

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CHAPTER 6: MANAGEMENT IMPLICATIONS

Mallard (*Anas platyrhynchos*) abundance in the Great Lakes region declined by approximately 30% from 2000 to 2023 based on spring aerial surveys in Michigan, Minnesota, and Wisconsin (U. S. Fish and Wildlife Service 2023b). The decline in Great Lakes mallards raises concern among agencies and organizations implementing the North American Waterfowl Management Plan (NAWMP; NAWMP 2018b) because mallards have ecological (Ackerman 2002, Kleyheeg et al. 2019), social, and economic (Carver 2013, 2015) value. Great Lakes mallards are managed as part of the midcontinent mallard population, where an objective is to maximize sustainable harvest (U. S. Fish and Wildlife Service 2023a). Declining mallard abundance conflicts with a continental goal of maintaining abundant waterfowl populations which support hunting and other uses (NAWMP 2018). More broadly, habitats that support mallards and other waterfowl provide ecosystem services that benefit society (Olewiler 2004). Therefore, waterfowl and wetland managers seek to understand the factors causing the Great Lakes mallard population to decline so management actions can work towards stabilizing or increasing mallard abundance.

Previous analyses of Great Lakes mallard female survival and productivity did not draw clear links between these parameters and population decline, and novel changes in anthropogenic and environmental factors raised new questions. Emigration was an understudied population parameter and a logical area for research given that survival and productivity had not been considered limiting. Additionally, anecdotal increases in the number of mallards observed in urban areas raised the possibility of mallard distribution change between rural and urban habitat types. A distribution shift from rural to urban areas could result in underestimation of mallard abundance as aerial surveys used to detect population trends were not designed to survey waterfowl within metropolitan areas (U.S. Fish and Wildlife Service 1987). Although Great Lakes female mallard harvest rates had declined (Singer 2014) and adult female harvest was likely to be partially compensatory (T. Arnold, University of Minnesota, unpublished), some stakeholders and managers voiced concern about liberalization of the female mallard daily harvest limits from one to two hens. Lastly, a major question was whether releases of domestic game-farm mallards in eastern North America (Huesmann 1974, U. S. Fish and Wildlife Service 2013, Lavretsky et al. 2020, 2023) conferred maladaptive traits or behaviors which negatively affected demographic parameters of wild x game-farm mallard hybrids. In this study we used GPS-GSM transmitters to monitor female Great Lakes mallard movement, migration, resource selection, survival, incubation initiation, nest survival, and breeding fidelity in relation to individual and landscape covariates during 2021–2024. We also used female mallard banding, band recovery, and aerial survey data collected from Michigan and Wisconsin during 1991–2022 to develop an Integrated Population Model (IPM) which identified parameters related to population decline, and ecological and anthropogenic factors affecting natural mortality, harvest mortality, and productivity.

OVERVIEW OF STUDY RESULTS

Analysis of stable hydrogen isotopes from GPS-marked hen mallard feather samples suggested 82% of female mallards captured during preseason (1 July–30 September) banding in 2021–2023 were likely to have molted or hatched at the latitudes of the Great Lakes region (Chapter 4). Nearly all (98%) surviving female mallards from the Great Lakes region remained in or returned to the region during the breeding period, suggesting breeding season fidelity is high (Chapter 4) and emigration recently contributed little to population decline. Our Great Lakes mallard IPM found that decline in mallard abundance from 2000 to 2022 was related to a decline in productivity and increase in adult and juvenile female natural mortality (and decline in annual survival). Adult and juvenile female mallard harvest mortality was a small component of total annual mortality compared to non-hunting mortality. Productivity was positively correlated with latitude and the annual area enrolled in the U. S. Department of Agriculture Conservation Reserve Program (CRP) in Michigan and Wisconsin, and negatively related to urban developed land cover (Chapter 5). Therefore, natural mortality outside of the hunting season and duckling production were the factors most limiting Great Lakes mallard population growth (Chapter 5).

