Spring migration and breeding distribution of female Ring-necked Ducks wintering in the southern Atlantic Flyway

Tori D. Mezebish1, Glenn H. Olsen2, Michele Goodman3, Frank Rohwer4 and Mark D. McConnell5

1University of Rhode Island, 2United States Geological Survey Eastern Ecological Research Center, 3Elmwood Park Zoo, 4Delta Waterfowl Foundation, 5College of Forest Resources, Mississippi State University

ABSTRACT. North American waterfowl conservation, management, and harvest regulation are delegated across administrative flyways and primarily guided by breeding population estimates. The Ring-necked Duck (Aythya collaris) is a late-nesting migratory species that winters and breeds across all of the United States Fish and Wildlife Service administrative flyways. We used satellite telemetry to characterize the spring migration and breeding distribution of 25 female Ring-necked Ducks marked in the southern Atlantic Flyway, USA in the winters of 2017-2018 and 2018-2019. Mean migratory initiation date was 17 March (range: 24 Feb - 5 April) and mean migratory completion date (i.e., arrival to a suspected breeding site) was 16 May (range: 17 April - 27 June), with migratory duration averaging 61.1 days (95% CI: 53.6 - 68.6 days). Total migratory distance averaged 3,409.6 km (95% CI: 2,956.7 - 3,862.6 km). Individuals took, on average, 3.3 stopovers (95% CI: 2.7 - 4.0 stopovers) that lasted an average of 13.5 days (95% CI: 13.3 - 13.8 days). The majority of individuals migrated northward and primarily traveled within the Mississippi Flyway prior to reaching Canada. Ten of 25 marked birds migrated through but did not settle in the Prairie Pothole Region (PPR) during the time when the Waterfowl Breeding Population and Habitat Survey (WBPHS) was conducted. Total indicated bird population estimates could be inflated if individuals are counted in multiple WBPHS strata. We also note that 24 of 25 marked birds bred outside of strata comprising the WBPHS eastern survey area, which suggests that more Ring-necked Ducks wintering in the Atlantic Flyway breed outside of the WBPHS eastern survey area than is currently assumed by a scaling parameter incorporated in Atlantic Flyway models used to estimate population size. Individuals from a single wintering site in the southern Atlantic Flyway dispersed widely across two states (USA), five provinces, and one territory (CAN) during the breeding season. Our results support concerns over the efficacy of the WBPHS for Ring-necked Ducks and other late-nesting waterfowl and suggest that the bounds of the scaling parameter incorporated in the Atlantic Flyway multi-stock population model may need to be widened to more accurately account for individuals breeding outside of the Flyway.

Migration printanière et répartition en nidification de Fuligules à collier femelles hivernant dans le Sud de la voie de migration de l’Atlantique

RÉSUMÉ. La conservation, la gestion et la réglementation de la récolte de la sauvagine d’Amérique du Nord sont réalisées par l’intermédiaire de voies de migration administratives et sont principalement guidées par les estimations d’effectifs des populations nicheuses. Le Fuligule à collier (Aythya collaris) est une espèce migratrice à nidification tardive qui hiverne et niche dans toutes les voies de migration administratives de l’United States Fish and Wildlife Service. Nous avons utilisé la télemétrie par satellite pour caractériser la migration printanière et la répartition de nidification de 25 Fuligules à collier femelles marquées dans le Sud de la voie de migration de l’Atlantique, aux États-Unis, au cours des hivers 2017-2018 et 2018-2019. La date moyenne de début de la migration était le 17 mars (étendue : 24 février - 5 avril) et la date moyenne de fin de migration (c.-à-d. l’arrivée sur un site de nidification présumé) était le 16 mai (étendue : 17 avril - 27 juin), la durée de migration moyenne étant de 61,1 jours (IC 95% : 53,6 - 68,6 jours). La distance de migration totale était en moyenne de 3 409,6 km (IC 95% : 2 956,7 - 3 862,6 km). Les individus ont fait, en moyenne, 3,3 escales (IC 95% : 2,7 - 4,0 escales) qui ont duré en moyenne 13,5 jours (IC 95% : 13,3 - 13,8 jours). La majorité des individus ont migré vers le nord-ouest et se sont principalement déplacés dans la voie de migration du Mississippi avant d’atteindre le Canada. Dix des 25 oiseaux marqués ont migré par la région des Cuvettes des Prairies, mais ne s’y sont pas établis, pendant la période où le relevé des populations nicheuses et des habitats de la sauvagine (RPNHS) a été effectué. La taille de la population totale d’oiseaux pourrait être surestimée si des individus sont comptés dans plusieurs strates du RPNHS. Nous avons aussi noté que 24 des 25 oiseaux marqués ont niché à l’extérieur des strates comprises dans la zone de l’Est du RPNHS, ce qui donne à penser qu’un plus grand nombre de Fuligules à collier hivernant dans la voie de migration de l’Atlantique nichent à l’extérieur de la zone de l’Est du RPNHS que ne le suppose actuellement un paramètre d’échelle intégré aux modèles de la voie de migration de l’Atlantique utilisés pour calculer la taille des populations. Les individus provenant d’un même site d’hivernage dans le Sud de la voie de migration de l’Atlantique se sont largement dispersés dans deux États (États-Unis), cinq provinces et un territoire (Canada) pendant la saison de nidification. Nos résultats confirment les inquiétudes quant à l’efficacité du RPNHS pour les Fuligules à collier et d’autres espèces de sauvagine dont la nidification est tardive et indiquent que les limites du paramètre d’échelle incorporé dans le modèle de population multi-stock pour la voie de migration de l’Atlantique doivent être élargies pour tenir compte plus précisément des individus qui nichent à l’extérieur de la voie de migration.

