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ARTICLE

Migratory connectivity of North American waterfowl across administrative flyways

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Abstract

Management of waterfowl that migrate seasonally across North America occurs within four flyways that were delineated in the early 1900s to include the annual movements of populations. Movements may have changed over the past century since the administrative flyways were established, and may do so while management plans are in use, so information about transitions among flyways through time can illustrate how management assumptions may change. Today there are more than 12 million records from 60 years of migratory waterfowl band recoveries to assess adaptive management approaches that will be most effective when they account for movements within and between flyways. We examined how much the movement of North American waterfowl occurs between flyways, whether those movements have changed through time, and whether movements of mallards are representative of multiple species, as suggested by current harvest management strategies. We estimated the probability a duck would transition from one flyway to another and the strength of migratory connectivity (MC) for each species within and among flyways. We used capture–mark–recovery models to estimate population-specific movement within and among flyways (transition probabilities) for 15 migratory waterfowl species that were banded during breeding and recovered during winter. We developed new functionality in the R package *MigConnectivity* to estimate the species-specific strength of MC using transition probability samples from the capture–mark–recovery models. We found the regular movement of duck populations among flyways, overall weak MC, and no consistent change in migratory movements through time. Mallard movements were median among all duck species, but significantly different from many species, particularly diving ducks. Despite the significant movement between flyways, our work suggests flyway management of waterfowl matches many of the seasonal movements of these species when considering mid-continent flyway management. We recommend models accounting for all transition probabilities between populations and regularly estimating harvest derivations, transition probabilities, and MC metrics to verify that the current movements match model assumptions.

KEYWORDS
duck, flyway-based management, harvest derivation, migration, migratory connectivity, seasonal movement, transition probabilities, waterfowl

INTRODUCTION

Management of migratory birds that move seasonally across North America is conducted within four flyways (Atlantic, Mississippi, Central, and Pacific; Figure 1) that were delineated to include the full annual cycle movements of populations (Nichols et al., 1995). When developing population models to guide harvest management within flyways, data from ducks banded across the continent are used to estimate relevant harvest derivations. These harvest derivations use band-recovery data and population abundance to estimate the proportion of the harvest in one management unit (i.e., flyway) that is derived from, or originated from, each source population (i.e., breeding area or flyway; Geis, 1972; Munro & Kimball, 1982). Harvest derivation analyses were originally conducted when population models were developed; this was in the early 1990s for the middle two flyways (Mississippi and Central), in 2007 for the Pacific Flyway, and in 2018 for the Atlantic Flyway. Formulating sustainable management plans requires accurate estimates of transitions among units (Johnson et al., 1992; Webster & Marra, 2005), however there is often no regular review of those movements, information about harvest derivations is difficult to find in technical reports, and the results are not easily accessible. Movements may have changed since the administrative flyways were established due to long-term regional reduction in wetland availability (Herbert et al., 2021; Wilen & Frayer, 1990), and may do so while management plans are in use due to increased prevalence of drought conditions (Sorenson et al., 1998), so information about cross-flyway movements through time can illustrate how management assumptions may change. It is recognized that there is a large degree of movement between waterfowl populations in each flyway, and so the challenge is to set flyway-specific hunting regulations in a way that recognizes general trends as well as the proportion of mixing that occurs (U.S. Fish and Wildlife Service, 2019a).

Nearly all the banding data used to establish flyway boundaries came from waterfowl, particularly species breeding in what Lincoln (1935) referred to as "the one great breeding ground." This area, the Prairie Pothole Region of North America, is the most prominent breeding area for many duck species in North America (Batt et al., 1989; Doherty et al., 2018). The overlap of geography and biological needs of individual waterfowl species breeding in the Prairie Pothole Region, along with similar geographical associations in other parts of the continent, potentially justifies the use of a single species representing the population dynamics of multiple species. This flyway-based umbrella approach allows many species to be managed based on population dynamics of a single species. Currently, most flyway waterfowl harvest management plans (strategies used to set hunting seasons) are based on population models of a single species, mallards (*Anas platyrhynchos*), and those models inform harvest regulations for 10 or more species (U.S. Fish and Wildlife Service, 2019a). For example, mallards are thought to be a representative species for mid-continent waterfowl populations and account for more than 30% of total duck harvest in the Mississippi and Central Flyways (Raftovich et al., 2019) and 35% of the harvest in the Pacific Flyway (U.S. Fish and Wildlife Service, 2019a). Because of this, the Mississippi and Central Flyways set hunting regulations for all waterfowl species based on a population model of mallards breeding largely in the Prairie Pothole Region (encompassing both the Mississippi and Central Flyways; Raftovich et al., 2019). Likewise, hunting regulations in the Pacific Flyway are based on a population model of mallards breeding within Alaska, British Columbia, California, Oregon, and Washington.

This single-species regulatory system provides a number of benefits to stakeholders, and is the simplest and most cost-effective approach to multispecies management if the assumption is correct that mallard population dynamics, including migratory movements, are representative of the suite of additional species. However, biologically, some species do not have the same geographic or habitat associations as mallards. For example, ducks in the genus *Aythya* typically feed by diving and require deeper water for breeding than mallards and other species in the genus *Anas*. Some species may have different geographic distributions, such as American black ducks (*Anas rubripes*) that primarily occur in eastern North America, or wood ducks (*Aix sponsa*) that have a more southerly distribution and are associated with forests during the breeding season (Hepp & Bellrose, 2020; Longcore et al., 2020). In these cases, a different management strategy is needed. In the Atlantic Flyway, reservations about using population dynamics of mallards breeding in eastern North America to set regulations for other species in the flyway arose because the eastern

