Migration routes and chronology of American Black Duck *Anas rubripes*

JOHN M. COLUCCY[1,*], KURT A. ANDERSON[2], TINA YERKES[3] & JACOB L. BOWMAN[4]

[1]Ducks Unlimited, Inc., 7322 Newman Boulevard, Building 1, Dexter, Michigan 48130, USA.
[2]Tompkins County Area Development, 401 East State Street #402b, Ithaca,
New York 14850, USA.
[3]3746 Arcadia Drive, Ann Arbor, Michigan 481808, USA.
[4]Department of Entomology and Wildlife Ecology, University of Delaware,
250 Townsend Hall, Newark, Delaware 19716, USA.
*Correspondence author. Email: jcoluccy@ducks.org

Abstract

Satellite telemetry was used to identify migration routes and stopovers, estimate migration chronology, and describe variation in movements among American Black Duck *Anas rubripes* marked in Delaware, New Jersey, New York, Ohio and Virginia between 2007–2009. Thirty-one transmitters each provided data for at least one spring migration. The ducks departed their wintering areas during 18 March–7 June ($\bar{x} \pm$ s.e. = 17 April ± 3.3 days), averaged 3.35 ± 0.3 stopovers (range = 1–5 stopovers) and spent 6.44 ± 0.8 days at stopover sites (range = 0.54–12.2 days), migrated 1,126.1 ± 89.5 km (range = 270–1,396 km), and arrived at inferred nesting areas during 16 April–28 June ($\bar{x}$ = 9 May ± 3.4 days). Black Duck on the South Atlantic Flyway migrated nearly twice as far ($P < 0.01$), made twice as many stopovers ($P < 0.01$) and arrived at their inferred nesting areas two weeks later than those on the North Atlantic and Mississippi Flyways ($P = 0.04$). Transmitters on 13 ducks provided at least partial data during autumn migrations. Black Duck departed inferred nesting or moulting areas during 5 October–1 December ($\bar{x}$ = 24 October ± 4.3 days), averaged 2.0 ± 0.3 stopovers (range = 1–4 stopovers), spent 12.6 ± 3.5 days at stopover sites (range = 0.25–41 days), migrated 993 ± 202.9 km (range = 277–1,485 km), and arrived at wintering areas during 18 November–18 December ($\bar{x}$ = 1 December ± 5.8 days). Our study confirmed known migration routes and stopovers and emphasises the need for habitat conservation and management along seasonal corridors, especially for Black Duck transitioning between their southern wintering and western breeding ranges. Furthermore, migration chronology and stopover duration of stay from our study should be incorporated into energetic carrying capacity models, to inform and direct habitat goals for Black Duck in north-eastern North America.

Key words: American Black Duck, migration, satellite telemetry.

American Black Duck *Anas rubripes* (hereafter Black Duck) populations have declined over the last 50 years. Numbers counted during mid-winter waterfowl surveys ranged from > 750,000 birds in 1954/55 to < 300,000 in 1983 and 1984 (USFWS 2012). The goal for Black Duck numbers was set at the 1970s level of 385,000 wintering birds in the 1986 North American Waterfowl Management Plan (NAWMP). The NAWMP also called for the formation of Joint Ventures (JV), including the Black Duck JV (BDJV), to help achieve the goal by 2000 (NAWMP 1986). Despite the increased focus on the species, the 1999/2000 mid-winter waterfowl survey counts recorded 260,372 Black Duck and as few as 246,334 were counted in winter 2011/12 (USFWS 2012). Their population remains more than 30% below the NAWMP goal (Fig. 1).

Several explanations for the Black Duck decline have been proposed, principal among them being overharvest, competition and hybridisation with Mallards *Anas platyrhynchos*, habitat loss and disease. Attempts to identify the primary factor have been inconclusive (Conroy *et al.* 2002). Previous studies have uncovered information regarding Black Duck breeding (Reed 1975; Seymour 1991; Merendino & Ankney 1994; McAuley *et al.* 2004; Link & Sauer 2006; Maisonneuve *et al.* 2006; Zimmerman *et al.* 2011), post-breeding (Parker 1991; Bowman & Brown 1992; Longcore *et al.* 2000) and wintering ecology (Morton *et al.* 1989; Brook *et al.* 2007; Plattner *et al.* 2010; Cramer *et al.* 2012;

