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Research Article

Exploring Fall Migratory Patterns of American Black Ducks Using Eight Decades of Band-Recovery Data

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ABSTRACT As regions of habitat used by migratory waterfowl are subjected to rising anthropogenic pressures, establishing patterns of landscape use during migratory cycles is becoming increasingly important for managing and maintaining populations. Although data collection strategies such as global positioning system (GPS) telemetry promise high-resolution insight on geographic use of contemporary populations, decades of available band recovery records on many species can provide a low-cost, multi-generational alternative for defining broad, historically informed patterns of landscape use. We used nearly a century of band-recovery data to reconstruct patterns of fall migratory landscape use for American black ducks in the Mississippi and Atlantic flyways. We partitioned band recovery positions by month from September to February and spatially analyzed positions using kernel density estimates (KDEs) to delineate geographic regions used by American black ducks and track changes in landscape use during migration. Additionally, we considered the appropriateness of current management strategies, which treat American black ducks as a single population, by testing for differences in month-specific landscape use between ducks banded in the Mississippi and Atlantic flyways, and between international management units (ducks banded in Canada or the U.S.). We found that geographic distributions during peak migration faithfully recovered regions previously hypothesized as migratory corridors. Furthermore, regardless of banding origin, we found highly similar distributions and strong flyway fidelity in Atlantic flyway American black ducks. Conversely, American black ducks banded in the Mississippi flyway displayed differences in landscape use between Canadian and U.S. populations, with Canadian ducks significantly more likely to winter in areas within the Atlantic flyway (i.e., migrate between flyways). Flyway- and population-specific patterns of black duck landscape use indicate populations behave more independently than currently treated by management models (including the Adaptive Harvest Management plan), and that population maintenance may be advanced by managing stocks separately.

KEY WORDS *Anas rubripes*, Atlantic flyway, banding records, Mississippi flyway.

Migratory species use many geographic regions and habitats throughout their annual cycles (Fryxell and Sinclair 1988, Beier and Noss 1998, Thirgood et al. 2004). For ducks, research has primarily focused on breeding, molting, and wintering areas (Serie et al. 1983, Bowman and Brown 1992, Yarris et al. 1994, Robertson and Cooke 1999, Nicolai et al. 2005), with little attention to delineating regions of important mid-migratory habitat (Newton 2006). However, the quality of mid-migratory habitat is critical to successful migration cycles (Raveling 1979, Krapu 1981, Ankney et al. 1991, Madsen 1995, Anteau et al. 2004). Management and conservation of waterfowl populations require high-quality data on their key migratory habitats and overall geographic requirements (Nichols et al. 1995*a*, Krementz et al. 2011). Although telemetry methods offer fine-resolution data for studying landscape use by duck populations (see Kendall and Nichols 2004), expense and technological complications limit sample sizes of individuals and temporal coverage. In contrast, banding records, which typically include decades of data on thousands of individuals, provide considerable temporal and spatial coverage. For example, using band recovery data, Calenge et al. (2010) were able to successfully delineate the timing and geography of fall and spring migratory corridors of Eurasian green-winged teal (*Anas crecca*) across southern France.

American black ducks (*Anas rubripes*) have been a species of management concern in eastern North America since

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population declines in the 1950s (Collins 1974). Although, harvest regulations are independently established by American and Canadian agencies (Fig. 1; United States Fish and Wildlife Service [USFWS] 2011), many decisions are driven by an Adaptive Harvest Management plan, which treats black ducks across the continent as a single population (Conroy et al. 2002). Past studies have indicated the existence of multiple, independently fluctuating black duck stocks, including stocks purported to include ducks from within only a few states or provinces, to those within whole flyways (Geis et al. 1971, Blandin 1982, Pendleton and Sauer 1992); however, the existence of different stocks has not been conclusively resolved. If independent stocks exist across North America, each with characteristic differences in population ecologies and patterns of landscape use, their formal recognition is an important component of successful future management (Conroy et al. 2004). Stock-specific management, for example, could be more responsive to changes in local population and/or habitat availability.