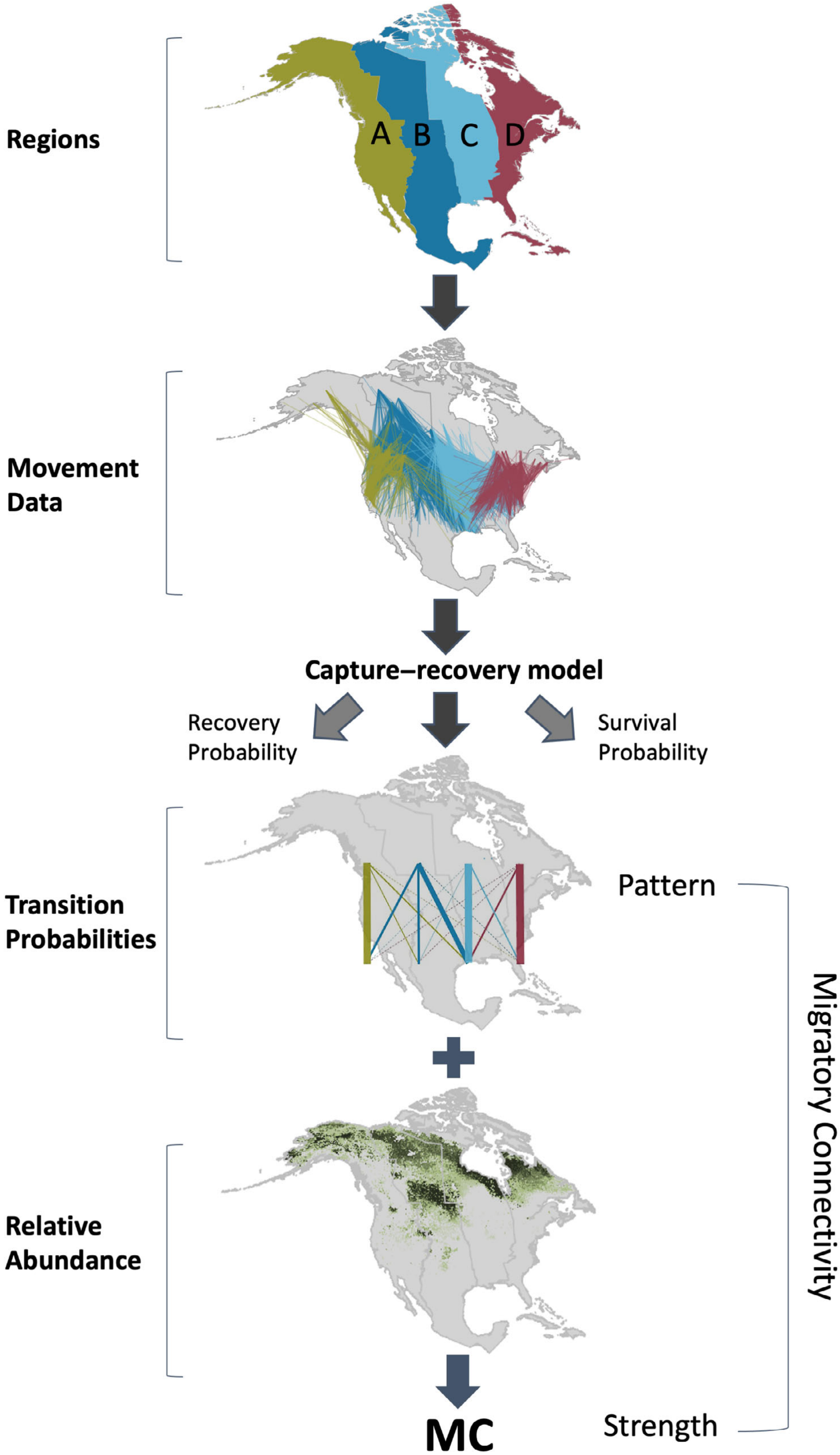

FIGURE 1 Conceptual figure illustrating the use of capture–recapture data to estimate transition probabilities and migratory connectivity. Regions (i.e., flyways) need to be defined according to areas of interest. Movement data (i.e., band and recovery data) are then used in a model to estimate transition probabilities, migratory connectivity (MC) patterns, between regions. Relative abundance among regions is combined with transition probabilities to estimate migratory connectivity strength. In the current case, regions are administrative flyways of Pacific (A), Central (B), Mississippi (C), and Atlantic (D).

mallard population did not adequately account for the composition of harvest (Johnson et al., 2019). This species variability led the Atlantic Flyway Council to adopt a multispecies management approach to setting harvest regulations based on the status of eastern breeding populations of common goldeneye (*Bucephala clangula*), green-winged teal (*Anas carolinensis*), ring-necked ducks (*Aythya collaris*), and wood ducks, as these species represent a variety of breeding habitats and together make up 45% of duck harvest in the flyway (Roberts, 2020). Another alternative to management based on a single species is species-specific cross-flyway population models. This strategy is currently used for American black duck, northern pintail (*Anas acuta*), and scaup (*Aythya affinis* and *A. marila*; U.S. Fish and Wildlife Service, 2019a). These two alternatives to single-species, flyway-based harvest strategies add a complexity to the promulgation of annual regulations, but may be necessary if no single species represents the population dynamics and movements of North American waterfowl.

Harvest derivations are a population-level metric used by managers to determine the source of harvested individuals. They incorporate information on population size and are centered around harvest, or wintering, areas. The result is an estimate of what proportion of the harvest in a given region is derived from each breeding area (Munro & Kimball, 1982). Harvest derivations are one of at least three methods of estimating the amount of movement of migratory species among defined regions. Transition probabilities are another population-level metric of migratory connectivity (MC) patterns, that describe the geographic patterns of population movement within and between regions (i.e., flyways), but do not account for variation in marking effort or population size. In contrast with harvest derivations, transition probabilities are often, as done here, defined as the likelihood that an individual from a specific breeding region or breeding population transitions to a specific wintering region (Frederiksen et al., 2018; Webster et al., 2002). Finally, MC strength is a species-level metric that quantifies the extent to which all populations remain together across seasons (Cohen et al., 2018; Marra et al., 2018). The MC metric incorporates the transition probabilities while accounting for the relative abundance of the source populations, given that sampling may not be proportional to the population size (i.e., amount of marking relative to abundance; Cohen et al., 2018). Knowledge of the pattern (transition probabilities) and strength of MC is necessary to guide annual cycle management because it describes the extent to which populations are exposed to the same environmental conditions and management practices (Webster et al., 2002; Woodworth et al., 2017). These may directly affect biological processes including reproductive success, survival, and dispersal (Esler, 2000; Hostetler et al., 2015; Marra et al., 2015). Knowledge of transition probabilities can describe potential disease transmission across the continent and among populations and species.

The four North American flyways were defined geographically using hundreds of band recoveries and survey data collected in the early 1900s (Lincoln, 1935). Frederick Lincoln's seminal work defined multiple migration routes that formed flyways, and he advocated for administrative units tied to those boundaries to manage migratory birds. In the late 1950s, Lincoln's flyways were formalized as administrative units, primarily to facilitate waterfowl management across multiple jurisdictions and agencies (Hawkins, 1984). Lincoln (1935) recognized that the flyways are not independent geographies and waterfowl migrate across administrative flyway boundaries, but changes or variability in migratory movements of waterfowl across the flyways are not regularly updated in management approaches (Blohm et al., 2006; Buhnerkempe et al., 2016; Crissey, 1955). It is now possible, with more than 12 million records from 60 years of migratory waterfowl band recoveries, to revisit movement among Lincoln's flyways among species and through time. Waterfowl and other migratory birds are often managed at the flyway scale; hence it is important to understand if management or monitoring is occurring at the appropriate scale and extent. For example, is harvest management targeting the expected population or how do we target habitat conservation to address regional population declines?

Our objectives were to address three questions about the movement of North American waterfowl as defined by both the pattern (transition probabilities) and strength of MC within and among flyways:

1. How much movement currently occurs between flyways and does the extent of inter-flyway movement vary among flyways? Specifically, we expected the most movement to occur between the Mississippi and Central Flyways, which are managed as a single population, compared with movement from the coastal flyways, which are managed individually.
2. Have the pattern and strength of MC changed through time? We did not have reason to expect specific or directional changes in MC from the time when the administrative flyways were established (~1960), to when the current mid-continent population model was implemented (1990), to the present day (2019). While there have been significant changes in the phenology of migration, there have not been large, disparate changes in habitat conditions across flyways (Guillemain et al., 2015; Thurber et al., 2020).

3. Are mallard transition probabilities and strength of MC representative of those measures for species managed according to mallard population models? We expected statistically similar transition probabilities and MC between mallards and species with similar breeding distributions (e.g., blue-winged teal [*Anas discors*], gadwall [*Mareca strepera*], and the northern shoveler [*Spatula clypeata*]). If the pattern and strength of MC are not the same among those species, we expected mallards to represent a median of all species. This result would suggest that the current management approach is appropriate for a suite of species, but we think differing biology of some species may result in different patterns and strength of MC, and knowledge of those differences could be applied to improve management.

METHODS

Species and study area

We modeled 60 years of transition probabilities for 15 migratory waterfowl species (Family Anatidae), including 10 dabbling ducks and five diving ducks (Table 1). We focused our analyses on these species because they are managed under the same set of harvest strategies, are migratory, and have sufficient banding data to model transition probabilities. We did not include geese and swans as those species are generally managed as subpopulations, not at the flyway or range-wide scale (U.S. Fish and Wildlife Service, 2019b).

Administrative flyways in the USA are defined primarily along State boundaries (Figure 1). There are four States that participate in both the Central and Pacific Flyway Councils, with the administrative boundary running along the Continental Divide (Colorado, Montana, New Mexico, and Wyoming). Within North America, the provinces and territories of Canada and the federal governments of both Canada and Mexico are partners on flyway committees, but set duck hunting regulations separately from their United States counterparts (https://www.fws.gov/partner/migratory-bird-program-administrative-flyways; accessed 27 June 2022). We assigned each Canadian province and territory to a flyway based on geography, participation in flyway councils, and assignment of birds breeding in their geography to harvest management population models (U.S. Fish and Wildlife Service, 2019a). Ontario east of 80° latitude, Quebec, and all provinces east were considered part of the Atlantic Flyway. Western Ontario, Manitoba, and Nunavut were grouped with the Mississippi Flyway while Alberta, Saskatchewan, and the Northwest Territories were grouped with the Central Flyway. British Columbia and Yukon Territory were considered part of the Pacific Flyway. South of the USA, Puerto Rico, the Virgin Islands, and Cuba were grouped with the Atlantic

TABLE 1 List of waterfowl species and associated information used in the 60-year migratory connectivity analyses.