Key Words: Aythya collaris; breeding distribution; Ring-necked Duck; satellite telemetry; spring migration; waterfowl management
INTRODUCTION

Waterfowl population monitoring and harvest management in North America reflects the notion that ecology during spring migration and on breeding grounds is a major predictor of population dynamics (Hoekman et al. 2002, Newton 2004, Drent et al. 2006, Devries et al. 2008). North American waterfowl management is regionally delegated across four United States Fish and Wildlife Service (USFWS) administrative flyways that longitudinally divide the continent (from east to west: Atlantic, Mississippi, Central, Pacific; Nichols et al. 1995, USFWS 2019a). Waterfowl harvest regulations across the flyways are largely informed by breeding population estimates, primarily derived from the annual Waterfowl Breeding Population and Habitat Survey (WBPHS; Smith 1995). Observations in the WBPHS are recorded in four classes: lone drakes, flocked drakes, pairs (associated male and female), or groups (three or more individuals of mixed sexes). Total indicated birds (TIB), used to estimate breeding waterfowl population sizes and guide management by the USFWS, is calculated as a combination of counts in the four classifications and may include migrants (Bordage et al. 2017). Total indicated pairs (TIP) is also calculated using counts in the four classifications but is weighted differently than TIB to minimize the prevalence of non-breeding birds in population estimates (Dzubin 1969). The aerial surveys conducted across WBPHS strata are timed to align with the spring migration and breeding chronology of the early-nesting Mallard Duck (Anas platyrhynchos). Consequently, the WBPHS may optimally inform the population statuses of early-nesting species while being less reliable for late-nesting species that may still be migrating during the surveys (Naugle et al. 2000, Schummer et al. 2018, Roy et al. 2019).

Data collected across WBPHS strata inform flyway-specific population models and harvest regulations (Smith 1995, USFWS 2019a, 2019b). In 2018, the Atlantic Flyway adopted a multi-stock harvest regulation strategy that considers the population status of Ring-necked Ducks (Aythya collaris), American Green-winged Teal (Anas carolinensis), Wood Ducks (Aix sponsa), and Goldeneye species (Bucephala spp.; USFWS 2018). The 4 species were chosen to reflect different life histories and habitat use across the flyway while constituting a large portion of the flyway’s duck harvest (Johnson et al. 2019). While sufficient banding data exist to directly estimate harvest rates and abundance for Wood Ducks and American Green-winged Teal in the Atlantic Flyway, banding data for Ring-necked Ducks and Goldeneye are insufficient (USFWS 2018). To account for insufficient data, the models used to estimate population size that guide harvest regulations for Atlantic Flyway Ring-necked Ducks and Goldeneye incorporate a scaling parameter that accounts for the portion of ducks harvested in the Atlantic Flyway that originate from outside of Atlantic Flyway survey strata. (USFWS 2018 and see Johnson 2019 Supporting Information S1). The scaling parameter is incorporated under a Bayesian framework and can vary annually. However, the scaling parameter is bounded under the assumption that at least 70% of Ring-necked Ducks or Goldeneye harvested in the Atlantic Flyway breed inside of the WBPHS eastern survey areas (Johnson et al. 2019). The multi-stock models used to estimate population size and guide effective waterfowl management and conservation in the Atlantic Flyway, therefore, rely upon understanding the spatiotemporal distributions of spring migrant and breeding waterfowl relative to the administrative flyways and WBPHS.

The phenology of waterfowl spring migrations is influenced by energetic demands, resource availability, and environmental conditions (Farmer and Wiens 1998, McWilliams et al. 2004, Van der Graaf et al. 2006, Newton 2008) and can reflect social learning and memory (Metteke-Hofmann and Gwinner 2003, Mueller et al. 2013). Waterfowl employ different migration strategies whereby the timing of movements relative to environmental conditions along migratory routes should ensure arrival to breeding sites at times corresponding with adequate resource availability for successful reproduction (Drent and Daan 1980, Drent et al. 2003, Alerstam 2011). Resources at northern stopover and breeding sites are initially limited by snow and ice cover until temperatures warm, making spring migrations particularly subject to temporal constraints (Newton 2008, Schummer et al. 2010). If temperatures early in spring limit resource availability at northern stopover sites, the number and duration of stopovers as well as overall migratory duration can be a function of migratory initiation date (Van der Graaf et al. 2006, Schummer et al. 2010, Shariatinafzhabadi et al. 2014). For example, individuals that closely follow changes in resource availability by initiating migration early may have long duration migrations with multiple stopover events. Alternatively, individuals may initiate spring migration late relative to changes in resource availability, make few or short duration stopovers, and have short duration migrations. Migratory timing for female waterfowl is particularly linked to breeding ecology, where the probability of nest success is generally higher for birds that initiate nesting early (Drent and Daan 1980, Drent et al. 2003 and 2006). Therefore, female waterfowl that initiate spring migration early might complete migration early to initiate nesting and increase potential reproductive success (Drent and Daan 1980). Finally, birds that initiate spring migration late might migrate a shorter total distance than those that initiate spring migrations earlier (Bregnballe et al. 2006).