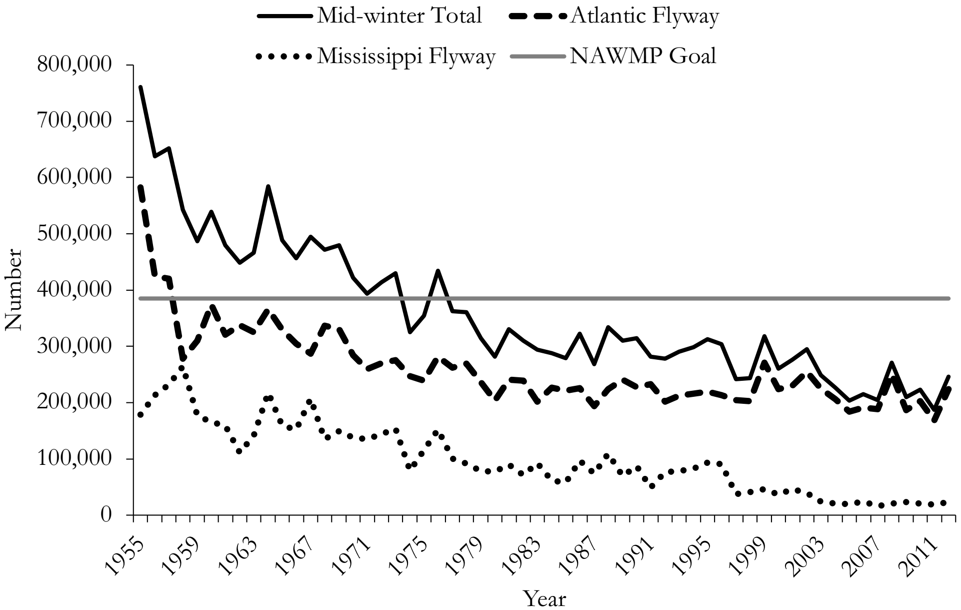

Figure 1. Number of American Black Duck counted during the mid-winter waterfowl survey, 1955–2012.

Newcomb *et al.* 2016). Those that have addressed migration are based on standard band recovery data, count data and population modelling (Robinson *et al.* 2016a,b,c), which provide rather general descriptions of migratory patterns. Migration influences the ecology, evolution and conservation of migratory animals (Webster *et al.* 2002), yet explicit data on the movements between migratory destinations (*i.e.* their inferred nesting and wintering areas) is virtually unknown for Black Duck.

Describing Black Duck migration routes and stopovers, along with the chronology, length and duration of their migrations, has been identified as a priority action by the BDJV (2008) and by the Upper Mississippi River and Great Lakes Region JV (UMRGLRJV; Soulliere *et al.* 2007). This information is required for developing regional Black Duck use day objectives, from which habitat objectives are estimated using energetics models. Additionally, an improved understanding of the connectivity between Black Duck migratory destinations can help waterfowl managers direct conservation efforts to key areas at the appropriate time (Robinson *et al.* 2016a,b,c).

We used satellite telemetry to identify migration routes and stopover sites, estimate migration chronology and describe variation among Black Duck migratory movements. Our study was not the first attempt to examine connectivity across their entire range, but is distinguished by the highly detailed individual-level data collected. Our study helps to address priority information needs of the BDJV and UMRGLRJV, and can aid population and habitat modelling and inform management decisions for Black Duck during their annual life cycle.

Methods

Study area

Black Duck were trapped during 4 January–14 March in winters 2007/08 and 2008/09 at multiple sites in northern Ohio (at Castalia, Mud Creek Bay and the Ottawa National Wildlife Refuge [NWR]), Virginia (at Brownsville Farm, Caledon Natural Area, Chincoteague NWR and the Eastern Shore NWR), and New Jersey (at Cape May NWR and the Edwin B. Forsythe NWR). In 2008/09, birds were also trapped in Delaware (at Prime Hook NWR) and Long Island, New York (at Hubbard County Park; Fig. 2). Trapping locations were selected on the basis that Black Duck could be caught there, in areas with the greatest known concentration of the species wintering in eastern North America (USFWS 2012).