Species	Scientific name	Group	Harvest management context	Breeding season	Wintering season
Wood duck	*Aix sponsa*	Dabbling	Species specific[a]	April–Aug	Nov–Jan
Blue-winged teal	*Anas discors*	Dabbling	Mallard umbrella	May–Aug	Nov–Feb
Cinnamon teal	*Anas cyanoptera*	Dabbling	Mallard umbrella	May–Aug	Nov–Feb
Northern shoveler	*Spatula clypeata*	Dabbling	Mallard umbrella	May–Aug	Dec–Feb
Gadwall	*Mareca strepera*	Dabbling	Mallard umbrella	May–Aug	Dec–Feb
American wigeon	*Mareca americana*	Dabbling	Mallard umbrella	May–Aug	Dec–Feb
Mallard	*Anas platyrhynchos*	Dabbling	Mallard umbrella	April–Aug	Dec–Jan
American black duck	*Anas rubripes*	Dabbling	Species specific	May–Aug	Dec–Feb
Northern pintail	*Anas acuta*	Dabbling	Species specific	April–Aug	Dec–Jan
Green-winged teal	*Anas carolinensis*	Dabbling	Mallard umbrella[a]	May–Aug	Nov–Feb
Canvasback	*Aythya valisineria*	Diving	Species specific	May–Aug	Dec–Feb
Redhead	*Aythya americana*	Diving	Species specific	May–Aug	Dec–Feb
Ring-necked duck	*Aythya collaris*	Diving	Species specific[a]	May–Aug	Dec–Feb
Greater scaup	*Aythya marila*	Diving	Species specific	May–Sep	Dec–Feb
Lesser scaup	*Aythya affinis*	Diving	Species specific	Jun–Aug	Dec–Feb

Note: Waterfowl are grouped into dabbling and diving ducks and harvest regulations for these species are based on population models of each species (species specific) or mallards (mallard umbrella). Marking and recovery records were assigned to individual flyways by breeding and wintering seasons as defined here.
[a]Except in the Atlantic Flyway where these species are managed as a group.

Flyway, Central America and all Mexican states not in the Pacific Flyway were grouped with the Central Flyway, and the Mexican states of Baja California, Baja California Sur, Senora, and Sinaloa were grouped with the Pacific Flyway.

Banding data

We obtained locations for all individuals of the 15 focal species that were banded during breeding and reported as shot or found dead >200 km from the banding location during winter (United States Geological Survey [USGS] Bird Banding Laboratory). We included all band types for birds banded during the breeding season, the timing of which was defined for each species using expert opinion and previous research (Table 1). We grouped recoveries by age (hatch year or adult), flyway where they were banded, flyway where they were recovered, and the decade of banding (1960–1969, 1970–1979, 1980–1989, 1990–1999, 2000–2009, 2010–2019).

All species we considered occurred almost exclusively in North and Central America. Some waterfowl that breed in Alaska may migrate to Asia, and some small proportion of blue-winged teal and cinnamon teal (*A. cyanoptera*) may migrate to South America. Because South American recoveries were very rare and were often derived from breeding populations outside the North American management areas, we excluded recoveries outside North and Central America.

Relative abundance

We obtained relative abundance measures for each species of dabbling duck using available breeding season estimates of the number of adults (U.S. Fish and Wildlife Service, 2019b). Mallard estimates are available for all flyways and are relatively precise, so if abundance was not available for a species in a flyway, we used the ratio of mallards in the Central Flyway to the appropriate flyway from breeding season estimates as an estimate of the species-specific flyway abundance. For example, northern pintail abundance is not estimated in the Atlantic Flyway, so we used the ratio of mallard abundance in the Central Flyway to the Atlantic Flyway (0.14) multiplied by the Central Flyway northern pintail abundance estimate to produce the Atlantic Flyway northern pintail abundance estimate. We compare transition probabilities as well as MC among species, and we may expect to see different patterns between transition comparisons and MC comparisons if this method had a strong bias. The relative abundance results from this method were similar to those found using other datasets (USGS Breeding Bird Survey and Cornell Laboratory of Ornithology eBird relative abundance). Diving duck abundance data were sparse and for these species we used USGS Breeding Bird Survey indices to estimate relative abundance (Link et al., 2020). Breeding Bird Survey indices were compiled for each flyway as described above. Abundance estimates for all species were only available during the most recent decade (2010–2019). Therefore, the strength of MC (see *Data analysis*) was only estimated for all species for a single decade. We used adult relative abundance for three species (mallard, green-winged teal, ring-necked duck) for the prior two decades (1990–1999 and 2000–2009) to compare the change in MC over the most recent 30 years. Two species have a geographic range that does not include all four flyways and, for that reason, these flyways were not included in the species' models: American black ducks are not present in the Pacific Flyway and cinnamon teal are rare in the Atlantic and Mississippi flyways.

Data analysis

We used a capture–mark–recovery model based on the division coefficient method to estimate bird distribution from banding and recovery data (Kania & Busse, 1987; Korner-Nievergelt et al., 2014). The specific model used here is modified from Frederiksen et al. (2018) to estimate species-specific transition probabilities among flyways, or the proportion of ducks banded (breeding) in each flyway that wintered in each flyway. The model uses a multidimensional array built from banding and recovery data to estimate the probability a bird survives, is recovered, and transitions within and among flyways. We built multidimensional arrays with dimensions of the breeding flyway, year banded, wintering flyway, and year recovered. We assumed that recoveries of banded birds in the same year and the same breeding area had a multinomial distribution. Cell probabilities of the array were then modeled as functions of survival, transition, and recovery probabilities. The associated code detailing all cell probabilities is available per the *Data availability statement*.

We estimated species-specific survival and transition probabilities for juveniles (hatch year) and adults. To reduce model parameters, we used a constant survival estimate for each juvenile and adult survival. Survival estimates were given a flat prior truncated at 0 and 1 as beta(1,1). The recovery probability represents the chance a duck transitions to a given wintering area, is shot or found dead during winter (rather than on migration), that it is recovered, and that the band number is reported. We kept the annual recovery probability constant across all years, wintering areas, and among the two age groups. Annual recovery probability was given a prior beta(1,1). Given current knowledge of waterfowl demographic rates, we considered using more informative priors for survival and recovery, but there was very little improvement in model convergence when we did this with a test data set. We also desired to compare survival and recovery rates to estimates from previous work to qualify model performance.

The juvenile and adult transition probabilities represent the probability that a bird banded in a particular flyway during breeding spends the winter in a particular flyway. The transition probabilities for one age group during one time period (decade) sum to one for each flyway where birds were banded, assuming the four flyways represent the entire wintering range of each species. We modeled transition probabilities as decadal changes using six 10-year periods starting in 1960. Priors for transition probability were beta(1,1) for transition between the flyway where the bird was banded and the same or neighboring flyway where the bird was recovered. We expected transitions to a nonadjacent flyway (e.g., Atlantic to Central or Pacific, Mississippi to Pacific) to be uncommon, so we assigned a prior beta(1,100) based on expert opinion and similar to Frederiksen et al. (2018). In regard to transition probabilities, the Frederiksen et al. (2018) model requires that the number of destination (wintering) areas does not exceed the number of origin (breeding) areas, which fits our objectives of estimating movement among the four administrative flyways. The model also assumes that each breeding area is connected to more than one wintering area, all individuals of a species winter within the designated areas, and recovery and reporting probabilities do not vary within wintering regions. The former two assumptions are met by the entire range of species existing within our study area and annual movements that occur, at least partially, between flyways. Although recovery and reporting rates may vary across geographic boundaries, these should be specific to a wintering area, not a breeding area (Boomer et al., 2013; Zimmerman et al., 2009). Harvest regulations are homogeneous within a flyway, so there is no evidence for differences in those rates among birds from different breeding areas.

For each species we estimated posterior parameter distributions using Markov chain Monte Carlo (MCMC) methods in JAGS (Plummer, 2003) with the *jagsUI* package (Kellner, 2019) for Program R. We ran three chains with the first 10,000 iterations discarded as burn-in and a thin rate of 5. Chains were run in sets of 10,000, and stopped when convergence was reached for all parameters. Thus, parameter estimates were based on a varying number of posterior samples by species. We assessed model convergence by visual inspection of posterior plots and estimating the Gelman statistic, $\hat{R}$. Following standard practice we considered values <1.1 as indicative of adequate model convergence (Gelman & Hill, 2006).