Once on the breeding grounds, the distribution of waterfowl populations can suggest important characteristics of their ecology to inform management and conservation. The population structure of breeding waterfowl can be investigated relative to annual movement patterns under the framework of metapopulation theory. When considering migratory species, metapopulation theory describes demographically independent subpopulations that converge spatiotemporally at one or more points during the annual cycle (Esler 2000). Specifically, migratory species that exist in metapopulations exhibit directed movement between spatially distinct breeding and non-breeding locales (Esler 2000, Taylor and Hall 2012). Metapopulation dynamics have been used to describe patterns of natal philopatry and dispersal in Black Brant (Branta bernicla nigricans; Lindberg et al. 1998). More recently, analyses of genetic structure in Eider (Somateria spp.) demonstrate that individuals disperse across multiple seasonal geographic locales and interact with individuals from other geographic locales throughout the year (Mehl et al. 2005, Sonsthagen et al. 2009). By elucidating the degree to which migratory populations interconnect throughout the annual cycle, metapopulation structure can reveal cross-seasonal life history

The Ring-necked Duck (*Aythya collaris*) is a mid-season migrant and late-season nester with wintering concentrations on inland freshwater along the Gulf Coast and southeastern United States and breeding concentrations in the northern United States and Canadian boreal forests (Baldassarre 2014, Roy et al. 2019). Initiation of Ring-necked Duck spring migration spans from early February through late April. Arrival at breeding grounds has been less thoroughly described, though breeding bird numbers in New Brunswick, CAN and Maine, USA peak from late April through early July (Baldassarre 2014). The continental Ring-necked Duck breeding population has been increasing since the WBPHS began in the mid-1950s and currently exceeds 2 million individuals. Ring-necked Ducks are the most abundant diving duck in the WBPHS eastern survey area (USFWS 2019b) and are consistently the most harvested diving duck in the United States (Raftovitch et al. 2011, 2014, 2016, 2018; Raftovitch and Wilkins 2013). From 2000-2010, 80.2% of Atlantic Flyway Ring-necked Ducks in the Midwinter Survey were counted in Florida and the Carolinas (Baldassarre 2014). Moreover, Florida, Georgia, and South Carolina account for a disproportionate amount (82% during the 1960s and 1970s) of Atlantic Flyway Ring-necked Duck harvest (Conroy and Eberhardt 1983, Montalbano et al. 1985, Raftovitch et al. 2018). Band recovery data suggest that while Ring-necked Ducks wintering in the Carolinas primarily migrate along the Atlantic coast and breed in Ontario, those that winter in Georgia may migrate to Canadian breeding grounds further west (Baldassarre 2014, G. D. Balkcom personal communication). The degree to which Ring-necked Ducks wintering in the southern Atlantic Flyway breed outside of the WBPHS eastern survey area has implications for the scaling parameter incorporated in Atlantic Flyway multi-stock population models. Specifically, if less than 70% of the Ring-necked Duck population that winters in and is subject to Atlantic Flyway harvest regulations consistently breeds within the WBPHS eastern survey area, the lower bound for the scaling parameter may need to be decreased accordingly.

Despite their abundance and importance in harvest, Ring-necked Ducks are one of the least-studied divers (e.g., Conroy and Eberhardt 1983; Roy et al. 2013, 2014, 2019; Roy 2018). No studies have delineated the spring migration and breeding locations of Ring-necked Ducks wintering in the Atlantic Flyway. Using satellite telemetry of marked birds, our objectives were to 1) identify spring migration routes relative to the USFWS administrative flyways and WBPHS survey strata, 2) quantify migratory timing relative to the WBPHS, and 3) delineate the breeding distribution of female Ring-necked Ducks wintering at a site in the southern Atlantic Flyway under the framework of metapopulation dynamics. Our analysis reveals important characteristics of the annual ecology of southern Atlantic Flyway Ring-necked Ducks to inform North American waterfowl survey designs and conservation and management efforts.

**METHODS**

### Captures and transmitter specifications

We captured female Ring-necked Ducks in the Red Hills physiographic region of southern Georgia and northern Florida (approximate geographic center: 30.67 ºN, 84.04 ºW; Fig. 1). The Red Hills region spans ~240,000 ha in the Gulf Coastal Plain on both sides of the Florida-Georgia state line (Palmer et al. 2019) and is largely composed of privately-owned plantations, primarily managed for hunting Northern Bobwhite (*Colinus virginianus*; Brennan et al. 2000). Managed habitat in the Red Hills is predominately upland pine (*Pinus* spp.) forest with old-field and wiregrass (*Aristida stricta*) ground cover, though bottomland hardwood drains and hammocks comprise notable portions of the landscape (Staller et al. 2005). Plantation owners manage wetlands in the region to attract Ring-necked Ducks and Wood Ducks through the waterfowl hunting season. Wintering ducks in the Red Hills exploit flooded agricultural fields (predominantly corn), moist soil impoundments, non-managed ponds, and lakes (Mezebish et al. 2021).

![Fig. 1. Capture site (star) in the Red Hills region, USA of female Ring-necked Ducks (*Aythya collaris*) implanted with platform terminal transmitters (PTTs) in winters 2017-2018 and 2018-2019.](http://www.ace-eco.org/vol17/iss2/art5/)

We captured female Ring-necked Ducks in November and December of 2017 and 2018. We captured additional female Ring-necked Ducks in early February 2019, shortly after the waterfowl hunting season ended but prior to spring migration. Captures in late fall coincided with splits in the Florida and Georgia waterfowl hunting seasons. To abide by federal baiting regulations, we did not use baited swim-in traps commonly used to capture waterfowl on private properties that landowners hunt (Finger et al. 2016, Schummer et al. 2018, USFWS 2021). Instead, we captured individuals via night-lighting techniques (Cummins and Hewitt 1964).

Upon capture, we banded (USGS aluminum leg band), weighed, and evaluated females for surgical candidacy. We rejected females if transmitters were >5% of their body mass (body mass \(x=649\)....
± 57 [SD] g, transmitter % of body mass 8=4.5 ± 0.3%; Fair et al. 2010, Schummer et al. 2018). We also rejected individuals if any physical injuries or abnormalities were extensive. On evenings that we captured more birds than could be processed within several hours, we kept individuals in a ~2 m x 2 m x 2 m wire holding pen on the edge of wetlands prior to surgery. We provided individuals with loafing mats and sorghum to reduce stress and maintain hydration and body mass.

