

RESEARCH ARTICLE

Spatiotemporal dynamics of duck harvest distributions in the Central and Mississippi flyways, 1960–2019

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Funding information

Mississippi Flyway Council; Ducks Unlimited, Inc.; Midwest Climate Adaptation Science Center

Abstract

Geographical distributions of waterfowl exhibit annual variation in response to spatiotemporal variation in weather conditions, habitat availability, and other factors. Continuing changes in climate and land use could lead to persistent shifts of waterfowl distributions, potentially causing a mismatch with habitat conservation planning, wetland restoration efforts, and harvest management decisions informed by historical distributions. We used band recoveries and harvest records (i.e., hunter-harvested wings) from the United States Fish and Wildlife Service Waterfowl Parts Collection Survey as indices of duck distribution in autumn and winter, and quantified intra-annual, interannual, and interspecific variation in their geographic distributions across 6 decades (1960–2019) for 15 duck species in the Central and Mississippi flyways in North America. Specifically, we tested for annual and decadal shifts in mean latitude and longitude of recoveries for each month (Oct–Jan) by species and taxonomic guild (i.e., dabbling, diving ducks). Overall, species varied in the extent, timing, and sometimes direction, of distributional change in recoveries. From 1960–2019, mean recovery locations for dabbling ducks shifted south 105–296 km in October and 27 km in November (wings only), whereas mean latitudes shifted north 144–234 km in December and 186–301 km in January. Mean recovery locations for diving ducks shifted north 162 km in October (wings only), 84–173 km in December, and 66–120 km in January, but shifted 99–512 km south in

November. Shifts in longitude were less consistent between guilds and data types. Finally, distributional change rarely accelerated during recent decades, except for southward shifts of band recoveries of diving ducks in November and northward shifts of band and wing recoveries of dabbling ducks in January. Although anecdotal accounts of large-scale northward shifts in duck distributions are prolific in the land management and hunting communities, our data demonstrate more subtle shifts that vary considerably by species and month. Observed changes in recovery distributions could necessitate changes in timing of habitat management practices throughout the Central and Mississippi flyways and may result in fewer hunting and recreational opportunities for some species in southern states. Quantifying patterns of historical change is a necessary first step to understanding temporal and inter-specific variation in waterfowl distributions, which will help with landscape-scale conservation and management efforts in the future and enable effective communication to core constituencies regarding ongoing changes and their implications for recreational engagement.

KEYWORDS

Anatidae, band recovery, distribution, duck, harvest, Parts Collection Survey, waterfowl

Shifts in the distributions of wildlife can have important implications for ecosystem functioning and can change conservation priorities and approaches. Distributional shifts can be caused by a variety of natural and anthropogenic factors, including changes in habitat resource quality, quantity, and juxtaposition (Studds et al. 2016, de Moreas et al. 2020), climate and weather conditions (Hickling et al. 2006, La Sorte and Thompson 2007, Horton et al. 2020), local predator and prey communities (Myers et al. 2007, Stantial et al. 2021), introduction of species into novel environments (Elliott and Arbib 1953), diseases or parasites (Anagnostakis 2001, Valenta et al. 2016), pesticide use (raptors; Rosenberg et al. 2019), and human disturbance (Burger and Niles 2013, Kays et al. 2016, Gallego-Zamorano et al. 2020). Because of the variety of underlying causes, distributional shifts can occur in multiple cardinal directions depending on which influence is changing and introduce a range of management challenges. For example, although the recovery of Canada goose (*Branta canadensis*) numbers in North America since the 1950s can be considered a conservation success story, several populations have increased in abundance and expanded their distributions at considerable rates, such that they now are a frequent source of human-wildlife conflicts, especially in urban areas (Balkcom 2010, Flockhart and Clarke 2017, Fox 2019, U.S. Fish and Wildlife Service [USFWS] 2022). Similarly, rising temperatures have caused numerous migratory bird species to alter migration timing and shift winter distributions toward the poles, thereby potentially abandoning protected areas closer to the equator and requiring management and conservation efforts in new places (La Sorte and Thompson 2007, Tayleur et al. 2015, Horton et al. 2020). Regardless of the underlying causes, quantifying distributional shifts of species is valuable because management efforts based on historical distributions may no longer be the most effective.

Understanding potential shifts in geographic distributions is especially important for waterfowl during autumn and winter. Most waterfowl populations in North America are actively managed and hunted, and decisions regarding habitat conservation and management require a thorough understanding of spatiotemporal patterns of waterfowl distributions and population dynamics (Alisauskas et al. 2013, Roy et al. 2017, Roberts et al. 2022, USFWS 2022). During autumn and winter, waterfowl distributions are largely determined by the number and diversity of available wetlands on the landscape, amount and types of accessible food within a landscape, and anthropogenic disturbance (Pearse et al. 2012, Beatty et al. 2014, Hagy et al. 2014, Haugen et al. 2014). Annual variation in weather conditions, hunting pressure, and availability of wetlands and food at local or regional scales can cause the extent and timing of migration and resulting waterfowl distributions to vary substantially across years (Schummer et al. 2010, Haugen et al. 2014, Masto et al. 2022, Weller et al. 2022). In contrast, combined effects of directional change in weather conditions, land use, the availability and hydrology of wetlands, expansion or shifts in primary grain crops, continued declines of coastal wetlands, and restoration of historically converted wetlands in other regions raise the potential for more substantial, persistent, and directional shifts in waterfowl distributions (Dale 1997; Duncan et al. 1999; King et al. 2006; Guillemain et al. 2015a, b; McKenna et al. 2017; National Oceanic and Atmospheric Administration 2022).

Waterfowl habitat is often managed at the taxonomic guild level, but because of differences in species traits and life-history strategies, waterfowl may exhibit substantial levels of variation in distributional patterns among species and at intra- and interannual scales. For example, in Europe and North America, winter distributions have shifted northwards for some species, as shown by surveys (Brook et al. 2009, Lehikoinen et al. 2013, Meehan et al. 2021) and band recoveries (Švažas et al. 2001, Sauter et al. 2010, Gunnarsson et al. 2012), or are predicted to do so in the future based on modeling efforts (Notaro et al. 2016, Reese and Skagen 2017). On the other hand, southward shifts or lack of distributional change have been observed for other waterfowl species and regions (Green and Kremetz 2008; Guillemain et al. 2015a, b). Extensive interannual variation in weather conditions could mask effects of long-term changes in weather and habitat conditions on winter distributions, especially when studies take place over a relatively short period (Green and Kremetz 2008, Schummer et al. 2010, Haugen et al. 2014). Moreover, migration behavior and spatiotemporal variation in factors affecting migration can cause intra-annual variation in waterfowl distributions (Green and Kremetz 2008, Schummer et al. 2017, Masto et al. 2022), necessitating assessment of shifts at finer temporal scales. Finally, life-history differences in breeding location, foraging ecology, adult survival, and migration timing, duration, and distance may produce species-specific responses in autumn and winter distributions to changing conditions (Baldassarre and Bolen 2006; Guillemain et al. 2015a, b; Schummer et al. 2017; Masto et al. 2022), which emphasizes the importance of assessing potential shifts in winter distribution for a variety of waterfowl species in a comparative framework.