Genetic ancestry analysis revealed that 44% of GPS-marked females were wild mallards and 56% were wild x domestic game-farm mallard hybrids. Hybrid mallards were more prevalent at urban developed capture sites in the southern Great Lakes region. Hen mallards with a higher proportion of game-farm mallard ancestry moved shorter daily distances, were less likely to engage in autumn migration, and had greater use and selection of urban developed land cover than did wild hen mallards (Chapter 2). Survival was positively associated with the proportion of locations in urban developed land cover for both wild and hybrid mallards, suggesting that semi-domestic characteristics of urban areas enabled early generational hybrids to survive at rates similar to those of wild mallards (Chapter 3). Increasing proportion of game-farm ancestry was also associated with lower incidence of initiating incubation, suggesting early generational hybrids contributed little to duckling production (Chapter 4), aligning with lower productivity indices at developed and southern banding locations (Chapter 5) where game-farm mallard hybrids were most prevalent (Chapter 2). Increasing proportions of urban developed land cover around nests was associated with higher nest survival probability in wild mallards (Chapter 4), suggesting that nest predation was higher in rural areas. Collectively, this study indicated that landscape-level habitat changes and hybridization with game-farm mallards have contributed to decline in Great Lakes mallard abundance.

MANAGEMENT IMPLICATIONS

Attempts to increase or maintain Great Lakes mallard abundance should consider regional quantity and quality of nesting and brood-rearing habitat types and population genetics. Processes acting during the spring and summer portion of the annual cycle which affect female mortality and productivity had the greatest impact on Great Lakes mallard population growth rate. Because mallards are highly studied, there exists a wealth of information which can inform efforts to increase female breeding season survival and nest and brood survival at the local (i.e., nest site, wetland, or upland-wetland complex) scale.

Options available to increase mallard nest, brood, and female breeding survival at local scales primarily include manipulating the amount, suitability, and or spatial arrangement of upland nesting cover and brood-rearing wetlands, and predator management. Mallards adapted to nesting in open prairie adjacent to emergent wetlands (Bent 1923, Bellrose 1976), meaning female mallards could be considered a grassland bird during a portion of their annual cycle. However, mallard nest success can be high when mallards use over-water nest sites (Arnold et al. 1993), but we did not observe any naturally constructed (i.e., outside of artificial nest structures) over-water nests in this study. Incubation, particularly in terrestrial environments, is hazardous and predation during nesting is considered a leading source of annual mortality in adult female mallards (Arnold et al. 2012). Predator management via meso-predator trapping can locally increase nest success (Pieron and Rohwer 2010), but benefits may be partially offset through other parameters, such as duckling survival, becoming limiting. Trapping can also be costly and labor intensive per individual added to the fall flight (Amundson et al. 2013). Decline in fur prices and public trapping participation (Bauder et al. 2020) is likely to further reduce the efficacy and cost-efficiency of meso-predator trapping at a regional scale required to influence population-level hen, nest, or brood survival in Great Lakes mallards. Additionally, avian predators likely account for a substantial portion of hen and duckling mortality (Devries et al. 2003). Therefore, focusing on upland nesting cover and brood-rearing wetland conservation may be most practical, but will require creating and maintaining habitat on private lands at a regional scale to have population-level influence.

Programs incentivizing grassland and wetland conservation, such as the Conservation Reserve Program (CRP) and Wetland Reserve Program (WRP), have demonstrated large-scale benefit to upland-nesting dabbling duck productivity (Reynolds et al. 2001). Effectiveness of agricultural land conservation incentive programs will likely depend on the relationship between program incentives and profitability of row-crop commodities (e.g., corn [Zea mays] and soybeans [Glycine max]), and on agricultural policies (King et al. 2021). Providing nesting and brood-rearing habitat in areas with the least forest cover (Simpson et al. 2007, Boyer et al. 2018) could be prioritized to minimize predation by perching avian predators. Grassland obligate birds have declined more than any other avian guild (Rosenberg et al. 2019), so grassland conservation represents a challenge and an opportunity with potential to provide diverse ecological benefits for many species.