Waterfowl habitat in the north-eastern (New York) and mid-Atlantic (New Jersey, Delaware, Virginia) states feature a mix of a saline tidal estuarine systems and freshwater tidal and non-tidal riverine and palustrine (depth < 2 m, size < 8 ha) systems. Coastal salt marshes consist of high and low marsh habitats, drained by shallow, meandering creeks to expose mud flats where periwinkles *Littorina* sp., Fiddler Crab *Uca pugnax* and Soft-shelled Clam *Mya arenaria* are abundant (Cramer *et al.* 2012). Cordgrass *Spartina* sp. is the dominant emergent vegetation. Inland, freshwater systems are dominated by smartweed *Polygonum* sp. and Buttonbush *Cephalanthus occidentalis*, with invertebrates such as copepods, amphipods, snails and

Figure 2. Approximate trapping locations for adult female American Black Duck PTT-tagged in New Jersey, Ohio, Virginia, Delaware and New York, USA during winters 2007/08 and 2008/09.

crabs (Jorde *et al.* 1989). Waterfowl habitat along the southwest shore of Lake Erie (Ohio) is almost entirely impounded marshes controlled for waterfowl hunting, consisting of several species of aquatic plants and surrounded by grain fields (Bookhout *et al.* 1989).

Study design

On catching and handling the Black Duck, protocols described by Fair *et al.* (2010) were followed to ensure that animal welfare was not jeopardised during scientific data collection. Three methods were used to catch Black Duck: cloverleaf (swim-in) traps, walk-in traps and rocket-nets baited with corn. Bill, cloacal and feather characteristics were used to identify and retain females in at least their third calendar year since hatch (*i.e.* adult birds; Ashley *et al.* 2006) in an effort to eliminate age-specific variability in a small sample. Additionally, females were weighed and those ≥ 1,000 g selected ($\bar{x} \pm$ s.e. = 1,134 ± 13.6 g; $n = 63$). Females with a lower body mass are considered more likely to be adversely affected on carrying satellite transmitters, because the mass and/or aerodynamic impacts of the devices may result in aberrant behaviour or mortality (Miller *et al.* 2005a).

Each selected female was fitted with a standard USGS leg-band and solar-powered, satellite Platform Transmitting Terminal (PTT; Model 100; Microwave Telemetry, Columbia, USA). The PTTs weighed 22 g, measured 62 × 22 × 21 mm and had a 178 mm nylon-coated flexible-stranded stainless-steel antenna that protruded posteriorly at a 45° angle. PTTs were attached mid-dorsally between the wings using a 13 g harness, 0.38 cm in width, made of Natural Tubular Teflon® tape (Bally Ribbon Mills, Bally, USA). The harness set included breast and belly loops, connected by a strap along the edge of the keel, similar to designs used by Malecki *et al.* (2001), Petrie & Wilcox (2003) and Miller *et al.* (2005a,b). The PTT and harness combined amounted to 3% of the ducks' average body mass at capture, which satisfied the guidelines established by Fair *et al.* (2010) and the U.S. Geological Survey Bird Banding Laboratory (http://www.pwrc.usgs.gov/bbl/MANUAL/aarequs.cfm). Marked females were kept in straw-lined poultry cages with food and water to afford them time to acclimatise to the harness and then released diurnally at the capture site within 24 h following capture. Because the PTTs were attached prior to spring departure, marked females had time to adjust to the transmitter (Cox & Afton 1998) and potentially find new mates if necessary (Miller *et al.* 2005a).

PTTs were programmed to acquire six GPS fixes daily, which were staggered to provide consistent 24 h coverage of bird movement throughout the year. GPS fixes were primarily used because of their accuracy (± 15 m) but Argos (Argos, Inc., Landover, USA) fixes were also used to supplement missing data when a transmitter recorded GPS fixes as either no fix, low voltage or battery drain. Argos estimates positional locations from the Doppler shift in transmission frequency and groups them by accuracy into Location Classes (LCs; Argos 2011), of which we used LCs 3, 2 and 1. Argos (2011) lists their accuracy as < 150, 150–350 and 350–1,000 m, respectively. Location data from GPS and Argos fixes were uploaded every 3rd day to the Argos satellite tracking system (CLS America, Inc., Largo, USA). Marked Black Duck were tracked until the PTT lost connection or the birds died, which was determined as ≥ 3 consecutive fixes in the same location simultaneous with on-board sensors indicating an irregular drop in body temperature (Krementz *et al.* 2011).