To estimate MC for each species, we used the R package *MigConnectivity* v.0.4.0 (Hostetler & Hallworth, 2021). We restricted MC estimates to include adult transition probabilities because we did not have independent estimates of relative abundance for juveniles. Migratory connectivity is an approximation of Mantel's correlation coefficient for discrete regions and, as such, its boundaries are −1 and 1 (Cohen et al., 2018). Due to the nature of discrete distance correlations, it is rare to get an MC estimate that is below 0, but variance estimates often overlap 0. If MC is strong (MC = 1), breeding populations remain within the same flyway in winter and if MC is weak (MC = 0), breeding populations spread out equally across flyways during winter. We added new flexibility to how the *MigConnectivity* package estimates MC in the new function "estStrength" for this analysis. Formerly, the package could only estimate MC from transition probabilities that were estimated using the R package *RMark* (Laake, 2013). The new function can alternatively incorporate transition probability estimates expressed as an array of samples (e.g., the posterior samples from MCMC). We applied this new MigConnectivity application here by estimating MC (95% credible interval [CI]) using the posterior samples from the model described above.

We estimated MC for 2000–2019 for all species and the three most recent decades for the three species for which we had relative abundance estimates during that period (mallards, green-winged teal, and ring-necked ducks). We tested for significant differences in MC among species and through time when appropriate with the "diffMC" function in the *MigConnectivity* R package that estimates the difference between the two independent estimates of MC (Cohen et al., 2019). We considered no significant difference between two estimates when the 95% confidence interval of the difference crossed zero. While it is generally true that lower numbers represent weak connectivity and higher strong connectivity, the meaning of the specific MC estimates presented here are best interpreted relative to each other as they all use the same geographical regions. The objective of the MC metric (Cohen et al., 2018) was to increase comparisons among taxa and studies with comparable methods that account for differences inherent to movement data used to estimate transition probabilities. However, the real-world range of variability in MC is still unclear. Therefore, the threshold values for "weak" or "strong" MC are yet to be determined.

Comparisons between transition probabilities were made by calculating the difference in posterior samples and examining the resulting 95% CIs of the difference.

Significant differences in transition probabilities are reported in the text if the 95% CI of the difference did not overlap 0. Significant differences are used to test two of our hypotheses, that pattern and strength of MC have not changed through time and that mallards are representative of species with similar life histories. Results are presented as the posterior median ± 95% credible interval, unless stated otherwise.

RESULTS

During the 60-year period from 1960, more than 12 million dabbling ducks and more than 700,000 diving ducks were banded in North American flyways during the breeding season (Appendix S1: Table S1). Of those, more than 300,000 dabbling ducks and more than 6000 diving ducks were recovered during winter (2.7% of the dabbling ducks and 0.79% of the diving ducks) and included in models of flyway-based movement. In support of the validity of the modeled transition probabilities, survival and recovery probabilities were similar to estimates from other research (Krementz et al., 1997). The posterior median annual adult survival probability for the 15 species of ducks ranged from 0.55 to 0.79, with diving ducks generally having higher annual survival probabilities than dabbling ducks (Appendix S1: Table S2). Median annual juvenile survival probabilities ranged from 0.29 to 0.48 (Appendix S1: Table S2) and were similar between dabbling and diving ducks. Recovery rates for 14 of the 15 species ranged from 0.001 to 0.039, while gadwall had a higher posterior median recovery rate of 0.081 (Appendix S1: Table S1). Across species, adult and juvenile transition probabilities were similar, with the exception of mallards in three of the flyways (Roberts, 2022). As compared with juvenile mallards, adult mallards were more likely to remain within the Mississippi and Pacific Flyways between seasons and less likely to remain in the Central Flyway between seasons (Figure 2). These differences were small (<0.10) and not seen in other species, therefore we discuss only adult transition probabilities for all species hereafter.

Migratory connectivity among flyways

Transition probabilities (the pattern of MC) were high within the coastal flyways; the probability of remaining within the Atlantic or Pacific Flyways between breeding and wintering seasons (e.g., banded in the Atlantic and recovered in the Atlantic) was >0.70 for all species during the most recent decade (2010–2019; Figures 2 and 3). In the most recent decade, about one-quarter of the birds breeding in the Pacific Flyway moved to winter in other flyways while around 30% of birds breeding in the Atlantic Flyway moved to winter in other flyways (Roberts, 2022). For dabbling ducks, the probability of remaining within the coastal flyways was higher than the probability of remaining within the middle two flyways (Figure 3). There was one exception to this pattern; blue-winged teal did not differ in the extent to which they remained within middle versus coastal flyways between seasons (Figure 3). The degree to which diving ducks remained in the same flyway between seasons was similar across species and flyways (Figure 3). There were two exceptions to this pattern, ring-necked ducks were more likely to remain within the Atlantic Flyway (0.87%–0.97 95% CI) than all other flyways and canvasbacks (*Aythya valisineria*) were more likely to remain within the Pacific Flyway (0.77–0.96) compared with all other flyways.

Management plans consider duck populations in the Central and Mississippi Flyways to be a single population (U.S. Fish and Wildlife Service, 2019a). When summed, the transition probabilities within and between the Central and Mississippi Flyways represent the combined mid-continent MC patterns. These were similar to, but still lower than, movement within the coastal flyways. For example, mallard movement from the Central to the Central or Mississippi had a median of 0.72 compared with transition probability within the Atlantic (0.85) and within the Pacific (0.97). This was true for all species, except blue-winged teal for which the movement from the Central to the Central or Mississippi (total median = 0.80) was higher than within the coastal flyways 2010–2019 (Atlantic Flyway = 0.53, Pacific Flyway = 0.46; Figure 2). For many species, movement from the Central Flyway to the Mississippi Flyway was the only among flyway movement that was higher than within-flyway movement (Roberts, 2022).

The strength of MC for adult movement between breeding and wintering flyways ranged from weak (with 95% CI crossing or close to zero) to low (median < 0.3 and CI above 0) to moderate (median 0.3–0.6), while no species had high MC (Figure 4). Species with weak MC included diving ducks (greater scaup and lesser scaup) and dabbling ducks (gadwall, blue-winged teal) and species with moderate MC included ring-necked duck, green-winged teal, American black duck, and wood duck (Figure 4).

Migratory connectivity through time

Transition probabilities for North American waterfowl species changed only moderately over six decades, from the time administrative flyways were established (~1960), to when the current mid-continent population model was