Within the Upper Mississippi/Great Lakes Joint Venture (UMGLJV) region, nesting and brood-rearing habitat conservation would be most effective in Bird Conservation Region (BCR) 23 (Prairie Hardwood Transition) because this area had the highest mallard density during the breeding period (Soulliere et al. 2017). Although per capita productivity was higher among banding sites in BCR 12 (Boreal Hardwood Transition; Chapter 5), this region had lower mallard nesting density and greater forest cover than BCR 23, reducing overall breeding habitat conservation efficiency relative to BCR 23. Providing artificial nesting structures, or mallard hen houses, could locally increase nest survival (Artmann et al. 2001, Stafford et al. 2002, Chouinard et al. 2005) where quality nesting cover is more limited than brood-rearing wetlands. Artificial nest structures could also be implemented when conversion of cropland to perennial cover was not economical or desired by private landowners. However, eight of nine mallards captured in hen houses in this study were hybrids and all captive-reared mallards released and monitored in a study in southwestern Manitoba (n = 5) nested in artificial nest structures (Yerkes and Bluhm 1998), suggesting possibility of disproportionate use of hen houses by hybrid or captive-reared mallards should be further evaluated.

Another factor potentially limiting hen mallard breeding survival and production are agricultural chemicals such as neonicotinoid insecticides. Insecticides could reduce availability of invertebrate food resources required by hens and ducklings (Hopwood et al. 2013, Morrissey et al. 2015, Soulliere et al. 2020). This hypothesis warrants further research given decline in Great Lakes mallard productivity in areas with greater agricultural land cover (Chapter 5). Neonicotinoid use has been correlated with declines in insectivorous passerines (Hallmann et al. 2014, Li et al. 2020) and aerial insectivores have declined in North America (Nebel et al. 2010). Hence, agricultural intensification could have broad implications for bird conservation (Soulliere et al. 2020). More broadly, elimination, consolidation, sedimentation, and degradation of wetlands resulting from agricultural practices and other anthropogenic factors such as the introduction of invasive species and urban development are landscape scale habitat changes potentially relevant to mallard productivity and survival. Ultimately, without addressing large-scale loss of upland nesting cover (Soulliere et al. 2017, 2020) and continued conservation of wetlands important for brood-rearing at a regional scale, the peak breeding abundance of Great

Lakes mallards observed in the late 1990s and early 2000s is an unrealistic future expectation.

This study suggested efforts to increase hen mallard survival via harvest management would be of limited effectiveness for several reasons. Relative to natural mortality, adult and juvenile female harvest mortality was a small component of annual mortality. Despite fluctuations in the number of waterfowl hunters and liberalization of season length and daily harvest limits, adult female harvest mortality remained constant from 1991–2022. Although juvenile female harvest mortality was related to the number of hunters, harvest mortality did not increase after daily hen mallard harvest limits were increased from one to two in Michigan and Wisconsin. Declines in the number of hunters are predicted to continue (Vrtiska et al. 2013), likely further reducing the effects of harvest. Lastly, high natural mortality (conditional on surviving harvest) and density dependence in productivity, indicate mechanisms that allow for female mallard harvest to be partially compensatory. Without substantial increase in the number of Great Lakes region duck hunters, restricting harvest regulations would likely provide little increase in female mallard survival or population growth rate.

In addition to conservation of the habitat types important to productivity, wildlife managers and policy makers should consider the implications of game-farm mallard releases and hybridization. Game-farm mallard releases which allow domestic mallards to leave release locations, become feral, and reproduce with wild mallards are incompatible with the objectives of maintaining abundant and resilient populations to support hunting and other uses (NAWMP 2018), maintaining the response of mallard populations to habitat conservation (NAWMP 2018, Ducks Unlimited 2023) and maintaining mallard migration in response to migratory cues. Based on findings in this study, continuing large-scale game-farm mallard releases conflicts with the mission and goals of the U. S. Fish and Wildlife Service (U. S. Fish and Wildlife Service 2024), the Great Lakes state natural resource management agencies (Illinois Department of Natural Resources 2024, Indiana Department of Natural Resources 2024, Michigan Department of Natural Resources 2024, Ohio Department of Natural Resources 2024, Wisconsin Department of Natural Resources 2024), and principles of the North American Model of Wildlife Conservation (Organ et al. 2012), which have common themes of equitable access to sustainable wildlife resources for current and future generations.