Although North American waterfowl have been extensively studied, limited empirical data are available to directly quantify their distributions during autumn and winter across large spatial scales and long (multi-decadal) periods. Location data from annual band recoveries and waterfowl harvest records (i.e., hunter-harvested wings) from the USFWS Waterfowl Parts Collection Survey (PCS; Padding et al. 2006, Pearse et al. 2014) may serve as useful indices of waterfowl distribution when viewed across large spatial and temporal scales (Green and Kremetz 2008).

In this descriptive study, our first objective was to quantify intra-annual, interannual, and interspecific variation and temporal trends in autumn and winter distributions of band recoveries and hunter-harvested wings (i.e., wings) for 15 species of migratory ducks in the Central and Mississippi flyways in North America across 6 decades (1960–2019). Specifically, we tested for annual shifts in mean latitude and longitude of band and wing recoveries for each month (Oct–Jan) and 2 taxonomic guilds (dabbling ducks [tribe Anatini], diving ducks [tribe Aythini]). As a second objective, we sought to test whether distributional shifts between 1960–2019 occurred gradually or could be attributed to rapid changes during distinct periods. We therefore compared decade-specific mean recovery latitude and longitude for each month and species to a decade-long baseline period (1960s).

STUDY AREA

To facilitate management and conservation of migratory birds and their habitat, the USFWS and its partners established 4 administrative flyways (Atlantic, Mississippi, Central, Pacific) during the late 1940s and early 1950s based on prevailing north–south bird migration routes. The Central and Mississippi flyways encompass the central United States from the Continental Divide in the west to Ohio in the east, the Canadian provinces of Alberta, Saskatchewan, Manitoba, Ontario, and the Northwest Territories to the north, and large portions of Mexico in the south. For our analysis, we included band and wing recovery data from only the 10 states in the United States within the Central Flyway (CO, KS, MT, NE, NM, ND, OK, SD, TX, WY) and the 14 states in the United States within the Mississippi Flyway (AL, AR, IL, IN, IO, KY, LA, MI, MN, MS, MO, OH, TN, WI). Major ecoregions in our study area include the Great Plains, parts of the Eastern Temperate Forests in the east, and parts of the Northern Forests in the north. Following a north–south gradient, average temperatures in October ranged from 6.8–22.2°C, in November from –0.8–16.8°C, in December from –8.6–13.1°C, and in January from –11.2–12.1°C (National Oceanic and Atmospheric Administration 2023).

METHODS

Our initial analysis included 15 migratory duck species that are commonly leg-banded and harvested throughout the Central and Mississippi flyways. We included 8 species of dabbling ducks (American black duck [*Anas rubripes*], American green-winged teal [*Anas crecca carolinensis*], American wigeon [*Mareca americana*], blue-winged teal [*Spatula discors*], gadwall [*Mareca strepera*], mallard [*Anas platyrhynchos*], northern pintail [*Anas acuta*], and northern shoveler [*Spatula clypeata*]) and 7 species of diving ducks (bufflehead [*Bucephala albeola*], canvasback [*Aythya valisineria*], common goldeneye [*Bucephala clangula*], greater scaup [*Aythya marila*], lesser scaup [*Aythya affinis*], redhead [*Aythya americana*], and ring-necked duck [*Aythya collaris*]).

Data handling

We obtained band recovery data for 15 species of ducks recovered within the United States portion of the Central or Mississippi flyway between 1960–2019 ($n = 656,383$ bands) from the United States Geological Survey (USGS) Bird Banding Laboratory (pwrc.usgs.gov/BBL/Bander_Portal, accessed 21 Sep 2021). We included direct and indirect band recoveries of ducks that were shot (89.66% of all bands) or found dead (1.77% of all bands) during the hunting season (Oct–Jan). We excluded band recoveries from September because of analytical difficulties caused by spatially inconsistent efforts resulting from the introduction of an early (i.e., Sep) teal hunting season in the late 1960s and early 1970s. Excluding bands recovered in September lowered the sample size by 5.81% (of which 68.71% were from blue-winged teal). Last, most band recoveries were reported with a spatial accuracy of a 10-minute latitude block or finer ($\sim 14 \times 19$ km), but we excluded a small proportion of bands whose recovery location was reported at coarser spatial scales (0.25% of all bands).

We included only band recoveries from ducks that were banded in the United States or Canada during the pre-hunting banding season (Jul–Sep). We excluded band recoveries from dabbling ducks banded in the winter because of potential differential survival probabilities and other unknown effects on distribution analyses, but for canvasback, greater scaup, lesser scaup, and redhead, we took advantage of more extensive banding efforts during spring migration (Feb–Apr) at Pool 19 of the Mississippi River in Illinois, and in other states (e.g., NY, MD, VA) to bolster sample sizes. Restricting our dataset by these banding month criteria reduced our sample size by 22.98%. Finally, to avoid potential effects that banding efforts may have on migration behavior and resulting winter distributions, we further restricted our data to include only birds that were held <24 hours during banding, did not

carry a nasal tag or radio-transmitter, and were released within the same 10-minute block from which they were captured (94.15% of all recoveries).

We obtained wing recovery records for the Central and Mississippi flyways from the USFWS PCS (B. Raftovich, USFWS, personal communication). Through the PCS, the USFWS receives duck wings from participating hunters (~90,000 wings/year nationwide), which are then identified to species, age-class, and sex by state and federal biologists (Carney 1992, Padding et al. 2006, Raftovich et al. 2009, Pearse et al. 2014). We included wings for ducks reported at the county level during the hunting seasons of 1961–2019 and considered the central point of the county as the recovery location for our analysis. The spatial accuracy of wing recovery locations was therefore equal to the area of the county of recovery ($\bar{x} = 2,237 \text{ km}^2$). Data for 1960 were unavailable because the PCS did not become fully operational nationwide until 1961. Because the PCS did not differentiate between wings from blue-winged teal and cinnamon teal (*Spatula cyanoptera*), we pooled data for these species. For both datasets, we pooled data across sex and age classes because of low sample sizes for some species.