We transported individuals to surgical locations <15 minutes distance from capture sites. Veterinarians followed standard sterile surgical procedures to implant ~26 g satellite Platform Terminal Transmitters (PTTs) with percutaneous antennas (Model GT-20GB; GeoTrak, Inc., Apex, NC, USA) into the coelomic cavity of each candidate female (Olsen et al. 1992, University of Georgia Institutional Animal Care and Use Committee Protocol A2016 08-026-A3, U.S. Geological Survey Federal Bird Banding Permit 06689, USFWS Scientific Collecting Permit MB14521C-0). Surgeries lasted ≤25 minutes with anesthetic time <60 minutes. We released all individuals at their capture sites after a 3-4-hour surgical recovery period. Implanted transmitters minimize the deleterious effects that traditional external transmitter attachments pose to waterfowl and diving ducks in particular (Perry 1981, Olsen et al. 1992, Iverson et al. 2006).

We censored all data from the first 14 days post-release to allow individuals to recover from surgery (Mulcahy and Esler 1999, Esler et al. 2000). We monitored body temperatures throughout the study period for indications of mortality (i.e., body temperatures below ~39-40 °C). PTT duty cycles varied over the course of the study to coincide with annual life history patterns and to maximize battery life. PTT locations were collected approximately every 2 days upon migratory initiation and approximately every 4 days during a portion of migration and upon arrival to the breeding grounds (Table 1).

### Table 1. Duty cycle programs for platform terminal transmitters (PTTs) deployed in female Ring-necked Ducks (Aythya collaris) captured in winters 2017-2018 and 2018-2019 in the Red Hills physiographic region, USA.

<table>
<thead>
<tr>
<th>Duty Cycle Duration</th>
<th>Hours On</th>
<th>Hours Off</th>
</tr>
</thead>
<tbody>
<tr>
<td>December - January</td>
<td>4</td>
<td>23</td>
</tr>
<tr>
<td>February - April</td>
<td>5</td>
<td>45</td>
</tr>
<tr>
<td>May - August</td>
<td>4</td>
<td>87</td>
</tr>
</tbody>
</table>

We collected PTT data through the Argos satellite system, including latitude, longitude, date, time, and estimated location error class (Service Argos 2016). Argos categorizes error distance associated with PTT locations into locations classes (LCs): estimated error distance <250 m (LC 3), 250-500 m (LC 2), 500-1500 m (LC 1), >1500 m (LC 0), and no error estimation (LCs A and B). We used the Douglas-Argos Filter (DAF) hybrid filter (HYB) in Movebank to remove implausible Ring-necked Duck locations and retain the most accurate location from each duty cycle based on spatial redundancy, movement rates, and turning angles between consecutive locations (Douglas et al. 2012). We set the filter parameters based on values reported in the literature and our PTT duty cycle (Appendix 1; Douglas et al. 2012, Finger et al. 2016).

### Migration phenology and breeding site delineation

We identified spatial classifiers indicating transitions between wintering, migration, stopovers, and breeding by investigating the distribution of step length values across the study period and examining movement paths in ArcMap 10.5 (ESRI 2016; De La Cruz et al. 2009, Lok et al. 2011, Meattey et al. 2018). We calculated all step lengths (i.e., the straight-line distance between consecutive relocations, km) in program R using the package adehabitatLT (Calenge 2006). We identified migratory initiation as a northward movement ≥150 km from the wintering grounds, stopovers as at least 2 consecutive locations ≤45 km apart during migration, and suspected nesting attempts as consecutive locations ≤22 km apart for ≥30 days. We identified transitions between wintering, migration, and breeding as the median Julian date between an individual’s final location in the area associated with one annual stage and the first location in the area associated with the next annual stage in program R 3.4.4 (R Core Team 2019). We used 30 days to temporally qualify suspected nesting attempts because it slightly exceeds the incubation period of Ring-necked Ducks (Baldassarre 2014, Finger et al. 2016). We used a temporal qualifier that slightly exceeds the incubation period of Ring-necked Ducks to increase confidence in our identification of suspected nest attempts and minimize the potential to incorrectly identify stopover events as suspected nest attempts. We were unable to quantify nest success and thus could not identify failed nest attempts that occurred prior to events defined as suspected nesting. We did not distinguish between stopover and staging events.

We calculated centroids of stopover events and breeding locations for each individual to account for movements within stopover and breeding areas and errors associated with PTT location data. Therefore, we represented each stopover event and breeding area for every individual with a single centroid. We identified simplified migration paths as the straight-line distances between the final location on the wintering grounds, stopover centroids, and breeding centroid for each individual and used these paths to quantify the distances (km) of total migration paths and single migratory step movements.

We quantified the number of birds that migrated through each USFWS administrative flyway by overlaying our simplified migration paths with the USFWS Administrative Flyway Boundaries layer (Parr 2015) in ArcMap. We quantified the number of birds that migrated through the Prairie Pothole Region (PPR) of North America but bred in the western boreal forested region of Canada by overlaying our simplified migration paths with polygon layers depicting the boundaries of each region (PPR, Mann 1974; boreal forest, Brandt 2009). To account for infrequency of data collection, we identified the date range that individuals could have been present in the PPR relative to WBPHS aerial flights as the date of the final location prior to entry into the PPR plus one-half of the duty cycle to the date of the first location beyond the PPR minus one-half of the duty cycle (Finger et al. 2016). Because of the infrequency in data collection (Table 1) and related uncertainty in our calculation of suspected nest initiation date, it is possible for the estimated final date a bird could have been present in the PPR to equal the suspected nest initiation date in the western boreal forest. To characterize the landscapes of suspected nest sites, we overlaid breeding centroids
with the Level II Ecoregions of North America layer (US EPA 2010) in ArcMap.