Data analyses

The birds' migratory destinations were described as sites where they remained with movement of ≤ 0.5 degrees latitude or longitude (Afton 2008) for ≥ 30 days (Miller *et al.* 2005b; Krementz *et al.* 2011). Migratory moves were defined as a flight > 0.5 degrees latitude or longitude, and each stopover site as a clustered location (> 1 fix) varying by ≤ 0.5 degrees (Afton 2008). Arrival was defined as the first fix at a clustered location and departure as the last fix at the same location (Miller *et al.* 2005a; Haukos *et al.* 2006), despite 4 h data gaps between daily fixes. When data gaps of > 1 day but < 10 days occurred, and an individual Black Duck made a migratory move during that time, departure was redefined as the median date and time between the last known fix at the previous location and the first known fix at the next clustered location; the original definition of arrival date was maintained. Departure from the previous clustered location, arrival at the next or length of stay at either were not calculated if the data gap was ≥ 10 days (Miller *et al.* 2005a; Haukos *et al.* 2006). The same criteria were followed to estimate the minimum number of stopovers, length of stay at stopovers and total straight-line distance between stopovers and terminal positions.

For comparison, Black Duck were grouped by wintering area (*i.e.* Mississippi Flyway = Ohio; North Atlantic Flyway = New Jersey and New York; South Atlantic Flyway = Delaware and Virginia), similar to evaluations by Rogers & Patterson (1984), Rusch *et al.* (1989), Petrie (1998) and Zimpfer & Conroy (2006). Also established were a latitudinal boundary at the 40th parallel and a longitudinal boundary at the 76th meridian to create north and south (*i.e.* north = Ohio and New York; south = New Jersey, Delaware and Virginia) and east and west (*i.e.* east = eastern shore of Virginia, Delaware, New Jersey and New York; west = Ohio and western Virginia) groups, respectively. The former was selected because the 40th parallel afforded even data distribution, whereas the latter was selected because the 76th meridian effectively cleaved the Chesapeake Bay.

The difference among geographic groups in the date and time of day at which Black Duck commenced spring migration, and also the date and time of day at which they arrived at their destinations, was investigated (Miller *et al.* 2005a; Haukos *et al.* 2006; Malecki *et al.* 2006). So, too, were the difference between minimum number of stopovers, duration of stay at stopover sites (days), distance of each migratory move (km), total distance travelled (km) and rate of movement (km/h) investigated among geographic groups. Analyses were conducted using Analysis of Variance with a block on year (*i.e.* the year in which the migration occurred, included as a factor) in JMP 9.0.1 (SAS Institute, Inc., Cary, USA). A Tukey's mean separation test was used to detect differences among treatment levels when significance was detected.

Finally, simple linear regression in JMP was used to evaluate the relationship between several migratory variables (*i.e.* main effects) and their responses irrespective of geographic group. Specifically, the combined data was analysed to determine the effect of: 1) departure date on the number of stopovers, duration of stay at stopover sites and the total distance of migration, 2) number of stopovers on the duration of stay at stopover sites, 3) total distance of migration on the number of stopovers and the duration of stay at stopover sites, 4) distance and duration of a migratory move on the duration of stay at the next stopover site, and 5) duration of stay at a stopover site on the distance and duration of the following migratory move. Mean values are given ± s.e. throughout. An *a priori* alpha of ≤ 0.05 was used to determine statistical significance.

Results

Twenty-nine PTTs were affixed to Black Duck during winter 2007/08 (New Jersey,

Table 1. Migratory variables (mean ± s.e.) of adult female American Black Duck by region during spring 2008 and 2009; levels not connected by the same letter within a row are significantly different.