Accounting for hunting effort and regulations

Using location data of band and wing recoveries as indices of duck distributions requires several assumptions and potential sampling bias corrections. First, sampling probability (i.e., probability of harvesting a banded duck) at any given location is directly dependent on duck hunting dates and zones within states, which have varied since the 1960s in non-random ways. The resulting sampling distribution might not fully represent the underlying duck distribution in the following scenarios: large numbers of ducks are present in states or zones not open for hunting at that time (i.e., inability to be sampled), states or zones are not open for the same duration during a period of interest (i.e., variable sampling probability), and hunting pressure or reporting probability of bands varies substantially among states or zones.

To assess and help correct potential sampling bias related to changes in hunting season dates and zones, we quantified changes in the hunting landscape (i.e., areas open to hunting on a given date or period) between 1960 and 2019. To accomplish this, we first obtained shapefiles or detailed geographic maps of current and historical duck hunting zones from state natural resource agencies within the Central and Mississippi flyways. In cases where shapefiles or maps were not available, we obtained hunting zone delineation descriptions from the Federal Register (<https://www.federalregister.gov>, accessed 23 Feb 2022) and used ArcGIS Pro to manually digitize hunting zones (Esri, Redlands, CA, USA). We then obtained zone-specific hunting season dates from the Federal Register for each year between 1960 and 2019. For each year-zone combination, we used hunting season dates to calculate the number of days that a given zone was open for hunting for each month of interest (Oct–Jan). Although our correction process assumes equal hunting pressure and duck densities within months (which is unlikely), potential effects of this assumption are likely minor relative to the distributional changes over time following our efforts to control for hunting regulation changes. Finally, for each year-zone combination, we assigned the number of open hunting days during a given month as a single value to individual band or wing recoveries based on their geographic location and date using the `over` function in the `sp` package in R (Pebesma and Bivand 2005, Bivand et al. 2013, R Core Team 2022).

We used the number of open hunting days within month of recovery as a correction factor to account for potential issues with sampling unavailability and unequal sampling probabilities. First, to correct for annual differences in open hunting days among zones, we used the inverse of the proportion of days that the hunting zone was open during the month of recovery as a weighting factor for individual recoveries in our statistical models. Second, to assess the proportion of ducks that occupy states or zones not open for hunting during the month of interest (and are therefore unavailable for sampling), we visually examined the residuals from models in which recoveries were weighted by the hunting correction factor for normality and the difference in distributional tail length when compared to a normal distribution with the same mean and standard deviation. Model residuals were normally distributed with <5% of the probability density missing in most species-year combinations, indicating that a

large majority of ducks were available for sampling in our analyses based on band or wing recoveries. Lastly, spatial variation in hunting pressure or closely related (but not identical) recovery probabilities could cause a mismatch between distributions of band or wing recoveries and the underlying duck distribution. However, although temporal trends in hunting pressure and recovery probabilities are affected by a range of factors, including changes in hunter numbers over time, within-year spatial variation in reporting probabilities is likely low for North American ducks (Arnold et al. 2020). Although we did not correct recovery locations for changes in bag limits over time, we believe this is unlikely to greatly bias our findings because bag limits are often set at similar values among states and zones within a given year and are therefore unlikely to cause spatial variation in sampling. A possible exception is if hunters are more likely to achieve their bag limits in certain states or zones than in others, which could cause stricter bag limits to constrain sampling efforts in some locations more than in others. Even so, bias of this type would be expected to be small because changes in season length are likely to have greater effects on harvest within a state.

Statistical analysis

For each species, we used linear models in R (Kutner et al. 2004, R Core Team 2022) to test whether the average recovery location of bands or wings (weighted by the hunting correction factor described above) changed during 1960–2019. We modeled latitude and longitude (separately) of band recoveries as a function of year (continuous), month (categorical), banding latitude or longitude (continuous), and interactions between year and month, and month and banding latitude or longitude, all as fixed effects. We included banding latitude or longitude in all band recovery models to correct for potential effects of banding location on recovery location. We modeled latitude and longitude of wing recoveries as a function of year, month, and their interactions only because wing origins were unknown. To test whether latitude or longitude of band and wing recoveries varied across decades, we included decade as a categorical explanatory variable instead of year as continuous variable in a series of species-specific linear models. By using the county centroid, we ignored some additional within-county variation in wing recovery locations, but potential increases in confidence intervals around parameter estimates are likely to be small when describing multiflyway-wide shifts. We visually examined quantile-quantile and residual plots for normality and homoscedasticity in residuals for all species-month and species-month-decade combinations. Lastly, we considered slope coefficients significant if their 95% confidence interval did not overlap zero.

We used parametric bootstrapping to compare temporal patterns in average latitude or longitude of band or wing recovery locations between dabbling and diving ducks. In each iteration, we first obtained a month-specific estimate of annual or decadal change in latitude or longitude for each species from a normal distribution with a mean and standard deviation based on parameter estimates from the species-specific linear models described above. When sampling estimates from linear models based on band recoveries, we set banding latitude or longitude to its mean value for that month. We then calculated the mean temporal change in recovery latitude or longitude for dabbling and diving ducks separately by averaging estimates across species within each guild. We repeated this process for 100,000 iterations to create a bootstrap distribution of the average temporal change in recovery latitude or longitude for dabbling and diving ducks, and calculated means and standard errors of the resulting distributions. Lastly, we evaluated whether the bootstrapped distributions were significantly different between diving and dabbling ducks by assessing whether the 95% quantile range of the distribution of the difference between both guilds overlapped zero.

RESULTS

Our analysis included 439,880 band and 1,965,461 wing recoveries from 15 duck species (Table 1). A preliminary power analysis using within-month variation in band recovery locations showed that >300 band recoveries/month provided a power of >0.8 to identify significant ($\alpha = 0.05$) latitudinal or longitudinal shifts of 2 degrees across

TABLE 1 Number of band and wing recoveries for 15 duck species in the United States portion of the Central and Mississippi flyways in North America during October–January, 1960–2019.

Category	Species	Code	Bands	Wings
Dabbling ducks	American black duck	ABDU	6,021	23,481
	American green-winged teal	AGWT	8,921	233,785
	American wigeon	AMWI	2,954	104,197
	Blue-winged and cinnamon teal	BCTE		90,441
	Blue-winged teal	BWTE	16,086	
	Gadwall	GADW	5,186	230,445
	Mallard	MALL	351,438	887,603
	Northern pintail	NOPI	20,660	75,646
	Northern shoveler	NSHO	618	66,395
Diving ducks	Bufflehead	BUFF	114	23,948
	Canvasback	CANV	2,170	13,414
	Common goldeneye	COGO	1,178	12,349
	Greater scaup	GRSC	280	8,214
	Lesser scaup	LESC	8,124	74,075
	Redhead	REDH	10,667	37,781
	Ring-necked duck	RNDU	5,463	83,687

60 years, which we considered biologically meaningful (Table S1, available in Supporting Information). Thus, band recovery sample sizes for bufflehead ($n = 114$), greater scaup ($n = 280$), northern shoveler ($n = 618$), and common goldeneye ($n = 1,178$) were too sparse to be included in month-specific analyses. We were also unable to estimate regression coefficients based on band recoveries for common goldeneyes, northern shovelers, and ring-necked ducks for certain month-decade combinations because of small sample sizes ($n < 20$; Table S2, available in Supporting Information). Averaged across months (Oct–Jan) and species, mean band recovery location of ducks harvested in the Central and Mississippi flyways shifted 1 ± 9 km (SE) north and 53 ± 9 km east between 1960 and 2019, whereas the mean wing recovery location shifted 62 ± 3 km north and 41 ± 3 km west during the same period.