We estimated overall migratory duration as the difference between migratory initiation date and migratory completion date, plus one day to account for the possibility that individuals were present in migratory areas on both the initiation and completion dates (De La Cruz et al. 2009, Meattey et al. 2018). We similarly calculated duration of stopovers as the difference between the first and last days at a stopover location, plus one day. We investigated Pearson correlation coefficients and p-values for relationships between migratory initiation date and migratory duration, migratory completion date, total migration distance, average stopover duration, the duration of the first stopover an individual made, and the total number of stopovers made. We natural-log transformed migratory duration, total migration distance, average stopover duration, and the total number of stopovers made to normalize each variable before testing for correlations.

RESULTS

Our initial sample included 14 female Ring-necked Ducks marked in winter 2017-2018 and 30 marked in winter 2018-2019. We removed one bird from the 2017-2018 sample due to harvest on the wintering grounds and 4 birds due to transmitter failure during spring migration. We removed three birds from the 2018-2019 sample due to harvest on the wintering grounds, two birds due to transmitter failure on the wintering grounds, seven birds due to transmitter failure during spring migration, and two birds due to mortality before the individuals remained at a breeding location long enough to confirm a suspected nesting attempt. Our final sample size included 25 female Ring-necked Ducks, nine marked in the winter of 2017-2018 and 16 marked in the winter of 2018-2019. One bird in the 2018-2019 sample died after the individual remained at the same breeding location long enough to confirm a suspected nesting attempt, so the bird was included in the sample.

On average, individuals started spring migration on 17 March (Julian day 75.5, n = 25, 95% CI: 71.5 - 79.5; Fig. 2A) and initiation dates were similar across study years. Average completion date of spring migration (i.e., arrival to a suspected breeding site) was 16 May (Julian day 135.8, n = 25, 95% CI: 128.5 - 143.2). Completion date was slightly later for individuals marked in 2017-2018 (x = 24 May, Julian day 143.9, n = 9, 95% CI: 130.7 - 157.1) than 2018-2019 (x = 11 May, Julian day 131.3, n = 16, 95% CI: 121.4 - 141.1; Fig. 2B). Migratory duration was similar across years, averaging 61.1 days (n = 25, 95% CI: 53.6 - 68.6 days; Fig. 2C). Total migratory distance averaged 3,409.6 km (n = 25, 95% CI: 2,956.7 - 3,862.6 km; Fig. 2D) and was similar across study years. Distances of individual migratory movements were also similar across years and averaged 468.4 km (n = 25, 95% CI: 419.2 - 517.6 km). We were unable to detect statistically significant correlations between the investigated natural-log transformed migration metrics. Migratory initiation date was not significantly correlated with overall migratory duration (r = -0.30, 95% CI: -0.62 - 0.11, P = 0.15), migratory completion date (r = 0.24, 95% CI: -0.17 - 0.58, P = 0.24), and total migration distance (r = -0.02, 95% CI: -0.41 - 0.38, P = 0.91). However, the correlation of migratory initiation date with migratory completion date (r = 0.24) was relatively large and in the expected direction. The number of stopovers individuals made was similar across study years, ranging from 1-7 stopovers during spring migration, with the average number of stopovers being 3.3 (n = 25, 95% CI: 2.7 - 4.0 stopovers; Fig. 2E). Stopovers ranged from 3-42 days but lasted an average of 13.5 days (n = 25, 95% CI: 13.3 - 13.8 days; Fig. 2F) and were similar in duration across years (Table 2). Migratory initiation date was not significantly correlated with the average duration of stopovers (r = -0.20, 95% CI: -0.55 - 0.21, P = 0.33), the duration of the first stopover (r = -0.02, 95% CI: -0.41 - 0.38, P = 0.94), and the number of stopovers (r = -0.19, 95% CI: -0.54 - 0.22, P = 0.36). However, the correlations of migratory initiation date with the average duration of stopovers (r = -0.20) and the number of stopovers made (r = -0.19) were relatively large and in the expected direction.

Table 2. Means, standard errors (SE), and 95% confidence intervals (95% CI) of metrics characterizing the spring migration of Female Ring-necked Ducks (Aythya collaris) marked with platform terminal transmitters (PTTs) in the Red Hills physiographic region, USA during winter 2017-2018, winter 2018-2019, and combined.