Zimpfer and Conroy (2006) attempted to identify black duck stocks using banding data. Concentrating on patterns of flyway fidelity for Atlantic and Mississippi flyway ducks, they found qualitative distinctions between these populations. Specifically, the analyses of Zimpfer and Conroy (2006) indicated that whereas Atlantic flyway ducks showed high flyway fidelity, Mississippi flyway ducks more-commonly engaged in movement between the flyways. However, because they analyzed band recovery records from across fall months, they noted that individuals killed in mid-migration may have inflated perceptions of flyway fidelity (i.e., some ducks that would have moved outside their home flyway were killed before doing so). This could have led to underestimates of inter-flyway movement. Thus, as we present here, an added benefit of evaluating the timing of migration and changes in associated distributions across different regions is a refined understanding of inter-flyway migration.

Figure 1. Map of the Mississippi and Atlantic flyways according to Baldassarre and Bolen (1994), with flyways partitioned into Canadian and U.S. management units. Key regions are highlighted and numbered: 1) Prairie Pothole Region; 2) Great Lakes Region; 3) Mississippi Alluvial Valley; 4) Junction of St. Lawrence and Lake Champlain Bay; 5) Chesapeake and Delaware Bays; and 6) Lake Marion, Lake Moultrie leading to Bulls Bays, and Charleston Harbor.

Using band recovery data from 1922 to 2007, we created the first maps of monthly (Sep–Feb) patterns of landscape use for migrating black ducks in the Mississippi and Atlantic Flyways, and investigated migration phenology and flyway fidelity. Specifically, we delineated changes in landscape use during fall migration and identified regions of habitat connecting pre-migratory and wintering regions. To test the consistency of black duck landscape use within flyways, we partitioned banding data by international management units, distinguishing between ducks banded in Canada from those banded in the United States. Although separating ducks by political boundaries is largely arbitrary, these political boundaries also longitudinally separate pre-migratory regions across landscape features (e.g., eastern and western boundaries of Lake Ontario, eastern and western regions of Lake Michigan). Thus, whether taken as arbitrary or as a distinction between potentially meaningful breeding regions, this sampling scheme provided a test of black duck population structure. If black ducks act as a single continental population (supported by the Adaptive Harvest Management plan), we expected similar patterns in landscape use, migration timing, and flyway fidelity regardless of data partition (at least at the flyway level). Thus, differences between Canadian and U.S. ducks would provide evidence of multiple stocks, though precise stock definitions would likely require additional work.

METHODS

Data

We obtained banding records from GameBirds software provided by Patuxent Wildlife Research Center. We used only records categorized as normal, wild individuals banded from June to August 1922–2007. To maintain data independence, we restricted analyses to ducks with a single recovery record (i.e., excluding catch-and-released birds with multiple sightings). Because we were interested in patterns of fall migration (traveling from rearing grounds to wintering grounds), we limited the dataset to direct recoveries (ducks recovered within the same year they were banded; Bellrose and Crompton 1970). The total dataset comprised 20,850 direct recoveries (Table S1; available online at www.onlinelibrary.wiley.com).

We first partitioned samples into those banded in the Mississippi or Atlantic flyways according to Baldassarre and Bolen (1994). Following international management units (USFWS 2011), we further partitioned ducks into Canadian (banded in Canada) and U.S. (banded in the contiguous USA) groups within each flyway (Fig. 1). Finally, we partitioned banding data by recapture month: 1) September, 2) October, 3) November, 4) December, and 5) January–February. We pooled data from January and mid-February because ducks are generally on their wintering grounds by January (Johnsgard 1978). Spring migration starts largely in late-February, peaking in late-March (Johnsgard 1978), so our combined January to mid-February dataset likely included only wintering individuals. We used the original banding locations of all analyzed ducks to establish the geographic distribution of staging areas (pre-migratory regions used in May–Aug).