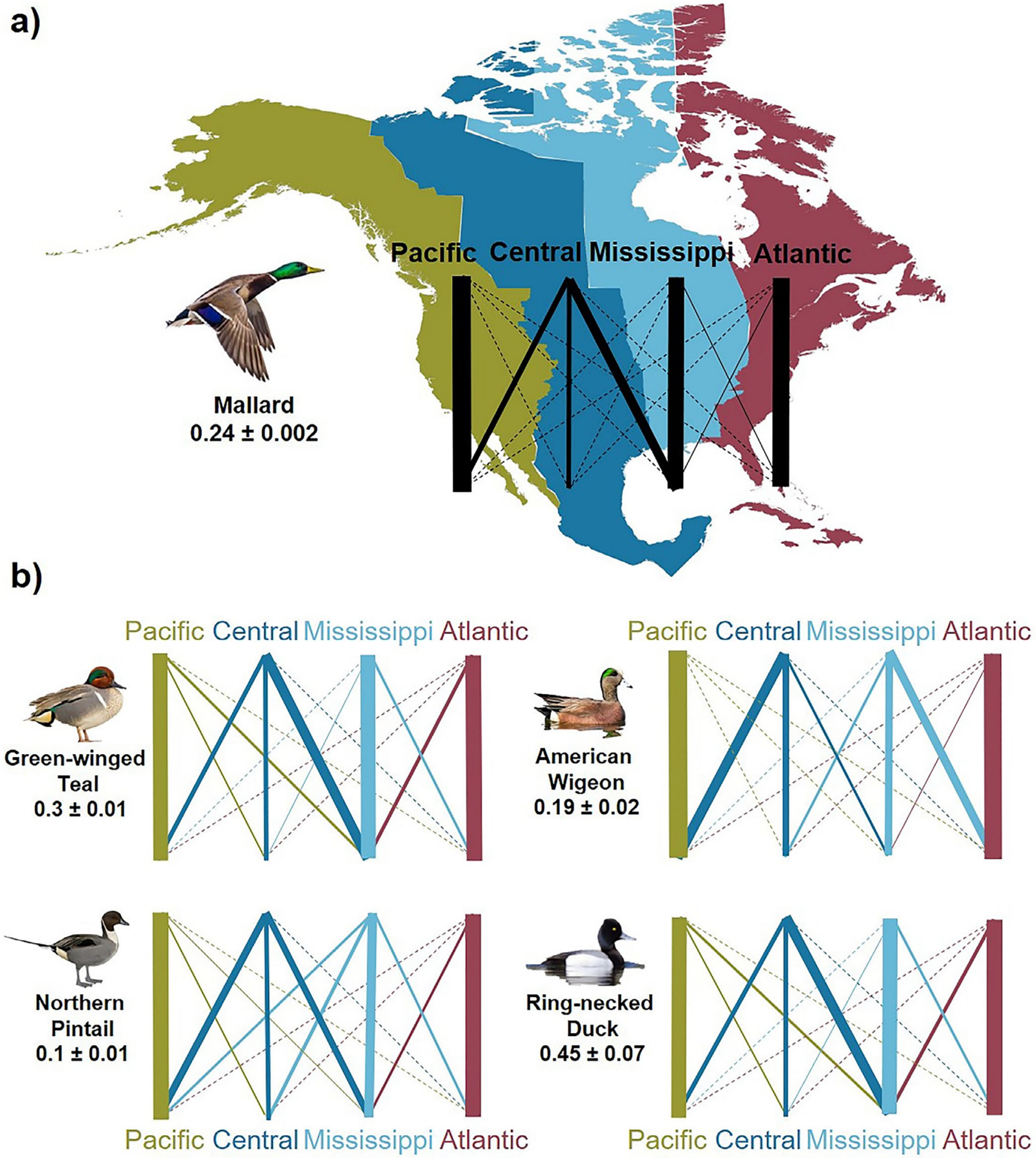

FIGURE 2 North American administrative flyways with breeding to nonbreeding wintering transition probabilities for mallards (a) and four representative species (b). Movement among flyways (i.e., median transition probabilities) are depicted by the width of the line, during 2010–2019. The strength of migratory connectivity (MC) incorporates range-wide transition probabilities and relative breeding abundance among flyways and is reported for each species as the median ± SE.

implemented (1990), to the present day (2019). There were no clear cross-species patterns, although some species showed decadal differences in specific movements between flyways (Appendix S1: Figure S1). The proportion of mallards that remained within the Mississippi Flyway increased from the 1960s (0.68–0.73 95% CI) to the 2010s (0.79–0.81) with a corresponding decrease in movement from the Mississippi Flyway to the Atlantic Flyway

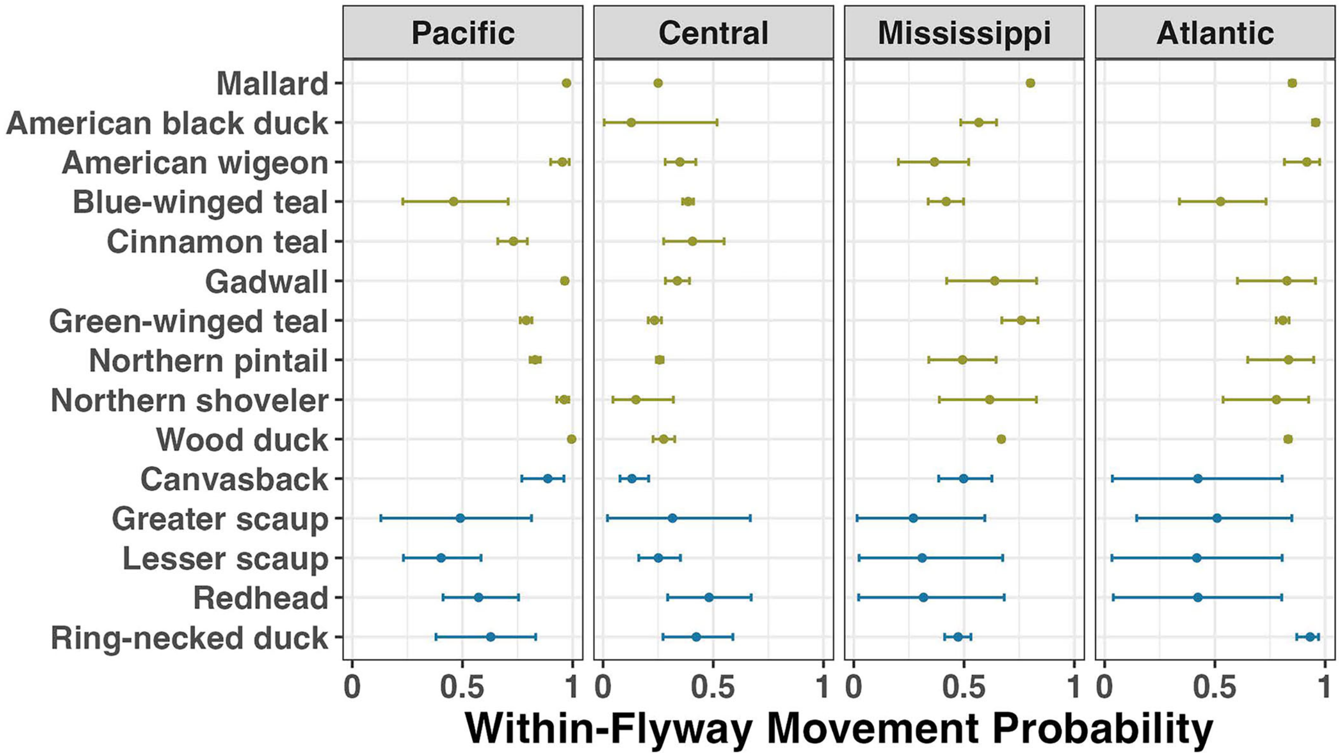

FIGURE 3 Movement within the same flyway from breeding to wintering defined as the transition probabilities for the four North American administrative flyways (median ± 95% credible interval of within-flyway transition probabilities) during 2010–2019 as estimated from breeding banding and wintering band-recovery records. Species with yellow lines are classified as dabbling ducks and those with blue lines are diving ducks. [Correction added on 10 February 2023, after first online publication: Figure 3 has been updated in this version.]

(1960s = 0.23–0.28, 2010s = 0.15–0.16; Roberts, 2022). Mallard movement probability from the Central Flyway to the Pacific Flyway also increased during that period (1960s = 0.22–0.25, 2010s = 0.27–0.28), while the opposite movement from the Pacific to the Central decreased (1960s = 0.01–0.05, 2010s = 0.00–0.02; Roberts, 2022). Gadwall transition within the Pacific Flyway increased (1960s = 0.43–0.73, 2010s = 0.95–0.97) with a corresponding decrease in movement from the Pacific to the Central Flyway (1960s = 0.23–0.52, 2010s = 0.02–0.04). Green-winged teal exhibited the opposite movement patterns to gadwall, with a decrease in the extent to which they remained within the Pacific Flyway (1960s = 0.82–0.95, 2010s = 0.76–0.81) and from the Central to the Pacific (1960s = 0.35–0.44, 2010s = 0.19–0.25; Figure 4). Correspondingly, green-winged teal movement from the Central to the Mississippi Flyway increased (1960s = 0.22–0.31, 2010s = 0.49–0.56) and, similar to mallards, the probability they remained within the Mississippi Flyway increased (1960s = 0.41–0.65, 2010s = 0.67–0.84). The probability of northern pintails remaining within the Central Flyway between seasons had decreased over the past six decades (1960s = 0.31–0.37, 2010s = 0.24–0.27). Finally, canvasbacks transition probability increased within the Mississippi Flyway (1960s = 0.12–0.42, 2010s = 0.38–0.63), while movement from the Central to the Mississippi also increased (1960s = 0.09–0.31, 2010s = 0.41–0.59).

MC strength differed through time for two species, mallards and green-winged teal, but not for the third species, ring-necked duck (Figure 5; Appendix S1: Table S2). For both mallards and green-winged teal, the strength of MC increased from 1990–1999 to 2000–2009 but then decreased from 2000–2009 to 2010–2019 (Figure 4). Ring-necked duck MC was more uncertain than either of the two dabbling duck species and did not change over the three decades (Figure 5).