<table>
<thead>
<tr>
<th>Metric</th>
<th>Mean</th>
<th>SE</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Migratory Initiation Date (Julian day)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2017-2018</td>
<td>78.1</td>
<td>4.3</td>
<td>69.6 - 86.6</td>
</tr>
<tr>
<td>2018-2019</td>
<td>74.1</td>
<td>3.3</td>
<td>67.7 - 80.4</td>
</tr>
<tr>
<td>Combined</td>
<td>75.5</td>
<td>2.0</td>
<td>71.5 - 79.5</td>
</tr>
<tr>
<td>Migratory Completion Date (Julian day)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2017-2018</td>
<td>143.9</td>
<td>6.7</td>
<td>130.7 - 157.1</td>
</tr>
<tr>
<td>2018-2019</td>
<td>131.3</td>
<td>5.0</td>
<td>121.4 - 141.1</td>
</tr>
<tr>
<td>Combined</td>
<td>135.8</td>
<td>3.8</td>
<td>128.5 - 143.2</td>
</tr>
<tr>
<td>Migratory Duration (days)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2017-2018</td>
<td>66.6</td>
<td>7.1</td>
<td>52.6 - 80.5</td>
</tr>
<tr>
<td>2018-2019</td>
<td>58.0</td>
<td>5.4</td>
<td>47.5 - 68.5</td>
</tr>
<tr>
<td>Combined</td>
<td>61.1</td>
<td>3.8</td>
<td>53.6 - 68.6</td>
</tr>
<tr>
<td>Total Migratory Distance (km)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2017-2018</td>
<td>3,777.1</td>
<td>427.3</td>
<td>2,939.6 - 4,614.6</td>
</tr>
<tr>
<td>2018-2019</td>
<td>3,202.9</td>
<td>320.6</td>
<td>2,574.8 - 3,831.1</td>
</tr>
<tr>
<td>Combined</td>
<td>3,406.6</td>
<td>231.1</td>
<td>2,956.7 - 3,862.6</td>
</tr>
<tr>
<td>Single Migratory Movement Distance (km)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2017-2018</td>
<td>485.6</td>
<td>41.5</td>
<td>404.2 - 567.0</td>
</tr>
<tr>
<td>2018-2019</td>
<td>457.6</td>
<td>31.6</td>
<td>395.7 - 516.5</td>
</tr>
<tr>
<td>Combined</td>
<td>468.4</td>
<td>25.1</td>
<td>419.2 - 517.6</td>
</tr>
<tr>
<td>Number of Stopovers</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2017-2018</td>
<td>3.6</td>
<td>0.4</td>
<td>2.8 - 4.4</td>
</tr>
<tr>
<td>2018-2019</td>
<td>3.2</td>
<td>0.3</td>
<td>2.6 - 3.8</td>
</tr>
<tr>
<td>Combined</td>
<td>3.3</td>
<td>0.3</td>
<td>2.7 - 4.0</td>
</tr>
<tr>
<td>Stopover Duration (days)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2017-2018</td>
<td>13.5</td>
<td>0.4</td>
<td>12.8 - 14.0</td>
</tr>
<tr>
<td>2018-2019</td>
<td>13.6</td>
<td>0.2</td>
<td>13.2 - 14.0</td>
</tr>
<tr>
<td>Combined</td>
<td>13.5</td>
<td>0.1</td>
<td>13.3 - 13.8</td>
</tr>
</tbody>
</table>

Only one individual migrated strictly within the Atlantic Flyway before crossing into Canada. Twenty-four individuals migrated within the Mississippi Flyway and six of those individuals migrated within the northeastern extent of the Central Flyway before crossing into Canada. Only one individual bled in the WBPHS strata was used to define the eastern waterfowl stock that guides Atlantic Flyway adaptive harvest management (AHM; Fig. 3). Thirteen individuals migrated through the PPR but bled in the western boreal forest. Of those 13 females, 10 were present in the PPR and then present in the western boreal forest within the approximate time frame that WBPHS aerial surveys are flown in each respective area, indicating that those individuals could have been counted twice in the survey (Table 3 and Fig. 4).
Fig. 2. Histograms of six metrics characterizing the spring migration of female Ring-necked Ducks (*Aythya collaris*) marked with platform terminal transmitters (PTTs) in the Red Hills physiographic region, USA. Black bars indicate the sample marked in winter 2017-2018 and gray bars indicate the sample marked in winter 2018-2019.

![Histograms](image.png)

Table 3. Capture year (winter 2017-2018 or 2018-2019), the range of dates individuals could have been present in the Prairie Pothole Region (PPR), and the date of suspected nest initiation in the boreal forest of female Ring-necked Ducks (*Aythya collaris*) implanted with platform terminal transmitters (PTTs) in the Red Hills physiographic region, USA that migrated through the PPR but bred in the boreal forest of North America.

<table>
<thead>
<tr>
<th>Individual Identifier</th>
<th>Capture Year</th>
<th>Date(s) Present in PPR</th>
<th>Suspected Nest Initiation Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>173008</td>
<td>2017-2018</td>
<td>8 May</td>
<td>8 May</td>
</tr>
<tr>
<td>173011</td>
<td>2017-2018</td>
<td>6 May</td>
<td>17 May</td>
</tr>
<tr>
<td>173012</td>
<td>2017-2018</td>
<td>8 May - 19 May</td>
<td>23 May</td>
</tr>
<tr>
<td>173013</td>
<td>2017-2018</td>
<td>24 April - 4 May</td>
<td>4 May</td>
</tr>
<tr>
<td>173017</td>
<td>2017-2018</td>
<td>12 May</td>
<td>15 May</td>
</tr>
<tr>
<td>177189</td>
<td>2018-2019</td>
<td>24 March - 20 May</td>
<td>20 May</td>
</tr>
<tr>
<td>177191</td>
<td>2018-2019</td>
<td>20 April - 10 May</td>
<td>14 May</td>
</tr>
<tr>
<td>177203</td>
<td>2018-2019</td>
<td>9 April - 15 May</td>
<td>11 June</td>
</tr>
<tr>
<td>177206</td>
<td>2018-2019</td>
<td>12 May</td>
<td>2 June</td>
</tr>
</tbody>
</table>

Suspected breeding sites ranged in latitude from 45.51 °N to 66.94 °N and ranged in longitude from 122.07 °W to 83.18 °W (Fig. 5 and 6). We identified 21 breeding centroids in Canada: one in the Northwest Territories, one in British Columbia, two in Alberta, five in Saskatchewan, five in Manitoba, and six in Ontario. We identified 4 breeding centroids in the USA: three in Minnesota and one in Michigan. Breeding centroids were identified across seven ecoregions: one in the southern Arctic, one in the taiga plain, one in the taiga shield, seven in the boreal plain, nine in the softwood shield, one in the temperate prairies, four in the mixed wood shield, and one mixed wood plains (Fig. 6).