Analysis

To visualize spatio-temporal patterns of black duck landscape use (geographic distributions), we calculated kernel density estimates (KDE) of band recovery positions. Although the geographic expanse of the entire population can be very large because of behaviors of individual ducks or stochastic climatic events (e.g., ducks falling out of migration, staggered migration), we were most interested in patterns of landscape use for the majority of ducks. With this in mind, we calculated the 50% and 95% KDEs that represented the geographic boundaries encompassing half and the majority of recovered ducks. We then overlaid kernel density contours on North American maps and used them as indicators of broadly important regions of habitat. All spatial calculations were performed in ArcGIS 10.0 (ESRI, Redlands, CA). We used the location of 50% KDEs to identify regions of particular high use. We used the 95% KDEs to define regions of general use at the decadal- and population-scales. We used shifts in the geographic placement of the 95% KDEs to signal changes in pre-, peak-, and post-migration. For instance, we defined the initiation of migration as the month when geographic distributions (95% KDE) first extended from pre-migratory or staging areas. We defined peak migration by the month(s) when the 95% KDE extended between staging areas and known wintering regions, which reflected when the population was the most geographically dispersed between these biogeographic boundaries. We also used the 95% KDE to examine geographic pathways (connections) between pre-migratory habitats and wintering grounds. During peak migration, if the area defined by the 95% KDE included multiple branches, we described each of these branches as individual connections.

Known changes in black duck population, regional avian community composition, habitat availability, and management (Johnsgard 1967, Dahl 1990, Merendino and Ankney 1994) across our study interval (1922–2007) suggest the possibility of secular changes in black duck landscape use. If true, pooling all available data could mask true contemporary distributions. Zimpfer and Conroy (2006), however, found no significant changes in black duck landscape use between 1965 and 1998. Building on this work, and to further test whether simultaneously analyzing all data would bias reconstructed distributions, we compared kernel density estimates for banding records pooled between 1922 and 1964 to those calculated from records between 1965 and 2007.

Evaluating the tendency for ducks to migrate within the flyway in which they were banded (flyway fidelity) as opposed to migrating to other flyways is an important aspect of duck management, including estimating local-to-regional habitat requirements for maintaining populations. We used chi-square tests to test for differences in the frequencies of ducks banded in the Atlantic or Mississippi flyways that 1) wintered within their home flyway, or 2) were recovered in the other flyway. Within individual flyways, we additionally tested for differences in flyway fidelity between Canadian and U.S. ducks.

RESULTS

Overall patterns of landscape use (particularly with respect to the 95% KDE) showed remarkable consistency between pre- and post-1965 time periods, though some differences in the placement and number of 50% KDEs may indicate shifts in regions of particularly high use (Table S1; Fig. S1a–d available online at www.onlinelibrary.wiley.com). Based on the close agreement in the geographic and temporal patterns of the 95% KDE between time periods, all further results are based on data from across the entire time interval (1922–2007).