The trend in expanding urban land area and comingling of domestic and wild mallard gene pools raises important waterfowl conservation concerns for the Great Lakes region and beyond. Yet, potential positive consequences resulting from human-wildlife interaction in urban settings must also be considered, especially regarding the continental objective to grow public support for waterfowl conservation (NAWMP 2018). The bird conservation community recently identified the relevancy of better integrating the needs of birds and people in habitat decisions (e.g., Soulliere et al. 2020). New efforts guided by conservation social science are improving public outreach and advocacy for habitats that benefit birds and people, while conservation planners are concurrently developing model-based spatially explicit strategies to achieve these multiple benefits (Soulliere et al. 2017). Scientists, resource managers, and policy makers must consider that stakeholders in urban areas can build the critical mass necessary to achieve policy change (e.g., Manfredo et al. 1999, Burnett 2004) and political support for conservation. Although hybridization between wild and game-farm mallards poses ecological threats, urban mallards may foster public value for waterfowl. Social science could help discern how public interaction with urban mallards influences behaviors which support conservation. This study suggests managing sustainable wild mallard populations is not incompatible with maintaining the presence of mallards in developed areas.

Our modeling predicted local-scale movement, migration, habitat selection, and nesting behaviors would become similar to those of wild mallards in about three generations of backcrossing of hybrid with wild mallards. However, the realized effects of reducing hybridization between wild and game-farm mallards is likely to be scale dependent. Some research suggested emigration of mallards banded in the Atlantic Flyway into the Mississippi Flyway (Lavretsky and Sedinger 2023) was a mechanism for westward movement of domestic genes. Thus, effects of reducing the number of game-farm mallards which survive and leave release sites would depend on spatial scale and magnitude of regulations. As nearly 60% of mallards sampled from rural capture sites were wild, there remains a sizeable component of the Great Lakes mallard population comprised of wild individuals. Assuming domestic genes confer traits which are generally less adaptive than traits coded in wild genes, reducing releases of game-farm mallards at a large scale is expected to increase the proportion of the Great Lakes mallard population comprised of wild individuals. Long-term continuous input of domestic ducks has likely contributed to maintaining domestic genes in mallard populations in eastern North America.

Theoretical models have predicted that gene flow from domesticated animals into wild populations adversely affects population growth and viability (Tufto 2001, 2010). Numerous examples provide evidence that interbreeding between wild and domesticated congeners negatively impacted genetic diversity and or life history traits in fish and wildlife. Studies examining captive rearing programs to domesticate fish for farming or to supplement wild populations through stocking have raised concerns about detrimental population consequences (e.g., Leitwein et al. 2018). For example, escape and hybridization of farmed Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*) with native fishes negatively altered age at maturation (Bolstad et al. 2017) and growth rates, spawning timing, and sex ratio (Johnston and Wilson 2015). In a laboratory experiment using steelhead (anadromous rainbow trout), domestic x wild hybrids had increased foraging behavior and greater exposure to predators than did wild steelhead (Johnsson and Abrahams 1991). Introgressive hybridization can also threaten persistence of wild species, such as American plains bison (*Bison bison*), where gene flow from cattle (Halbert et al. 2005) modified phenotypes (Derr et al. 2012). Introductions of gamebirds to non-native ranges can threaten genetic integrity of native species (Taysom et al. 2014, Wells et al. 2019) and extensive stocking can reduce fitness in wild populations (Barbanera et al. 2010, Puigcerver et al. 2014). Expanding human development can also increase contact and hybridization between domestic and wild forms, as in red junglefowl (*Gallus gallus*), where domestic chickens threaten genetic diversity (Wu et al. 2020, 2023). There is repeated evidence across taxa that introgressive hybridization with domesticated organisms is a conservation concern which merits continued research to inform policy. This study builds on previous understanding and recommends federal and state wildlife management agencies should regulate game-farm mallard releases to reduce hybridization with wild mallards.