**DISCUSSION**

We provide the first detailed delineation of Ring-necked Duck spring migration and breeding distributions for birds wintering in Georgia and Florida, USA. Using satellite telemetry to track females wintering in the southern Atlantic Flyway, we 1) identified spring migration routes relative to the USFWS administrative flyways and WBPHS survey strata, 2) quantified migratory timing relative to the WBPHS, and 3) delineated the breeding distribution relative to metapopulation dynamics theory. Our findings from a sample of females wintering at a single southern Atlantic Flyway site indicate that the timing and distribution of
Fig. 4. Spring migration paths of female Ring-necked Ducks (*Aythya collaris*) implanted with platform terminal transmitters (PTTs) in winter 2017-2018 and 2018-2019 in the Red Hills physiographic region, USA through the Prairie Pothole Region (PPR) and boreal forest of North America. Waterfowl Breeding Population and Habitat Survey (WBPHS) strata (data retrieved from USFWS Division of Migratory Birds Branch of Population and Habitat Assessment, 2019) are outlined and numbered. Individuals that migrated through the PPR during the timeframe that surveys are conducted in the associated strata but bred in the boreal forest are shown in black. All other individuals are shown in gray. Suspected nesting locations are indicated by circles.

The WBPHS may not be appropriate for Ring-necked Ducks and other late-nesting species and that a higher portion of the winter population than currently accounted for by Atlantic Flyway models used to estimate population size may breed outside of the WBPHS eastern survey strata. Finally, our results indicate that Ring-necked Ducks from concentrated wintering sites disperse across large breeding ranges.

Four administrative flyways were established in the mid-1900s with boundaries based upon band recovery and survey data to coordinate waterfowl management and conservation across North America (Nichols et al. 1995). While all female Ring-necked Ducks in our sample wintered at one location in the

Atlantic Flyway, the majority (24 of 25 individuals) migrated and made most stopovers in the Mississippi Flyway rather than moving northward within the Atlantic Flyway (Fig. 3). Moreover, all but one individual settled at breeding sites west of the Atlantic Flyway and the WBPHS eastern survey strata (Fig. 3). A GPS study of Minnesota Sandhill cranes found similar use of multiple administrative flyways that define population segments across the annual cycle (Wolfson et al. 2017).

Our finding of inter-flyway movement supports the continued use of a scaling parameter in the population model guiding Atlantic Flyway Ring-necked Duck harvest to account for the portion of harvested Ring-necked Ducks originating from breeding areas outside of the WBPHS eastern survey strata (USFWS 2018, Johnson 2019). The scaling parameter incorporated in models for both Ring-necked Ducks and Goldeneye is bounded under the
assumption that at least 70% of ducks harvested in the Atlantic Flyway originate from within the WBPHS eastern survey areas (Johnson et al. 2019). The current lower bound of the scaling parameter may require updating based on a more thorough investigation of the spatiotemporal scale and prevalence of multi-flyway migratory behavior by Ring-necked Ducks across the Atlantic Flyway. Ninety-six percent of individuals from a wintering site in the southern Atlantic Flyway bred outside of the WBPHS eastern survey strata. We recognize that our results are limited to a single wintering population and relatively small sample of Ring-necked Ducks. Therefore, we currently do not have sufficient spatial replication across the Atlantic Flyway wintering Ring-necked Duck population to make specific recommendations as to the appropriate value for the lower bound of the scaling parameter. However, given the large numbers of Ring-necked Ducks that winter across the southern Atlantic Flyway and spatial distribution of limited available band reporting data (G. D. Balkcom personal communication) we suspect that a larger portion of the population than is currently accounted for breeds outside of the WBPHS eastern survey strata. Continued transmitter-tagging efforts should seek to obtain a representative sample of Ring-necked Ducks wintering across the Atlantic Flyway to improve the ecological accuracy of this scaling parameter. Similar investigations of the annual cycle movement patterns of Goldeneyes wintering in the Atlantic Flyway could inform the scaling parameter included in that species-specific population model. An exploratory analysis may also be warranted to determine how sensitive the population model is to the choice of bounds for the scaling parameter.

Our estimates of mean spring migration initiation (\( \bar{x} = 17 \) March) and completion (\( \bar{x} = 16 \) May) dates fall within the range of published observations and confirm that Ring-necked ducks are a late-nesting species (Table 2; Baldassarre 2014). Our dates of arrival to suspected breeding sites are similar to Lesser Scaup (\( Aythya affinis \); Finger et al. 2016) but are roughly one month later than Mallards (Kirby and Cowardin 1986, Krementz et al. 2011), for which the timing of the WBPHS is targeted (Naugle et al. 2000, USFWS 2018). WBPHS aerial surveys are conducted in the PPR and boreal forested region of Canada from ~1 May to 25 May and May to 12 June, respectively (Smith 1995). Ten of 25 females in our sample migrated through the PPR during the period that aerial surveys are conducted in that region. These individuals continued migration to suspected nesting sites in the western boreal forest, where they could be counted again in later-timed surveys (Table 3 and Fig. 4). Historic data suggest that the timing of the WBPHS is appropriate as only 14.7% of Ring-necked Duck observations were counted as groups in the PPR (Smith 1995). This suggests that only 14.7% of individuals were migrants and could have been counted in both PPR and boreal WBPHS strata. We do not know if our marked birds were counted as breeding pairs or migrant groups in the PPR. However, our findings indicate that up to 40% of Ring-necked Ducks (10 of 25 females) could have been counted in both PPR and boreal survey strata and included twice in the USFWS TIB population estimate for the species. Future studies should seek to update data reported by Smith (1995) and quantify the proportion of Ring-necked Ducks counted as breeding pairs versus groups in the PPR. Such information would inform annual variation in survey efficacy and address concerns over inflated TIB population estimates for Ring-necked Ducks and other late-nesting ducks in the traditional survey area (Naugle et al. 2000, Schummer et al. 2018, Roy et al. 2019). Alternatively, it may be appropriate for the USFWS to utilize estimates of total indicated pairs (TIP), which excludes Ring-necked Ducks counted as groups, rather than TIB to estimate breeding population sizes of Ring-necked Ducks and other late-nesting ducks.