Mississippi Flyway

From May through October, black ducks banded in the Mississippi Flyway were concentrated along the Great Lakes (Fig. 2); however, Canadian ducks were primarily found in eastern Ontario around Lake Erie and Lake Ontario. In November, the geographic distribution of U.S. ducks extended from the Great Lakes region along the Mississippi river to the Mississippi Alluvial Valley (MAV). During this same period, the geographic distribution of Canadian black ducks included the Chesapeake and Delaware Bays, as well as some shift in landscape use towards the Mississippi River. Although the 2 groups of the Mississippi flyway clearly showed differences in November landscape use, both used the eastern portion of Lake Erie as indicated by their 50% KDEs. In December, the 95% KDEs for Canada and U.S. populations encapsulated both pre-migratory and wintering regions, signaling synchronous peak migration. Furthermore, 6 separate geographic connections between breeding and wintering areas were revealed (Figs. 2 and 3) including 1) along the Mississippi River to the MAV (U.S. ducks only), 2) from Lake Michigan towards the MAV (Canadian and U.S. ducks), 3) Lake Erie to the Mississippi River, which then projected to the MAV (Canadian and U.S. ducks), 4) Lake Erie to the Chesapeake and Delaware Bays (Canadian ducks only), 5) Lake Ontario to the Chesapeake and Delaware Bays (Canadian ducks only), and 6) the MAV to the Atlantic flyway (Canadian and U.S. ducks). The location of 50% KDEs were more complex in December than in previous months with 2 main areas of concentration for both Canadian and U.S. ducks. Although Canadian and U.S. ducks maintained a portion of their 50% KDE on the western end of Lake Erie, Canadian ducks had a secondary concentration on the Chesapeake and Delaware Bays, whereas U.S. ducks had a secondary concentration in the northern portion of the MAV. In winter (Jan–Feb), although the 95% KDE still extended to Lake Erie, neither Canadian nor U.S. ducks had a 50% KDE so far north. In general, although January–February distributions were largely shifted south, the 95% KDE showed that Mississippi flyway black ducks could be found in many regions of the United States, including from Lake Erie to the MAV and from the MAV to