Comparisons between mallards and other species

In the most recent decade, patterns of MC for mallards and other dabbling ducks were often similar (Figures 2, 3). Differences in transition probabilities within flyways were most common. Within-flyway transition probability of mallards in the Central Flyway (0.24–0.26) was lower than gadwall (0.28–0.39), American wigeon (*Mareca americana*; 0.28–0.42), and blue-winged teal (0.36–0.41; Figure 4). In the Pacific Flyway, the within-flyway transition probability of mallards (0.97–0.98) was higher than green-

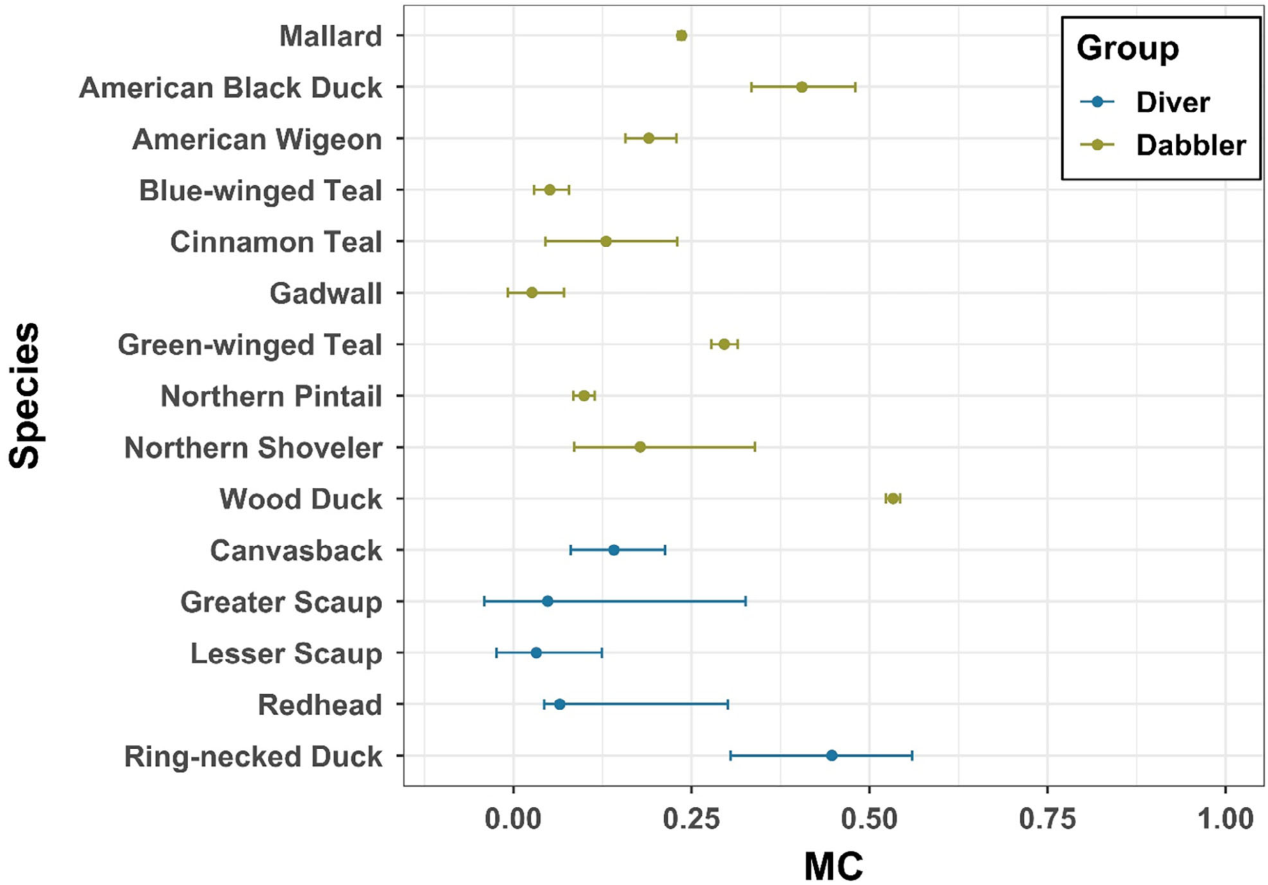

FIGURE 4 The strength of breeding to wintering migratory connectivity (MC; median ± 95% confidence interval) for North American waterfowl species during 2010–2019 within the four management flyways as estimated from banding and recovery records and relative abundance among flyways.

winged teal (0.76–0.81), blue-winged teal (0.23–0.71), and northern pintail (0.81–0.85). Other significant differences were within the mid-continent flyways, and would not affect management.

There were a few differences in mallard among flyway transition probabilities compared with other species. The movement to the coastal flyways from the mid-continent was lower for mallards than American wigeon in both the Mississippi to Atlantic movement and the Central to Pacific movement (Roberts, 2022). There were no differences between mallards and other dabbling ducks for movements to or from the Atlantic Flyway, rather differences were found in transitions to and from the Pacific Flyway. Mallards had a higher transition probability from the Central Flyway to the Pacific Flyway (0.27–0.28) than gadwall (0.03–0.07), green-winged teal (0.20–0.25), blue-winged teal (0.00–0.01), and wood ducks (0.00–0.02). In contrast, mallards had a lower transition probability from the Central to the Pacific than northern pintail (0.38–0.41). In addition, mallards had a lower transition probability from the Pacific to the Central (0.01–0.02) than gadwall (0.02–0.04), green-winged teal (0.01–0.10), blue-winged teal (0.16–0.63), and northern pintail (0.08–0.12).

Diving duck transition probability estimates were less precise due to fewer banding records, but median estimates for each species were similar to mallards (Roberts, 2022). Between-flyway movements of mallards were not different from diving ducks, but there were a number of within-flyway differences (Figure 3). Mallards had higher transitional probabilities within all flyways compared with all diving duck species except redheads (*Aythya americana*) in the Central Flyway and ring-necked ducks in the Atlantic and Central Flyways (Figure 3).

Mallard MC strength was within the range of values of the other species. The large number of marking and recovery records for mallards, compared with other species, is reflected in the high precision of the MC estimate compared with other species (Figure 4). Nevertheless, MC values for mallards differed significantly from all of the dabbling ducks with the exception of the northern shoveler, as measured by diffMC confidence intervals (Appendix S1: Table S2). Among the dabbler species,

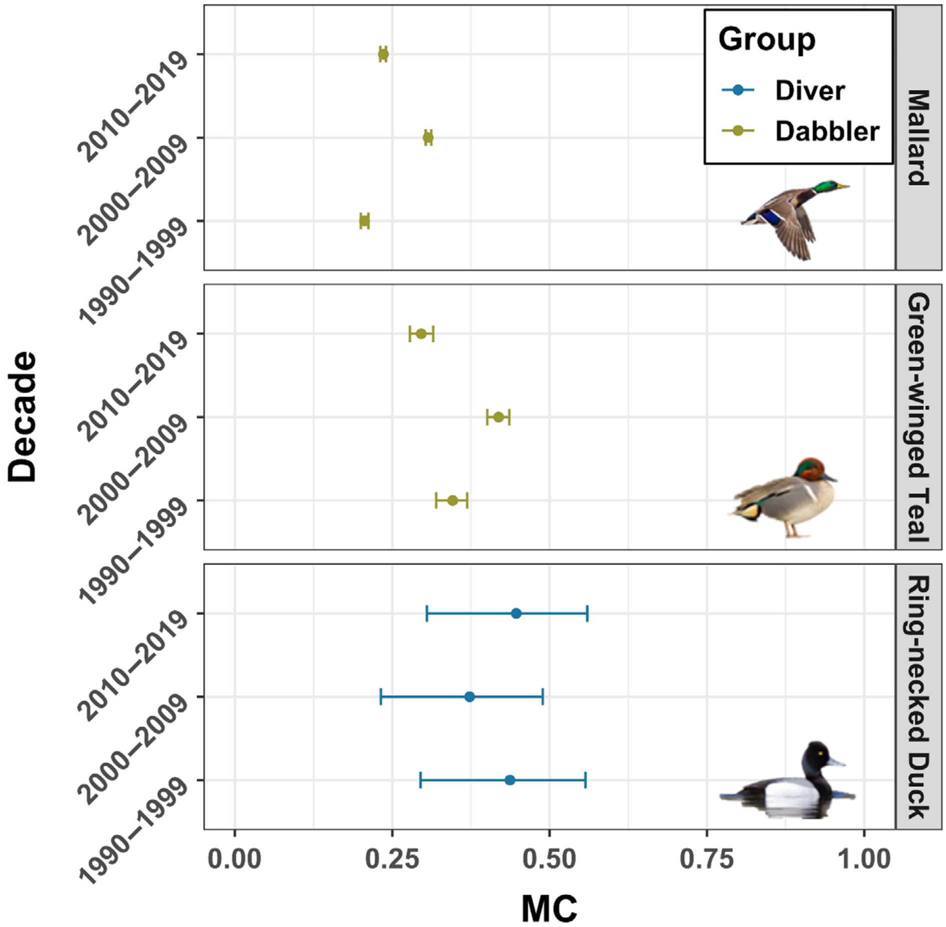

FIGURE 5 Breeding to wintering strength of migratory connectivity (MC; median ± 95% confidence interval) among the four North American management flyways over three decades (1990–1999, 2000–2009, 2010–2019) for three North American waterfowl species.