Month-specific trends in latitude and longitude

For most species, recovery location of bands or wings was affected by year of recovery, banding location (bands only), month of recovery, and their interactions (Tables S3 and S4, available in Supporting Information). During 1960–2019, recovery locations of dabbling ducks shifted south in October by 105 ± 4 km (wings) to 296 ± 13 km (bands) and November by 27 ± 5 km (wings), while they shifted north in December by 144 ± 7 km (wings) to 234 ± 14 km (bands) and January by 186 ± 8 km (wings) to 301 ± 15 km (bands). Over the same period, mean recovery locations of diving duck in October shifted south by 92 ± 19 km (bands) or north by 162 ± 9 km (wings), south in November by 99 ± 8 km (wings) to 512 ± 20 km (bands), and north in December by 84 ± 26 km (bands) to 173 ± 12 km (wings) and January by 66 ± 16 km (wings) to 120 ± 28 km (bands; Figure 1; Figure S1, available in Supporting Information).

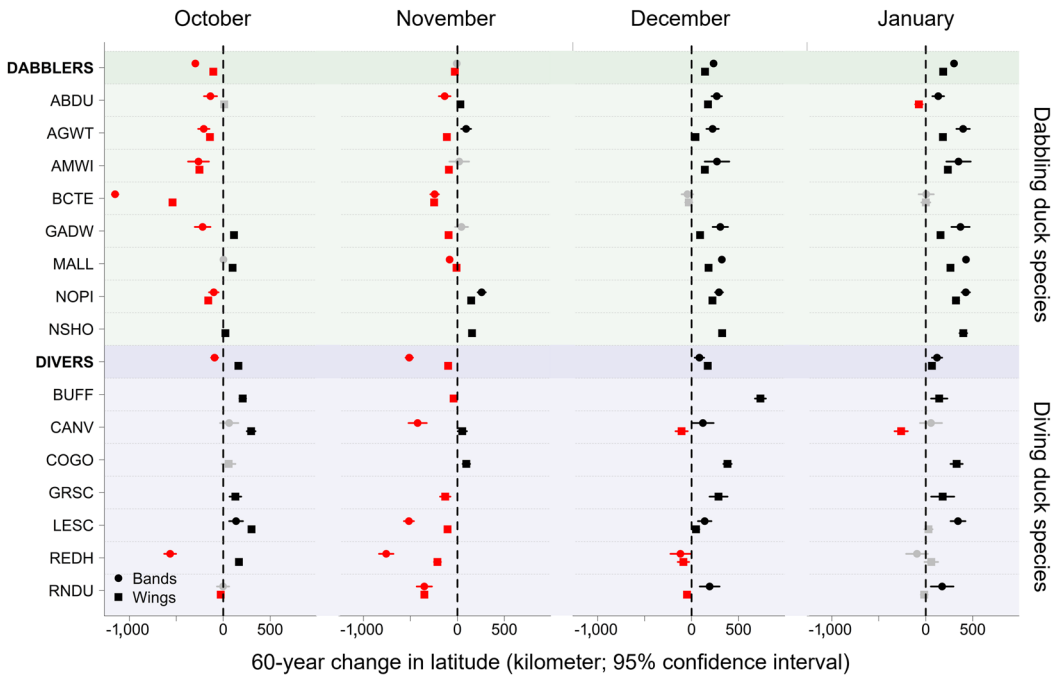


FIGURE 1 Estimated month-specific shifts in average latitude with 95% confidence intervals of band (circles) and wing (squares) recoveries for 15 duck species in the Central and Mississippi flyways in North America during October–January, 1960–2019. Black symbols indicate a significant northward shift, red symbols indicate a significant southward shift, and grey symbols indicate a non-significant shift in either direction. Species include American black duck (ABDU), American green-winged teal (AGWT), American wigeon (AMWI), bufflehead (BUFF), blue-winged teal (BCTE; bands), blue-winged and cinnamon teal (BCTE; wings), canvasback (CANV), common goldeneye (COGO), gadwall (GADW), greater scaup (GRSC), lesser scaup (LESC), mallard (MALL), northern pintail (NOPI), northern shoveler (NSHO), redhead (REDH), and ring-necked duck (RNDU). Sample sizes for bufflehead, common goldeneye, greater scaup, and northern shoveler were insufficient for band recovery analyses.

Overall, latitudinal shifts for individual species matched dabbling or diving duck mean responses, but species response of dabbling ducks in October (wings) and diving ducks in January (bands, wings) were more variable (Figure 1; Table S5, available in Supporting Information). The most extreme northward shifts in mean band and wing recovery location were observed for bufflehead in December (731 ± 30 km; wings), mallard in January (428 ± 6 km; bands), northern pintail in January (425 ± 23 km; bands), and northern shoveler in January (399 ± 21 km; wings), whereas the most extreme southward shifts were observed for redhead in October (563 ± 32 km; bands) and November (756 ± 39 km; bands), blue-winged teal in October (538 ± 12 km; wings), and lesser scaup in November (515 ± 27 km; bands; Figure 1, S1; Table S5).

In October, recovery locations of dabbling ducks shifted either east by 124 ± 10 km (bands) or west by 105 ± 3 km (wings), and east in November by 111 ± 10 km (bands) to 117 ± 4 km (wings), in December by 29 ± 5 km (wings) to 46 ± 12 km (bands), and in January by 17 ± 6 km (wings) to 69 ± 13 km (bands). At the same time, mean recovery locations of diving ducks shifted west in October by 137 ± 13 km (bands) to 240 ± 10 km (wings), west in November by 43 ± 7 km (wings), east in December by 59 ± 20 km (bands) and either east by 72 ± 22 km (bands) or west by 114 ± 16 km (wings) in January (Figure 2; Table S6, available in Supporting Information).