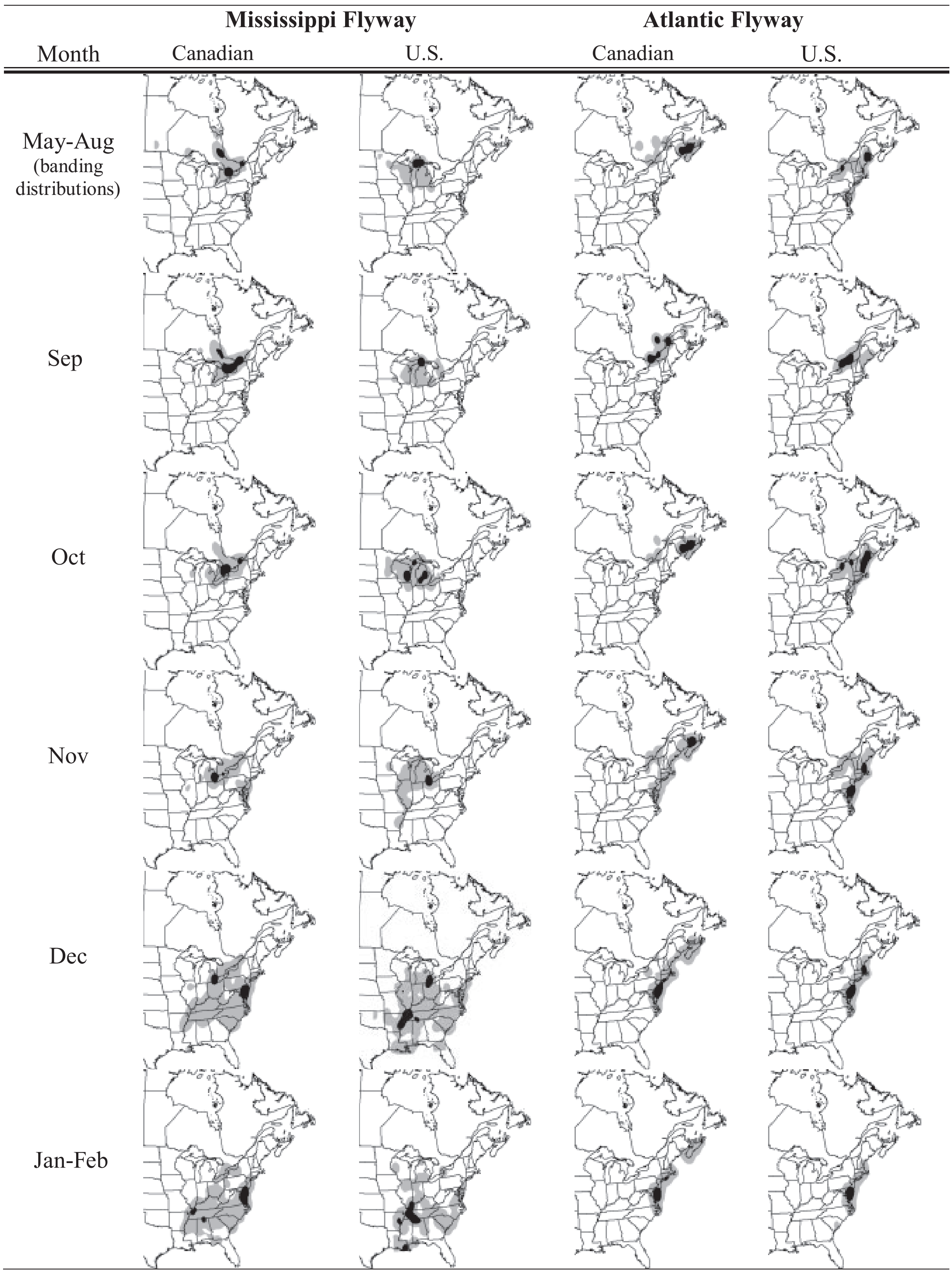

Figure 2. Kernel-density estimates (KDEs) derived from direct black duck recoveries banded in the Mississippi or Atlantic Flyways from 1922 to 2007. We provide the 95% (light gray), and 50% KDEs (black) for each month. The 50% KDE defines core regions of habitat for each month, and the 95% KDEs provide the overall migratory envelope. We calculated May–August distributions from banding localities of recovered ducks (i.e., for each group, May–Aug sample sizes equal the sum of duck recoveries from Sep through mid-Feb; see Table S1; available online at www.onlinelibrary.wiley.com).

the coastline of South Carolina. For U.S. ducks, geographic distributions in winter revealed a single 50% KDE centered on the northern edge of the MAV, whereas, based on location of 50% KDEs, Canadian ducks were concentrated on the Chesapeake and Delaware Bays as well as 3 regions on and near the MAV.

Atlantic Flyway

Black ducks in the Atlantic Flyway showed stable geographic distributions indicated by minimal landscape use outside of banding localities through October. Peak migration for both Canadian and U.S. ducks occurred in November, with a connection from the junction of the St. Lawrence River and