three were significantly higher than mallards, American black duck, green-winged teal, and wood duck, while five dabbler species were significantly lower than mallards (Figure 4). The strength of mallard MC differed from three of five diving duck species (Appendix S1: Table S2). Among the diving duck species, there was no difference in MC between mallards and either greater scaup or redheads, while ring-necked ducks had stronger MC and both lesser scaup and canvasback had weaker MC (Figure 4).

DISCUSSION

Using 60 years of band-recovery data across North America, we found regular movement of duck species among flyway management units, overall weak MC, and no consistent change in migratory movements across flyways through time. Despite regular movement between flyways, movement within management units (two coastal flyways and the mid-continent region) was high, and there was little evidence of long-term trends in MC. Although it is important to consider species- and flyway-specific MC in management, particularly for species with declining populations, we believe our analysis validates the stability of the flyways as management units with little evidence of long-term trends in MC. Unlike climate-induced effects on the movement of many species at smaller scales (Brisson-Curadeau et al., 2019; Charmantier & Gienapp, 2014; Haest et al., 2019), we found that transition probabilities among administrative flyways have been relatively stable across multiple decades. While North American administrative flyway boundaries have not changed over time, there may be other ways to integrate these new movement results into intergovernmental management units. For example, flyway-specific harvest regulations could represent a jointly optimized strategy across all populations by weighting the relative size of each population exposed to harvest. Given current monitoring programs, relative weights can be estimated annually to track changing environmental conditions.

Migratory connectivity among flyways

Despite the significant movement between flyways, our work suggests that flyway administrative boundaries largely reflect the seasonal movements of these species, because within-flyway transition probabilities were high. Although there are four administrative flyways, population models used to set harvest regulations recognized three distinct populations, the Pacific Flyway, the mid-continent (Central and Mississippi Flyways), and the Atlantic Flyway (U.S. Fish and Wildlife Service, 2019a). Within-flyway transition probabilities were high in both the Atlantic and Pacific Flyways, suggesting that unique management units are appropriate. Transition probabilities were lower within each of the middle two flyways, and managing duck populations by individual flyway in this region would not represent the movements of those birds. Combined with movements between those two flyways, ducks that originated in either the Central or Mississippi Flyways stayed within the mid-continent region during winter. Other studies have used banding data to identify biological flyways and found significant overlap between the biological network and the current administrative flyways for dabbling ducks (Buhnerkempe et al., 2016). Biological flyway boundaries for dabbling ducks from that study had some discrepancies with administrative boundaries, but mostly matched the three populations of the Atlantic, mid-continent, and Pacific. Within the administrative flyways, they found that the Mississippi Flyway had the highest mixing, similar to our results (Buhnerkempe et al., 2016).

Although transition probabilities were often high within individual flyways, at the species level, we found weak and low MC estimates that suggested that no species primarily remained within individual flyways between seasons. Despite high transition probabilities within the two coastal flyways, MC estimates were low due to movements among flyways in the mid-continent. MC also accounted for marking relative to abundance and was influenced by the high population abundance of all species in the Central Flyway. The Central Flyway encompasses the highest density of breeding ducks in North America, largely in the Prairie Pothole Region (Doherty et al., 2018); the large numbers of ducks originating there transition to all other flyways (Batt et al., 1989; U.S. Fish and Wildlife Service, 1986). Although many birds travel south and stay in the Central Flyway during winter, others migrate to the Pacific Flyway to utilize important wetland landscapes (U.S. Fish and Wildlife Service, 1986). This was seen in our relatively high estimates of transition probabilities from the Central to the Pacific Flyway.

The three species with the strongest MC, American black duck, wood duck, and ring-necked duck, have a life cycle that leads to a more restricted distribution than most waterfowl species, and do not have breeding distributions that are skewed toward the Central Flyway (Baldassarre, 2014). American black ducks and wood ducks breed primarily in the two easternmost flyways (Hepp & Bellrose, 2020; Longcore et al., 2020), and remain largely within these flyways throughout their annual cycle (Diefenbach et al., 1988; Hepp & Hines, 1991), as supported by the relatively high and precise transition probability estimates in our study. Ring-necked ducks breed across the continent, but are not as reliant on the Prairie Pothole Region as other dabbling and diving ducks (Roy et al., 2020). They also had the highest within-flyway movements of all diving ducks. These species do not represent the life histories of other ducks, and are not well represented by movements of other species, which further suggests they should be managed independently (Johnson et al., 2019; Roy et al., 2020). Current harvest management of these species acknowledges these differences, as American black ducks have their own adaptive harvest management strategy, and in the Atlantic Flyway wood ducks and ring-necked ducks are managed as part of a multispecies strategy (U.S. Fish and Wildlife Service, 2019a). Ring-necked ducks may benefit from a species-level, cross-flyway management plan based on their unique distribution.

Migratory connectivity through time

We found very little change and no clear trends in transition probabilities over six decades from 1960 to 2019, or in MC over three decades from 1990 to 2019. The former period starts with the formation of administrative flyways, and the latter period reflects changes since the adoption of adaptive harvest management, the system that established three mallard populations used to set harvest regulations currently (Johnson & Williams, 1999). Network models of waterfowl biological flyway boundaries using banding and recovery data also found no temporal change over a single 10-year period (2004–2013; Buhnerkempe et al., 2016). Significant changes in migratory movements through time would signal the need to revisit assumptions about population models and harvest strategies. Overall, we found more birds staying within the same flyway from breeding to wintering periods, with mallards, green-winged teal, and canvasbacks all more likely to remain within the Mississippi Flyway currently, compared with 60 years ago. While we did find occasional among-decade changes in transition probabilities, there were no directional trends in the proportion of ducks that crossed flyway boundaries. Therefore, models or decision frameworks that were developed based on harvest derivations conducted when they were implemented continue to represent the current distributions.

Within the last three decades, there were some differences in MC for mallards and green-winged teal. Both species showed an increase in MC from 1990–1999 to 2000–2009, then a decrease from 2000–2009 to 2010–2019. One hypothesis for this pattern is that plasticity in migration behavior allows ducks to utilize different areas of the continent based on environmental conditions (Hagy et al., 2014; Schummer et al., 2010). We did not test the effect of landscape composition or climate patterns, but the 1990s and the 2010s had wetter landscapes compared with the 2000s as measured by the Palmer Drought Severity Index (Niemuth et al., 2014). More wetland habitat in the primary breeding areas may allow ducks to stay within the same flyway, while during drought conditions they may migrate longitudinally to find appropriate wetlands. Knowledge of the relationship between transition probabilities or MC and landscape variables would allow managers to adjust harvest strategies based on expected changes to movements. Even though we found no impactful changes over the past 60 years, patterns may change in the future along with shifts in human populations, climate, and available habitats. Therefore, we recommend regular monitoring of transition probabilities and MC in concert with adaptive frameworks of flyway-based conservation.