Species-specific responses in longitudinal shifts were more variable than in latitudinal shifts, especially for diving ducks in October, December, and January (bands), and for dabbling ducks in December (bands only) and January (bands and wings; Figure 2; Table S6). We observed the most extreme eastward shifts in band and wing

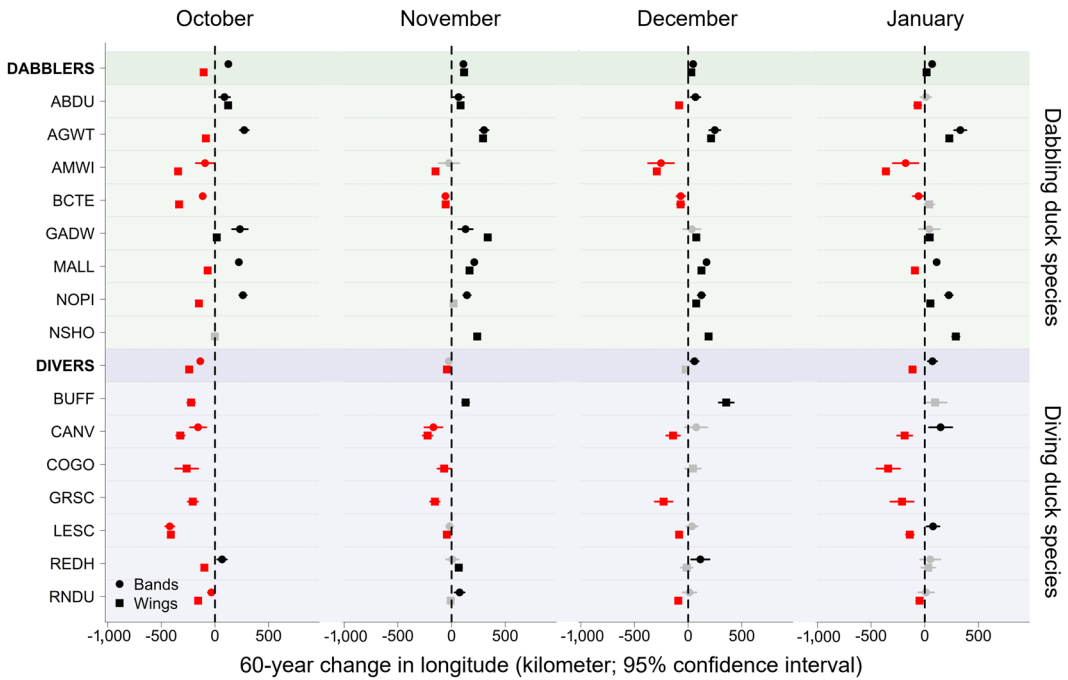


FIGURE 2 Estimated month-specific shifts in average longitude with 95% confidence intervals of band (circles) and wing (squares) recoveries for 15 duck species in the Central and Mississippi flyways in North America during October–January, 1960–2019. Black symbols indicate a significant eastward shift, red symbols indicate a significant westward shift, and grey symbols indicate a non-significant shift in either direction. Species include American black duck (ABDU), American green-winged teal (AGWT), American wigeon (AMWI), bufflehead (BUFF), blue-winged teal (BCTE; bands), blue-winged and cinnamon teal (BCTE; wings), canvasback (CANV), common goldeneye (COGO), gadwall (GADW), greater scaup (GRSC), lesser scaup (LESC), mallard (MALL), northern pintail (NOPI), northern shoveler (NSHO), redhead (REDH), and ring-necked duck (RNDU). Sample sizes for bufflehead, common goldeneye, greater scaup, and northern shoveler were insufficient for band recovery analyses.

recoveries in canvasback in January (471 ± 80 km; bands), gadwall in November (337 ± 5 km; wings), bufflehead in December (355 ± 36 km; wings), and American green-winged teal in October (273 ± 23 km; bands), November (303 ± 23 km; bands), and January (331 ± 32 km; bands; Figure 2; Table S6). Westward shifts in distributions were most extreme for lesser scaup in October (421 ± 22 km; bands, 411 ± 10 km; wings) and American wigeon in October (343 ± 8 km; wings) and January (362 ± 18 km; wings; Figure 2; Figure S2, available in Supporting Information).

Decadal changes in latitude and longitude

The direction and magnitude of latitudinal and longitudinal shifts in band and wing recoveries assessed at a decade-by-decade basis were largely comparable to estimates from linear regression models (Figures 3 and 4; Tables S7 and S8, available in Supporting Information). Compared to the 1960s, band and wing recovery locations of dabbling ducks in October shifted farther south each decade (except the 2010s), whereas wing recoveries of diving ducks continued to shift north. Band recoveries of diving ducks in November steadily shifted south across decades, whereas band and wing recoveries in December shifted north over time for both dabbling and diving ducks. In January, band and wing recoveries of dabbling ducks continually shifted north across decades, whereas

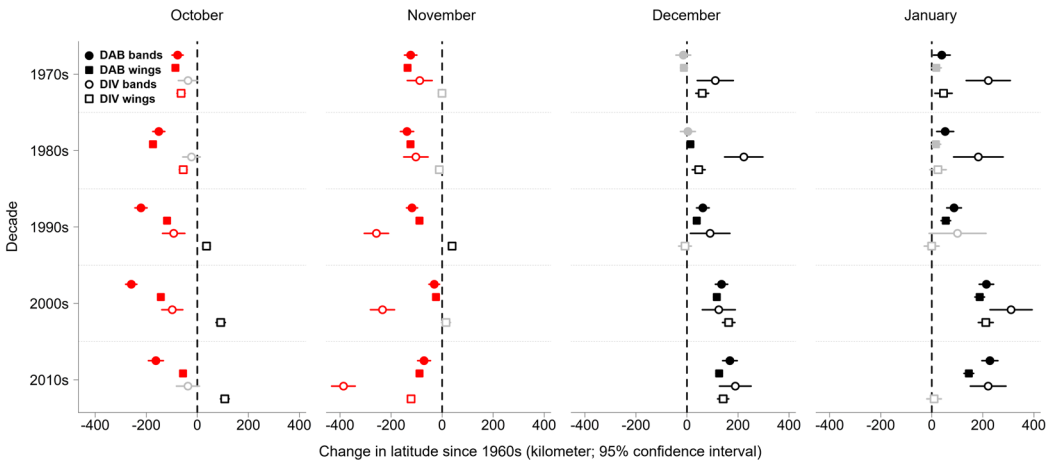


FIGURE 3 Average latitudinal shifts of band (circles) and wing (squares) recoveries for 15 duck species in the Central and Mississippi flyways in North America during October–January for each decade, 1960–2019. Shown are the average responses for 8 species of dabbling ducks (DAB; solid symbols) and 7 species of diving ducks (DIV; open symbols). Means and 95% confidence intervals for each decade indicate a shift in kilometers from the average latitude of recoveries from 1960–1969. Positive values in black represent significant northward shifts and negative values in red represent significant southward shifts. The following species were not included in estimates: bufflehead, greater scaup, and northern shoveler for October and November; bufflehead, common goldeneye, greater scaup, and northern shoveler for December; and bufflehead, canvasback, common goldeneye, greater scaup, northern shoveler, and ring-necked duck for January.