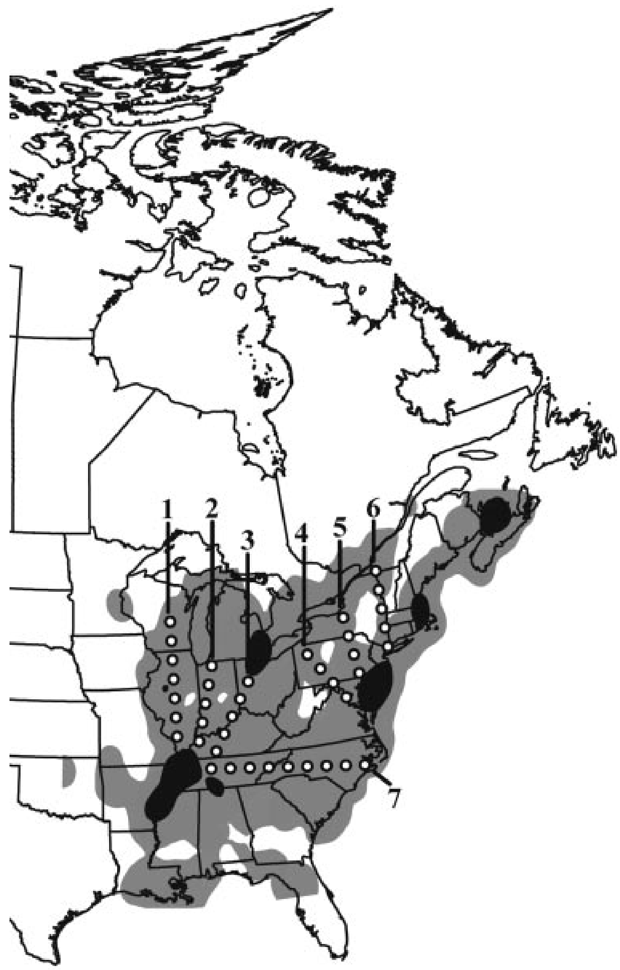

Figure 3. Combined 95% (gray) and 50% (black) kernel-density estimate (KDE) distributions for the 4 American black duck groups using recoveries from 1922 to 2007. We combined kernel density estimates from all geographic distributions from peak migration through February. The 7 geographic connections linking pre-migratory and wintering areas include 1) along the Mississippi River to the Mississippi Alluvial Valley (MAV); 2) from Lake Michigan towards the MAV; 3) Lake Erie to the Mississippi River; 4) Lake Erie to the Chesapeake and Delaware Bays; 5) Lake Ontario to the Chesapeake and Delaware Bays; 6) along Lake Champlain to the Chesapeake and Delaware Bays; and 7) the MAV with the Atlantic flyway. Putative corridors based on these connections are schematically represented by dotted lines. More detailed assessments of particular pathways will require finer-scaled investigation (i.e., GPS tracking).

Lake Champlain, along Lake Champlain's drainages to the Chesapeake and Delaware Bays (Fig. 2). Simultaneously, the geographic distributions of both groups encompassed habitat along the Atlantic coastline. By December, Canadian and U.S. ducks were on wintering grounds, with the 95% KDE revealing isolation of these wintering areas from pre-migratory staging grounds. The 50% KDE for both groups primarily encompassed the Chesapeake and Delaware Bays, with secondary concentrations on the coasts of Massachusetts and New Hampshire. Although highly similar to December distributions, black duck distributions in January–February also included a 95% KDE encompassing habitat along the South Carolina coastline (e.g., Lake Marion, Lake Moultrie, and Bulls Bay; Figs. 1 and 2).

Mississippi Flyway Ducks Exhibit Lower Flyway Fidelity

Of all ducks banded in the Mississippi flyway, 20% (835 ducks) migrated between flyways and were recovered in the Atlantic flyway, whereas only ~6% (943 ducks) of ducks banded in the Atlantic flyway were recovered in the Mississippi flyway. The difference between flyway fidelity was strongly significant ($\chi^2_1 = 875$, $P \leq 0.001$; Table 1). Additional tests within flyways revealed that the weaker flyway fidelity of the Mississppi flyway was most profound for Canadian ducks with 26% (769 ducks) recovered in the Atlantic flyway compared to 6% (66 ducks) of U.S. Mississippi flyway ducks ($\chi^2_1 = 206$, $P \leq 0.001$; Table 1). Rates of interflyway migration for both U.S. and Canadian ducks in the Atlantic flyway were roughly equal to the rate found in the flyway as a whole (approx. 6%) and not different between international management units ($\chi^2_1 = 2$, $P = 0.15$; Table 1).

DISCUSSION

Intra-Population Structuring and Putative Black Duck Stocks

Differences in the timing, flyway fidelity, and overall patterns of landscape use for black ducks reared in the Mississippi and Atlantic flyways indicate that western (Mississippi flyway) and eastern (Atlantic flyway) black ducks may warrant subpopulation status and separate management plans. Atlantic flyway ducks (both Canadian and U.S.) simultaneously reach peak migration in November, whereas the initiation of peak migration for Mississippi flyway ducks is varied and prolonged across late-fall and winter (i.e., Nov–Feb; Fig. 2). The transition to post-migration is also variable between the flyways; Atlantic flyway ducks are primarily on wintering habitat (i.e., all connections with pre-migratory regions are severed) in December, whereas Mississippi flyway black ducks maintain distributions across the Mississippi and Atlantic flyway regions into late winter. Regional differences in flyway fidelity for ducks in the Mississippi flyway, which are not found in the Atlantic flyway, point to additional, previously undocumented population structuring. Specifically, U.S. ducks primarily move from the Great Lakes to the MAV and then, to some extent, to the central and southern Atlantic coastlines along