We did not find statistically significant correlations between female Ring-necked Duck migratory initiation date and other migration metrics that could reflect adjustments to migratory timing relative to arrival to the breeding grounds. Species' ability to shift their migratory phenology in response to environmental conditions can be reflected in relationships between migratory initiation date, completion date, and migratory duration (Drent et al. 2003 and 2006), the number and duration of stopover events (Farmer and Wiens 1998, Schummer et al. 2010, Shariatinajafabadi et al. 2014), and total migratory distance (Bregnballe et al. 2006). While we were unable to detect any statistically significant relationships, the correlations of migratory initiation date with migratory completion date (\( r = 0.24 \)) the average duration of stopovers (\( r = -0.20 \)), and the number of stopovers made (\( r = -0.19 \)) were relatively large and in the expected direction. As migratory initiation date increased, overall migratory duration and migratory completion date also increased. As migratory initiation date increased, the average duration of stopovers and number of stopovers made decreased. The lack of significant relationships between migration metrics may simply reflect our relatively small sample size and the behavioral plasticity in migration displayed by Ring-necked Ducks. Moreover, we recognize that we only tracked individuals through a single breeding season and were unable to quantify potential long-term (i.e., cross-seasonal) effects of transmitter implantation. Implanted transmitters may delay migratory timing, influence selection of stopover and breeding sites, and
reduce the breeding propensity of avian species, particularly during the first year of transmitter deployment (Barron et al. 2010, Lamb et al. 2020). To quantify potential impacts of transmitter implantation on Ring-necked Duck migration phenology and breeding ecology, future studies should employ transmitter programs that allow multi-year tracking and conduct on-the-ground verification of suspected nest attempts. Such efforts were beyond the scope of this study given additional research objectives and the remote nature of ring-necked duck breeding sites.

The distribution of suspected breeding locations provides evidence that Ring-necked Ducks may exhibit metapopulation dynamics (Esler 2000). Individuals that utilized the same geographic wintering area dispersed across two states (USA), five provinces, and one territory (CAN), in areas comprised of six ecoregions during the breeding season. That individuals in our sample bred across such a wide geographic area suggests that the continental Ring-necked Duck population could have relatively high variation in migratory and breeding strategies, responsiveness to environmental stressors and selection pressures, and genetic diversity (Esler 2000). We cannot make claims in reference to how Ring-necked Ducks beyond our limited sample from a single wintering site disperse during the breeding season. However, our findings are consistent with the suggestion that some breeding populations of Ring-necked ducks may be maintained by immigration (Roy et al. 2019). Our findings support conducting investigations into the genetic and stable isotope structure of a larger and more representative sample of Ring-necked Ducks tracked across multiple years to validate the demographic independence of breeding subpopulations and quantify the degree of interspersion across the continental population (e.g., Fleskes et al. 2010, Asante et al. 2017).

The highest frequency of Ring-necked Duck breeding concentrations is in the boreal forested region of Canada (Baldassarre 2014). Our results support this assertion, as 16 breeding centroids were in the boreal plain, softwood shield, and mixed wood shield Level II North American Ecoregions, which are more broadly categorized as the northern forest Level I Ecoregion (Fig. 6; US EPA 2010, Omernik and Griffith 2014). We also note that 3 breeding centroids were in northern Minnesota where Ring-necked Ducks have been identified as a species of management concern due to high harvest rates and declines in local survey counts (Zicus et al. 2008, Roy et al. 2019). Four of 25 individuals bred in Minnesota and Michigan, USA, which fall outside of the WBPHS survey areas (Fig. 4 and 6; USFWS 2019b). This finding supports reported inconsistencies in local surveys and WBPHS population trends for Ring-necked Ducks breeding in Minnesota (Zicus et al. 2008) and suggests that WBPHS strata boundaries may not adequately reflect the species’ breeding distribution. Future studies could seek to quantify the density of Ring-necked Ducks across their breeding range relative to WBPHS strata locations to determine the portion of the Ring-necked Duck breeding population that is not counted in the WBPHS.

While we recognize that no single survey design or model can simultaneously and adequately assess all waterfowl, we reveal limitations of the current WBPHS and Atlantic Flyway multi-stock population model for Ring-necked Ducks wintering in the southern Atlantic Flyway. Specifically, greater attention should be given to the timing of the WBPHS and scaling parameter used to account for Ring-necked Ducks originating from outside of the Atlantic Flyway. Our findings suggest a need for continued Ring-necked Duck banding and telemetry efforts across the Atlantic Flyway to guide ecologically accurate and informed management decisions.

Responses to this article can be read online at: https://www.ace-eco.org/issues/responses.php/2185

Author Contributions:
MDM, FCR, GHO, MG, and TDM conducted fieldwork. GHO and MG conducted transmitter implant surgeries. TDM and MDM analyzed the data. TDM wrote the first draft of the manuscript. All authors contributed to manuscript revisions.

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LITERATURE CITED


Appendix 1. Parameter values used to run the hybrid (HYB) Douglas-Argos Filter in Movebank to remove implausible locations of female Ring-necked Duck implanted with platform terminal transmitters (PTTs) in winters 2017-2018 and 2018-2019 in the Red Hills physiogeographic region, USA.

Please click here to download file ‘appendix1.docx’.