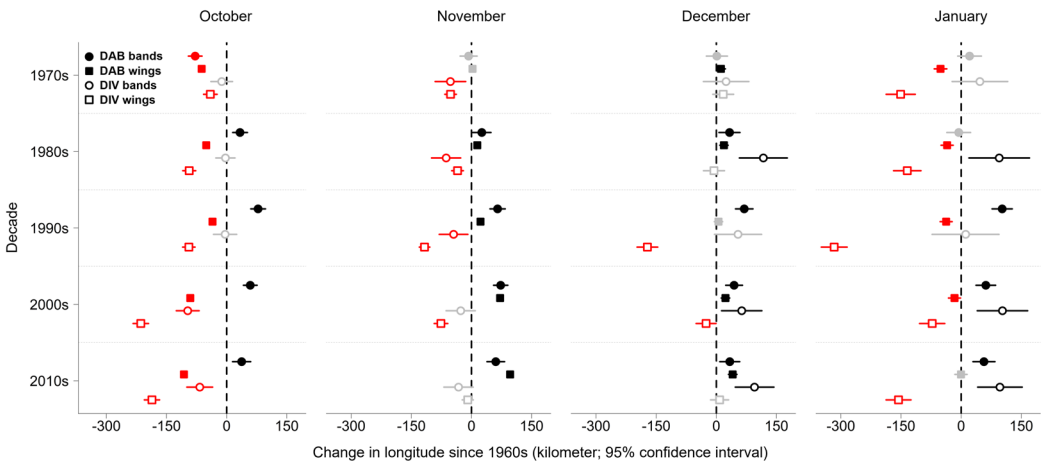


FIGURE 4 Average longitudinal shifts of band (circles) and wing (squares) recoveries for 15 duck species in the Central and Mississippi flyways in North America during October–January for each decade, 1960–2019. Shown are the average responses for 8 species of dabbling ducks (DAB; solid symbols) and 7 species of diving ducks (DIV; open symbols). Means and 95% confidence intervals for each decade indicate a shift in kilometers from the average longitude of recoveries from 1960–1969. Positive values in black represent significant eastward shifts and negative values in red represent significant westward shifts. The following species were not included in estimates: bufflehead, greater scaup, and northern shoveler for October and November; bufflehead, common goldeneye, greater scaup, and northern shoveler for December; and bufflehead, canvasback, common goldeneye, greater scaup, northern shoveler, and ring-necked duck for January.

band recoveries of diving ducks initially shifted northwards in the 1970s, but this shift did not continue during later decades (Figure 3; Table S7). Overall, distributional change rarely accelerated during recent decades, except for southward shifts of band recoveries of diving ducks in November and northward shifts of band and wing recoveries of dabbling ducks in January.

Decade-specific shifts in latitude of recoveries for individual species were consistent with estimates for their associated dabbling or diving duck guilds but were overall more variable (Table S5). The species with the most extreme northward shift in band or wing recovery distribution between the 1960s and 2010s include bufflehead in December (535 ± 32 km; wings), canvasback in December (395 ± 91 km; bands), common goldeneye in January (343 ± 35 km; wings), northern pintail in January (340 ± 23 km; bands), American black duck in December (318 ± 22 km; wings), greater scaup in December (315 ± 47 km; wings), and northern shoveler in January (313 ± 26 km; wings; Table S5). Southward shifts in distributions were most extreme for redhead in November (587 ± 36 km; bands), blue-winged and cinnamon teal in October (565 ± 19 km; bands, 333 ± 13 km; wings), lesser scaup in November (431 ± 25 km; bands), and ring-necked duck in November (387 ± 44 km; bands; Table S7).

Longitudinal changes in band and wing recoveries showed few continued shifts across decades since the 1960s, except for a persistent westward shift by diving ducks in October and an eastward shift by dabbling ducks in November (Figure 4; Table S8). We observed the most extreme eastward shifts in band and wing recovery distributions between the 1960s and 2010s in bufflehead in December (313 ± 38 km; wings) and American green-winged teal in November (215 ± 22 km; bands) and January (268 ± 33 km; bands; Table S8). Species with the most extreme westward shifts included common goldeneye in January (373 ± 59 km; wings), and lesser scaup in October (338 ± 20 km; bands, 345 ± 10 km; wings), American wigeon in October (303 ± 9 km; wings), December (209 ± 64 km; bands), and January (213 ± 63 km; bands, 339 ± 18 km; wings), and canvasback in November (251 ± 62 km; bands; Table S8).

DISCUSSION

Using 60 years of band and wing recovery data from 15 duck species in the Central and Mississippi flyways of central North America, there were minimal shifts in recovery distributions over time when considering the entire autumn and winter period (Oct–Jan), which was consistent with previous research on mallards on a more limited timescale (Green and Kremetz 2008). But when examined monthly, the mean latitude of band and wing recovery distributions has shifted south in October and November, and north in December and January by several hundred kilometers for most species. Moreover, there was considerable variation among species and taxonomic guilds (dabbling vs. diving ducks) in the extent, and sometimes direction, of distributional change over time. Our December and January data join a growing body of work indicating that winter distributions of several duck species have shifted north (Švažas et al. 2001, LaSorte and Thompson 2007, Gunnarsson et al. 2012, Lehtikoinen et al. 2013, Meehan et al. 2021) or are likely to do so in the future (Notaro et al. 2016, Reese and Skagen 2017). Previously reported inconsistencies in the extent and direction of distributional change (Green and Kremetz 2008; Guillemain et al. 2015a, b) correspond to the interspecific and intra-annual variation in distributional change observed in our study. We therefore conclude that summarizing distribution shifts across species and months within the nonbreeding season could mask underlying finer-scale patterns important for habitat conservation and useful in recreational hunting and viewing opportunities.

The observed lack of consistency in species response among months might help explain why Green and Kremetz (2008) did not observe latitudinal trends in mallard band and wing recovery distributions in the Mississippi Flyway between 1980 and 2003, a period in which we observed northward shifts in recovery distributions for mallards, but only in December and January (Table S5). In contrast, Schummer et al. (2017) reported decreases in area with weather severe enough to encourage southward migration during autumn and early winter (Oct–Dec) and mid-winter (Nov–Jan), suggesting that northward shifts in duck distributions are expected

during both periods, not just during December–January as observed in our study. Both the act of migration itself and spatiotemporal variation in factors affecting winter distributions can result in intra-annual variation in waterfowl distributions during autumn and winter (Schummer et al. 2017). For instance, greater pressure to move south in late autumn by worsening weather could be replaced by an increased need to find open water and available food in a (relatively stable) mid-winter landscape. Observed intra-annual variation in distributions emphasizes the importance of assessing shifts at finer temporal scales than the entire autumn-winter season and indicates that drivers important in determining duck distributions might vary across months.