Comparisons between mallards and other species

In the three western flyways, the population dynamics of mallards determine harvest regulations for many other duck species (U.S. Fish and Wildlife Service, 2019a). This assumes that the population fluctuations of mallards accurately track the trajectory of the additional species and that the movement patterns among populations are similar. We found dabbling ducks that primarily nest in seasonal wetlands in the Prairie Pothole Region have similar transition probabilities as mallards, with some exceptions. Gadwall, blue-winged teal, and green-winged teal were less likely to transition to and within the Pacific Flyway than mallards. These species are more closely linked to small, shallow wetlands than mallards, and have wintering distributions concentrated in the central US (Baldassarre, 2014). American wigeon had higher transition probabilities to both coastal flyways than mallards, while northern pintail had lower within-flyway transition probabilities. American wigeon nest further north than many dabbling ducks, and likely use distinct migration routes compared with mallards (Mini et al., 2020). Northern pintails nest further west than mallards and their populations have been declining for many years, and thus they are managed with a population-specific harvest strategy (Podruzny et al., 2002; Runge & Boomer, 2005). Transition probabilities of diving ducks were difficult to compare with mallards due to their low precision, but MC strength estimates were generally lower than mallards, suggesting that species-specific management strategies may be appropriate. Diving ducks have similar breeding distributions as dabbling ducks, but during winter they migrate to areas with more permanent, open water. Scaup, canvasbacks, and redheads all have winter concentrations along large rivers, reservoirs, or coastal bays (Adair et al., 1996; Torrence & Butler, 2006).

Mallard MC was near the middle of most duck species estimates, but many species had values significantly higher or lower. Three species had significantly higher MC than mallards, American black duck, green-winged teal, and wood duck, while five species were significantly lower. A stronger MC makes it easier to manage harvest within an administrative flyway, as the entire population is subject to the same management actions (Webster & Marra, 2005). Unless a group of species has similarly weak MC values, managing species that disperse widely after breeding may best be done with species-specific strategies (Nichols et al., 2007). Accurately determining differences among species is difficult due to large variations in the number of markings and recoveries (Johnson et al., 2015). Therefore, the uncertainty in MC estimates for many species may require additional banding data to obtain more precise estimates, and determine species groupings.

Our results suggest that mallards have transition probabilities similar to many other species and an MC value near the average. However, some species have unique migratory movements and occupy different habitats, necessitating specific management plans. For those species there are costs and benefits to alternative management strategies. Currently single-species harvest management strategies exist for American black ducks, northern pintail, and scaup species (U.S. Fish and Wildlife Service, 2019a). Each of these management strategies was put into place due to declining populations (Johnson et al., 2019). In addition to declining populations, scaup and other divers either breed further north than mallards, or have different habitat associations throughout the annual cycle (Austin et al., 2000; Podruzny et al., 2002). These life-cycle differences mean that population models that are focused on shallow-water nesting dabbling duck population dynamics are not representative of diving duck population dynamics. As such, scaup, canvasbacks, and redheads all have either a separate harvest strategy (scaup) or daily harvest limits that are not influenced by mallard population models. Although the latter strategies are not species specific, they are a step toward recognizing the difference in population dynamics between these species and mallards.

As an alternative to species-specific regulations, harvest regulations could be optimized over a suite of species that represent a broader spectrum of life histories. The Atlantic Flyway detached its harvest regulations from the population status of mallards when it became apparent that those populations did not represent duck species conservation in the eastern USA (Johnson et al., 2019). Our work confirms the low transition probabilities of all ducks from the Mississippi and Central Flyways to the Atlantic Flyway and vice versa. The objectives of this multispecies harvest management strategy are not to match the population dynamics of all other species, but rather to monitor the status of important habitats for waterfowl in the Atlantic Flyway based on the differential habitat preferences, while also acknowledging the importance of some species to hunters. In addition, the species represented in Atlantic Flyway management were shown to have low transition probabilities to flyways further west when first developing the models (Johnson et al., 2019).

Broader implications

In this effort, we demonstrated how to estimate transition probabilities and MC of multiple species with overlapping ranges and similar life histories for management purposes. We added new functionality to the *MigConnectivity* package, making it possible to propagate uncertainty from transition probability estimates using MCMC approaches into MC. This added functionality will improve cross-species comparisons of the strength of migratory connectivity broadly and will the support use of the MC metric in adaptive management frameworks (Brown et al., 2017; Jones et al., 2008). Further, while this abundance of data is not available for many migratory species, tracking and intrinsic markers (i.e., stable isotopes and genetics) are becoming increasingly available to measure the movements of additional species (Contina et al., 2022; Nathan et al., 2022; Ruegg et al., 2021). The methods developed here will facilitate the quantitative exploration of the strength of MC across species and studies by accounting for relative abundance among regions and incorporating the uncertainty inherent to each data type (Cohen et al., 2018).

This approach is highly applicable to other taxa and species in other geographies. However, there are limitations to the approach that should be considered. Low banding, and more importantly re-encounter, sample sizes may lead to less precise estimates with limited inference, as was the case for diving ducks in our study. Real differences between estimates that have low precision are unlikely to be detected, potentially leading to the erroneous conclusion that they are similar. As always, significance tests should be considered alongside estimated effect size (Nakagawa & Cuthill, 2007), with the caveat that low precision can also lead to poorly estimated effect sizes. The effects of sample size on estimates of MC have been explored previously (Cohen et al., 2018). In addition, sample sizes may be limited across regions, not just individual species, but in this case it is the proportion of sampling that is important, not the absolute sample size. Where fewer birds are banded or otherwise marked there will be fewer re-encounters, reducing the precision of the resulting transition probability. Additional potential sources of error that should be considered and have been addressed elsewhere include location error of marking or recovery, or uncertainty in relative abundance (Cohen et al., 2018; Korner-Nievergelt et al., 2014; Thorup et al., 2014). The limitations do not reduce the utility of the methods, as even when recovery rates are relatively low, the accumulations of recaptures in the 100-year banding dataset can still capture important aspects of migration behaviors. Looking forward, integration of these data with additional sources of information about MC (i.e., tracking, intrinsic markers like genetics) can improve estimates.

Our focus is waterfowl, but administrative flyways are also used for the management of other migratory birds, particularly for regulatory decisions like take. Previous research has found that transition probabilities of populations other than waterfowl match administrative flyway boundaries (Kimble et al., 2020; Knight et al., 2018). For example, models have been used to identify three flyways, two coastal and a mid-continent population for shorebirds, waterbirds, songbirds, and raptors (Knight et al., 2018; Lott & Smith, 2006; Morrison & Gill, 2001). This may be the result of vegetation communities available and physical barriers between coastal areas on the mid-continent. However, species-specific MC among these identified flyways is still lacking (Marra et al., 2015). Future work should examine population movements of species other than waterfowl among flyways to determine whether flyways, subspecies, or other scales are most appropriate for management decisions (Kimble et al., 2020). For example, if transition probabilities between regions regularly exceed 75% or MC is near 0, managers likely want to consider different management regions.

Conclusions

Multiple populations are regularly exposed to the same management action at a single point in the annual cycle, thus it is important to understand the MC for these species. This is often true with the harvest of migratory or widespread species besides waterfowl including fisheries (Perruso et al., 2005; Wilson, 1982), waterbirds (Christensen et al., 2017; Guillemain et al., 2014), and passerines (Johnson et al., 2012). Adaptive management approaches will be most effective when they account for the extent to which flyway boundaries match the observed migratory movement between flyways and try to manage in a way that explicitly recognizes the strength of MC. Decision rules for establishing a regulation based on the results of a model vary based on biological factors, including the abundance of waterfowl, and social factors such as the abundance of hunters (Brown & Hammack, 1973; Nichols et al., 2011). For example, the distribution of hunters in North America is skewed toward the Mississippi Flyway, which necessitates different harvest decisions to account for the higher harvest pressure compared with the Central Flyway (Nichols et al., 2007; Raftovich et al., 2019). Flyway-based surveys, data collection, and harvest management programs are uniquely successful examples of long-term evidence-based adaptive management (Nichols et al., 2007), although there are ways to improve inference. If multispecies harvest models are developed we recommend clearly accounting for all species-specific transition probabilities between populations rather than a single species representing many others. Regular estimates of harvest derivations, transition probabilities, and MC metrics allow managers to match current patterns to model assumptions. Additionally, the movement assumptions of population models should be clear, and the results of the estimates should be widely available to articulate the current state of knowledge and uncertainty in management decisions. Despite 60 years and millions of data points, it is still exceptional that migratory flyways established with limited data collected by Lincoln and others in the early 1900s match waterfowl distributions today.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Celis-Murillo et al., 2022) are available in a United States Geological Survey data release at https://doi.org/10.5066/P9BSM38F. Novel code (Roberts, 2022) is provided in the Open Science Framework at https://doi.org/10.17605/OSF.IO/JGAVH.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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