Table 1. Direct recoveries of American black ducks partitioned by banding origin (U.S. or Canada) and recovered in either the Mississippi (MISS) or Atlantic (ATL) flyways from 1922 to 2007.

	Recovered in	
Banded in	**MISS**	**ATL**
MISS		
Canada	2,204	769
U.S.	1,081	66
Total	3,285	835
ATL		
Canada	563	9,597
U.S.	380	5,857
Total	943	15,454

what appears to be a single route. Conversely, Canadian Mississippi flyway ducks show greater use of the Atlantic flyway (50% KDE surrounding the Cheseake and Delaware Bays in Dec through Jan–Feb), fed by a minimum of 3 pathways between pre-migratory Mississippi areas and wintering regions of the Atlantic flyway (i.e., from Lake Ontario, from Lake Erie, and from the MAV; Fig. 2).

We observed 7 connections between banding locations and wintering areas: a single connection for Atlantic flyway ducks, and a minimum of 6 in the Mississippi flyway (Fig. 3). The consistent location and timing of connections as documented by 95% KDEs within flyways and between Canadian and U.S. groups and between pre-migratory and wintering areas strongly indicates that these pathways represent important migration corridors (including stopover sites) that connect critical migratory endpoints (Alerstam and Hedenström 1998, Alerstam 2001). Moreover, months in which these connections are observable corresponded to periods when black duck numbers were known to increase in their respective wintering regions (Bellrose and Crompton 1970, Bellrose 1976), indicating that the majority of ducks were filtering into their wintering grounds along these connections. Telemetry studies targeting these areas can test if observed decadal-scale, population-level patterns correspond to annual-scale migration characteristics.

Observed spatial and temporal patterns in band recovery records provide a foundation for future corridor analysis by helping to improve the sampling efficiency of telemetry studies, winter banding, and other population assessment methods. For example, our analyses indicate that movement corridors can be effectively studied by targeting 2–3 months of the year. Such a constrained study interval reduces opportunities for technological failure or loss of individuals, and limits overall telemetry costs.

Understanding the movement of ducks between flyways is important for maintaining the future viability of populations. Our results provide an assessment of the occurrence and timing of inter-flyway landscape use (migration) for Mississippi flyway ducks (Fig. 2, Table 1). Although we observed several inter-flyway connections in Canadian Mississippi flyway black ducks, only the connection between the MAV and the southern Atlantic coastline was shared between both Canadian and U.S. individuals. We hypothesize that this shared pattern of landscape use suggests that the MAV is a primary mode of dispersal for Mississippi flyway ducks into the Atlantic flyway. Furthermore, the greatly reduced proportions of Atlantic flyway black ducks using regions within the Mississippi flyway indicate that inter-flyway movement is primarily from the Mississippi (i.e., MAV region) to the Atlantic coastline. Using GPS-tracked individuals arriving on the northern portions of the MAV and on the southern Atlantic coastline from December to February could help delineate how ducks move between the MAV and Atlantic coastline, including determining if ducks actively migrate across this region, which we predict, or if our result (Fig. 2) is the manifestation of stationary, widely distributed ducks across the landscape.