As expected, we observed variation in the direction and magnitude of latitudinal shifts among species and between taxonomic guilds during most months. Life-history differences among species, including diet and foraging strategy, propensity to forage on agricultural resources, and variation in response to changes in environmental conditions, may all contribute to species-specific responses in autumn and winter distributions (Baldassarre and Bolen 2006; Guillemain et al. 2015a, b; Schummer et al. 2017; Masto et al. 2022). Differences in foraging strategy could result in different responses to cold weather events, with wetland obligates showing a greater response than generalist species that have greater plasticity in foraging (Tidwell et al. 2013, Hitchcock et al. 2021, Masto et al. 2022). Similarly, Meehan et al. (2021) reported that although 12 of 16 duck species in the Atlantic and Mississippi flyways exhibited a negative relationship between change in abundance and average winter temperatures, blue-winged teal, canvasback, redhead, and wood duck (*Aix sponsa*) did not. Lastly, decreases in area with weather severe enough to cause southerly duck migration in the Atlantic and Mississippi flyways showed a >3-fold difference among several species (gadwall: 3,239 km², northern shoveler: 890 km²; Schummer et al. 2017). Both observed and previously reported interspecific variation in the magnitude, timing, and direction of distributional shifts highlight the importance of assessing winter distribution shifts for a variety of waterfowl species in a comparative framework.

At the taxonomic guild level, dabbling duck band and wing distributions shifted south in October, whereas those for diving ducks did so in November, and distributions for dabbling ducks in January shifted 2–3 times farther north than for diving ducks. Relative to dabbling ducks, research on distributional shifts of diving ducks is limited and conflicting. On one hand, Haugen et al. (2014) reported that average wing harvest latitudes and factors influencing latitude were similar between dabbling and diving ducks in the Central Flyway. Conversely, Meehan et al. (2021) documented that the inverse relationship between local abundance trends and average winter temperatures was about 1.5 times stronger for dabbling ducks than for diving ducks. Existing work on dabbling duck distributions might therefore not be a representative alternative for studying diving ducks.

The mallard is a common generalist species that occurs widespread throughout North America, but our results indicate that shifts in its harvest distribution do not adequately represent distributional shifts for other dabbling duck species. Observed distributional shifts by mallards resembled the mean response of dabbling ducks, but frequently differed from the response of individual species, with gadwall and northern pintail, the species most like mallards, showing comparable shifts only in approximately 50% of the cases (Figures S1–S2). Although researchers have previously reported similarities between mallards and other species in winter distributional shifts (Meehan et al. 2021), factors affecting those shifts (Haugen et al. 2014) or predicted future shifts (Reese and Skagen 2017), our data join a growing body of literature indicating that mallard responses might be similar to only some species (green-winged teal and pintail, but not gadwall and shoveler; Masto et al. 2022), during only some months (Oct–Nov, but not Dec–Jan; Schummer et al. 2017), or to no other species at all (Roberts et al. 2022). Mallards can differ from other dabbling duck species in many ways, including foraging strategy and winter habitat preferences, especially from wetland obligate species such as gadwall and northern shovelers (Tidwell et al. 2013, Hitchcock et al. 2021). Moreover, the timing and extent of fall migration by mallards may be more influenced by weather variables than photoperiodic cues compared to other species, with most mallards often not migrating farther south than necessary to obtain food (Bellrose 1980; Jorde et al. 1983, 1984; Schummer et al. 2010; Weller et al. 2022). That said, regardless of underlying factors influencing differences in distributional shift, our data highlight the challenges of relying on more commonly banded and hunted species such as the mallard when making management decisions for other species.

Although band and wing recovery distributions for blue-winged teal showed some of the greatest southward shifts for any species in October and November, recovery distributions for the species remained largely unchanged during December and January. Meehan et al. (2021) reported no relationship between trends in relative abundance of blue-winged teal and average winter temperatures, suggesting autumn migration and winter distributions may be affected more by changes in photoperiod than by weather-related factors (Van Den Elsen 2016, Meehan et al. 2021). Compared to other species considered in our study, blue-winged teal migrate south earlier and farther, with a large percentage of birds wintering in Central and South America (Rohwer et al. 2002, Baldassarre and Bolen 2006). Moreover, blue-winged teal (and green-winged teal to a lesser extent) are exposed to additional hunting pressure in autumn compared to other species, with the introduction of a September early teal season in most states in the United States since 1966–1967. Rather distinctive migratory tendencies, potential differences in drivers of migratory behavior, and additional exposure to hunting during migration pose unique challenges for explaining observed results but also provide avenues for future research.

There were only a few cases where distributional shifts accelerated during recent decades: southward shift of diving duck band recoveries in November and a northward shift of band and wing recoveries of dabbling ducks in January. Studies on decadal rates of distributional change of waterfowl during autumn and winter are sparse, and it is therefore unclear whether shifts are maintaining a constant pace or are accelerating. Moore et al. (2023) documented a shift in the distribution of band recoveries of greater white-fronted geese (*Anser albifrons*) in midcontinent North America that occurred largely in 3 discrete time periods from 1975–2018, with variable rates of change occurring through time and among study regions. Lehtikoinen et al. (2013) noted that increases in abundance in the northeastern parts of the range of 3 common species of ducks in Europe were greatest in the last 15–20 years of their 30-year study (1980–2010). Moreover, Notaro et al. (2016) predicted greater changes in mean migration dates between mid- and late-21st century versus late-20th century and mid-21st century for 6 out of 7 species of dabbling ducks examined in their study. That said, recent decades have seen slow yet persistent changes in weather conditions, agricultural land use, and the availability and hydrology of wetlands (Dale 1997; Duncan et al. 1999; King et al. 2006; Guillemain et al. 2015a, b; McKenna et al. 2017; National Oceanic and Atmospheric Administration 2022). Although linking distributional changes to underlying causes was beyond the objectives of this study, the relative lack of accelerations in distributional shifts of band and wing recoveries may indicate that such changes are influenced more strongly by factors operating gradually over longer time scales, rather than hunting regulations, banding efforts, or even population changes that act over shorter periods.