FUTURE RESEARCH

This study reduced uncertainty in our understanding of the factors contributing to the Great Lakes mallard population decline, but many opportunities remain for future research. Whereas the IPM and monitoring of GPS-marked female mallard nesting behavior identified land cover changes and domestic ancestry as factors associated with reduced productivity, the factors affecting natural mortality were less certain. Natural mortality increased for both adult and juvenile female mallards over the 32 years examined in the IPM. Although predation is a likely contributor considering mallard life history, additional research to clarify factors mediating increased natural mortality, such as hybridization with game-farm mallards, specific habitat changes, and agricultural practices (e.g., insecticide application) would be informative for directing specific management actions. Increasing natural mortality and declining productivity could have related drivers given they overlap during the spring and summer seasons of the annual cycle.

Our study related the proportion of wild ancestry to behavior and demographics but did not examine the functions of individual genes. Additional research using whole-genome sequencing could look for associations between genes and behaviors, such as migration or incubation. As genes have specific functions, relating behavior or demographic parameters to the proportion of wild ancestry could be an overly simplistic approach to quantifying the effects of hybridization. In addition to the potential for greater understanding of gene functions, this would also be a valuable opportunity to examine the interaction between genetics and environment in a wildlife population. In areas where domestic mallard releases ceased after feral mallard populations became established (e.g., Hawaii, New Zealand), there existed potential for local adaptation by feral domestic mallards, and this could be an area for further research in North America where environmental conditions differ from those of island ecosystems (Lavretsky et al. 2023).

Efforts to manage population genetics would benefit from increased understanding of the role of urban developed areas in hybridization. This study showed that early generational hybrids were most prevalent and survived in urban areas, but that later generational hybrids and wild mallards were also present in and used urban areas in the Great Lakes region. Urban areas could be hotspots for hybridization if these are locations where feral game-farm mallards survive long enough to reproduce, and if survival and nest success benefits create selective pressure for wild mallards to also use these areas. Additionally, as mallard ancestry became more domestic, use of urban areas increased, resulting in decreasing availability of early generational hybrids for harvest and likely limiting harvest as a tool for reducing hybrid mallard abundance. There could be greater harvest management potential for male mallards due to their higher harvest rates, and future genetic sampling of hunter-harvested mallards in the Great Lakes region could be used to estimate the proportion of harvest comprised of hybrid and wild mallards.

Enhanced understanding of the spatial distribution and magnitude of game-farm mallard releases would greatly aid in modeling their effects. Detailed information at the federal or state level on the number and locations of game-farm mallards released is lacking, in part due to inconsistent permitting and reporting requirements across jurisdictional boundaries. Further, public perceptions of game-farm mallard releases are generally unstudied. Outreach and education campaigns could help raise awareness of potential issues resulting from game-farm mallard releases, and human dimensions research could help determine the attitudes of stakeholders. Social and biological science will both be required to inform policy decisions.

Lastly, the methods used to monitor Great Lakes mallard abundance may have limited effectiveness for mallards using large urban areas during the breeding period. However, it could be undesirable or ineffective to modify aerial survey standard operating procedures to attempt improved coverage of urban areas. If estimating abundance or density of mallards using developed landscapes is an objective, managers may consider designing an additional survey. Although a portion of female mallards breeding in urban areas in the Great Lakes region were early generational hybrids and likely contributed little to production, late generational hybrids and wild mallards also used urban land cover. Designing and implementing surveys for urban coverage could enable managers to track trends in the relative abundance of mallards in urban areas, which could better inform whether these areas are used by an increasing component of the mallard population.

Regardless of any decisions to regulate game-farm mallard releases or manage breeding habitat types at the regional scale, continued monitoring of Great Lakes mallard population genetics and demography is warranted. Banding, population surveys, and harvest surveys form the foundation of North American waterfowl monitoring. Maintaining these datasets in conjunction with genetic sampling and analyses should be prioritized to quantify ecological and anthropogenic effects on mallard populations in an ever-changing landscape.

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