Banding Data Biases

Multi-decadal (or longer) datasets provide valuable biological perspectives with which to evaluate modern populations (Kidwell 2007, Terry 2010, Dietl and Flessa 2011, Miller 2011, Kidwell and Tomašových 2013, Miller et al. 2013). However, although we report many patterns in the averaged geographic distributions of black ducks, we acknowledge the limitations of band-recovery data and their biases, including differences among states and countries in banding programs, hunting seasons, and reporting rates (Crissey 1955, Conroy and Blandin 1984, Nichols et al. 1995*b*, Royle and Dubovsky 2001). The wide temporal expanse of the dataset also means it samples across important changes in management practices, which could affect our results. For example, management changes include the end of major U.S. waterfowl hunting in September after the 1970s. Thus, the September distributions of ducks recovered in the U.S. are temporally biased. However, major patterns of black duck landscape use have remained largely stable over the broader study interval (Supplementary Fig. S1; Zimpfer and Conroy 2006), and because duck migrations do not generally ramp-up until November (with some populations showing migratory movement in Oct), biased September sampling does not have important ramifications for understanding patterns of landscape use during the actual migration.

Because the majority of band recoveries are from ducks harvested and reported by hunters, an additional concern is that analyses of band recovery data may be skewed by hunter behavior, densities, and reporting rates. However, although hunting activity could be particularly important when analyzing band recovery data at small spatial scales (i.e., at the county- or even state-scale; Calenge et al. 2010), we suggest that their impacts may be dampened at flyway-scale analyses across multiple decades. Thus, at the broad spatial and temporal scales analyzed here, although hunter preferences or behaviors may change over time within a county, state, or even region, much of this high-frequency variability, and that associated with stochastic climatic events and population fluctuations, should be effectively averaged out (as observed in other studies of multi-decadal data; Western and Behrensmeyer 2009, Miller 2011, Behrensmeyer and Miller 2012, Miller 2012). This does not suggest that our analyses are free of bias (including hunter bias), but that our scale of analysis should limit some of their effects. Importantly, the 95% KDE, which we use to document landscape connections and corridors and define temporal patterns of the fall migration, should be particularly robust to these sorts of biases and high-frequency variability.

Known patterns of duck landscape use and migration characteristics also offer some indication as to how well our analyses track the temporal and spatial dynamics of duck landscape use (as opposed to hunter behavior). For example, although duck hunting is legal across the United States by November, the majority of banding recoveries are predominantly not reported in the southern reaches of the migration (e.g., Louisiana) until December. Moreover, months associated with the presence of each migratory connection closely correspond to when increasing numbers of black ducks are observed in regions downstream of these connections. For example, the 95% KDE defines peak migration for Atlantic flyway ducks in November and this is when ducks are known to reach peak numbers along the Lake Champlain complex and in the Chesapeake and Delaware Bays (Bellrose and Crompton 1970, Bellrose 1976).

Finally, dramatic changes in habitat availability through time, including reductions in wetlands over the last few decades, could have a seemingly greater impact on our results than hunting biases. However, the similarity in patterns of landscape use, particularly as judged by the 95% KDE (Fig. S1), between pre- and post-1965 suggest that our analytical framework is capable of reconstructing the overall trends of interest. Importantly, although the methods we employ at the flyway scale may be somewhat sheltered against the influences of some biases within the data, we are less confident that similar analyses at smaller geographic scales would fare as well, and caution against using our results to interpret how black ducks use specific localities at small geographic scales.

MANAGEMENT IMPLICATIONS

Monthly geographic distributions of band recovery positions provide patterns of fall and winter migratory landscape use for American black ducks. Geographic connections between pre-migratory and wintering ranges during peak migration likely approximate migration corridors (Fig. 3) and offer a way to prioritize management and focus future research efforts to particular geographic regions. In addition, geographic distributions of black ducks delineate clear differences between groups in the Mississippi and Atlantic flyways, which suggests some independence between these groups (i.e., stocks) and argues for region-specific management strategies. Our results also show that ducks from different regions of the Mississippi flyway (Canadian vs. U.S.) have significantly different degrees of flyway fidelity, with ducks banded in Canada more likely to migrate to the Atlantic flyway.

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