The distance of distributional shifts differed between data types (band vs. wing recoveries) in magnitude and, less frequently, direction. In the few species-month combinations where the direction of shifts differed between data types, wing recovery locations systematically moved north in October and November, south in December and January, and west during October, December, and January, whereas band recoveries shifted in the opposite direction (Figures 1 and 2). There could be several reasons for variation in distributional shifts between data types. In our analysis of band recoveries, we were able to account for changes in banding location over time, but breeding ground origins of recovered wings were indeterminable. The spatial distribution of breeding ducks varies annually in response to local habitat conditions and past reproductive success (USFWS 2022), potentially leading to spatial variation in local duck density and subsequent wing recoveries during winter. But when comparing models with and without banding latitude or longitude as covariates, we found that banding longitude (difference in mean adjusted $R^2 = 0.132$; range = 0.043–0.355) but not latitude (difference in mean adjusted $R^2 < 0.002$ for all species) explained some variation in recovery longitude, while neither banding latitude nor longitude explained much variation in recovery latitude (difference in mean adjusted $R^2 < 0.003$ for all species). Therefore, in combination with potential effects of spatial variation in breeding population distribution, banding location may more likely explain differences in longitudinal but not latitudinal shifts in recovery locations between data types. Finally, in contrast to previous studies evaluating band recovery distributions (Green and Kremetz 2008, Moore et al. 2023), our work empirically accounted for potential effects of banding location on recovery location in a manner that enables use of the entire geographic record of banded ducks, which has been demonstrated and encouraged by technical reports

(Munro and Kimball 1982, Szymanski and Dubovsky 2013). Although we can envision other approaches for accounting for potential effects of band location on recovery location, preliminary analyses lead us to believe that little additional precision would be gained by alternative approaches.

Discrepancies in distributional response between data types may also relate to methods by which wings are collected through the PCS. The USFWS selects a sample of hunters from across the United States to submit wings from harvested ducks, but the employed sampling design is chosen for its ability to achieve harvest estimation objectives at large spatial scales (i.e., state, flyway) and may not be optimal for estimating waterfowl distributions, or even harvest thereof, at smaller spatial or temporal scales as examined in this study. Moreover, processes such as urbanization or other social factors could have led to a within-state redistribution of hunters and therefore hunting efforts over time, potentially introducing some minor bias in our continent-wide analysis of wing recovery locations. Although observed discrepancies between data types introduced variation in the magnitude (but only rarely in the direction) of distributional shifts, our results highlight the importance of using multiple data sources to quantify these shifts. Overall, band and wing recoveries are only proxies for duck distributions, and their accuracy is directly related to the degree to which hunting efforts track the presence and abundance of ducks on the landscape over time. Nevertheless, band and wing recovery data provide large sample sizes for many duck species and therefore could offer a useful supplement to population surveys or global positioning system tracking studies in determining geographical shifts in duck distributions in autumn and winter.

MANAGEMENT IMPLICATIONS

Observed southward shifts in October and November, and northward shifts in December and January of several hundred kilometers have important implications for landscape-scale habitat conservation and population management. For example, between 1960 and 2019, January mean band recovery location of mallards shifted from east central Arkansas to southcentral Missouri and that of lesser scaup shifted from southcentral Louisiana to western Mississippi. Managers and hunters throughout the Central and Mississippi flyways will therefore likely encounter waterfowl at different times of the year compared to historical timing, which could affect the optimal timing of habitat management and hunting season dates. For example, southern states in the Central and Mississippi flyways might experience fewer ducks in management areas and therefore fewer hunting and recreational opportunities for some species in December and especially January, a period during which northward distribution shifts have accelerated in recent decades. Observed shifts in band and wing recovery distributions also suggest a potential mid-latitude convergence of ducks resulting in a greater number of birds using the region for longer periods of time than in previous decades, thereby raising the question of whether these landscapes will be able to meet the increased energy demand.

Additionally, large interspecific variation observed in our study presents challenges for generalizing observed distributional shifts across species, putting further emphasis on the necessity of species-specific assessments and consideration in management decisions. While these changes are often complex and vary by species, month, and decade, quantifying patterns of historical change is a necessary first step to understanding variation in waterfowl distributions. Identifying the implications of these changes for actionable habitat conservation and harvest management decisions remains a priority and requires an assessment of the relative importance of underlying mechanistic drivers of distributional shifts, including changes in weather conditions, land use, wetland availability, and human disturbance. Proactive adaptation to these changes will further benefit from mechanistic models capable of forecasting future changes and necessary adjustments to management decisions.

ACKNOWLEDGMENTS

The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the USFWS. Any use of trade, product, website, or firm names in this publication is for descriptive purposes only

and does not imply endorsement by the United States Government. We extend special thanks to all waterfowl banders and supporting agencies in the United States and Canada for over a half-century of work and investment in the waterfowl banding data stream and the USGS Bird Banding Laboratory for curating and providing band recovery location data. We similarly thank biologists in state agencies and the USFWS for curating and providing wing recovery location data from their Waterfowl Parts Collection Survey. We also thank the thousands of waterfowl hunters that enabled this study by taking the extra steps to report band recoveries and submit recovered wings. We are grateful to the state and provincial representatives of the Central and Mississippi Flyway Gamebird Technical Sections for their support, feedback, and for providing delineations of current and historical duck hunting zones. Finally, we thank D. E. Andersen, J. Gammonley, J. S. Lamb, B. E. Ross, E. L. Weiser, and 2 anonymous reviewers for helpful suggestions and feedback on previous versions of the manuscript. This project and B. H. F. Verheijen were funded by USGS Midwest Climate Adaption Science Center, Mississippi Flyway Council, and Ducks Unlimited grants administered through the USGS, the Missouri Cooperative Fish and Wildlife Research Unit, and the University of Missouri. The Missouri Cooperative Fish and Wildlife Research Unit is jointly sponsored by the Missouri Department of Conservation, the University of Missouri, the U.S. Fish and Wildlife Service, the USGS, and the Wildlife Management Institute.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Our research used publicly available band recovery data from the USGS Bird Banding Laboratory for ducks banded over 60 years by biologists and researchers across North America. All historical capture and banding efforts were conducted under the auspices of federal and state banding permits and Institutional Animal Care and Use Committee permits where required.

DATA AVAILABILITY STATEMENT

Our research used publicly available band recovery data curated by the United States Geological Survey Bird Banding Laboratory and wing harvest records curated by the United States Fish and Wildlife Service.

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Associate Editor: Daniel Collins.

SUPPORTING INFORMATION

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How to cite this article: Verheijen, B. H. F., E. B. Webb, M. G. Brasher, and H. M. Hagy. 2023. Spatiotemporal dynamics of duck harvest distributions in the Central and Mississippi flyways, 1960–2019. *Journal of Wildlife Management* e22521. <https://doi.org/10.1002/jwmg.22521>