	Region								
	Mississippi		**North Atlantic**		**South Atlantic**				
	n	$\bar{x}$ ± s.e.	*n*	$\bar{x}$ ± s.e.	*n*	$\bar{x}$ ± s.e.	*F*	d.f.	*P*
Departure date (s.e. in days)	14	14 Apr ± 3.6	4	25 Apr ± 17.6	14	16 Apr ± 5.0	0.39	2, 28	0.68
Departure time (s.e. in days)	14	1,921 ± 1.6	4	1,600 ± 7.9	14	1,750 ± 1.8	0.88	2, 28	0.42
Arrival date (s.e. in days)	14	30 Apr ± 3.4 **B**	4	26 May ± 12.6 **A**	14	14 May ± 5.3 **A**	3.74	2, 28	**0.04**
Arrival time (s.e. in days)	14	1,457 ± 4.0	4	1,225 ± 6.1	14	1,371 ± 4.1	0.10	2, 28	0.90
No. of stopovers	13	2.38 ± 0.4 **B**	4	2.75 ± 1.1 **B**	14	4.43 ± 0.4 **A**	6.23	2, 27	**< 0.01**
Duration of stay (days)	33	6.26 ± 1.2	11	10.75 ± 4.0	62	5.77 ± 0.9	1.92	2, 102	0.15
Total distance (km)	13	806.8 ± 72.5 **B**	4	877.7 ± 242.7 **B**	14	1,493.6 ± 116.2 **A**	12.4	2, 27	**< 0.01**
Distance (leg; km)	48	237.8 ± 27.5	15	234.1 ± 43.6	76	275.1 ± 20.0	0.78	2, 135	0.46
Rate of movement (km/h)	48	32.7 ± 3.5	15	31.8 ± 3.8	76	41.4 ± 3.3	2.08	2, 135	0.13

n = 10; Ohio, *n* = 9; Virginia, *n* = 10) and another 39 Black Duck during winter 2008/09 (New Jersey, *n* = 10; Ohio, *n* = 11; Virginia, *n* = 10; Delaware, *n* = 5; New York, *n* = 3). Of the 29 PTTs deployed in winter 2007/08, 12 provided a full data set during spring migration 2008 (New Jersey, *n* = 1; Ohio, *n* = 6; Virginia, *n* = 5). Two of the 2008 PTTs continued transmitting during winter 2008/09 and provided another full data set during spring migration 2009. Additionally, 17 of the 39 PTTs deployed during winter 2008/09 provided a full data set during spring migration 2009 (New Jersey, *n* = 1; Ohio, *n* = 5; Virginia, *n* = 4; Delaware, *n* = 5; New York, *n* = 2). Still another PTT provided partial data during spring migration 2009, which was included in the analyses where appropriate.

Black Duck departed their wintering areas during 18 March–7 June ($\bar{x}$ = 17 April ± 3.3 days) averaged 3.35 ± 0.3 stopovers (range = 1–5 stopovers) and spent 6.44 ± 0.8 days at stopover sites (range = 0.54–12.2 days) during spring migrations 2008 and 2009 combined. Of the 139 migratory moves identified in our study, only six needed adjustment to account for data gaps of > 1 day and < 10 days. The ducks migrated on average 1,126.1 ± 89.5 km (range = 270–1,396 km) and arrived at their inferred nesting areas during 16 April–28 June ($\bar{x}$ = 9 May ± 3.4 days). Departure dates, departure and arrival time of day, the duration of stay at stopover sites and the average distance of each migratory move did not vary by geographic group (Tables 1–3).

South Atlantic Flyway Black Duck migrated nearly twice as far ($P < 0.01$) and made twice as many stopovers ($P < 0.01$) than those from the Mississippi and North Atlantic Flyways (Table 1). Black Duck south of the 40th parallel migrated > 50% further ($P < 0.01$), took nearly twice as many stopovers ($P = 0.02$) and, despite migrating almost 10 km/h faster during each migratory move ($P = 0.03$), arrived at their inferred nesting areas two weeks after their counterparts ($P = 0.04$; Table 2). Although not statistically significant, Black Duck east of the 76th meridian migrated nearly 25% farther than those to the west ($P = 0.07$). They also arrived at their inferred nesting areas three weeks later ($P = 0.01$; Table 3).

Black Duck followed a variety of routes during spring migration in both years (Fig. 3). Among those wintering along the eastern seaboard, nine ducks spent all or part of their migration along the Atlantic Coast and 10 used the Hudson and St. Lawrence River valleys. Stopover sites included Long Island Sound, Narragansett Bay, Lake Champlain, Merrymeeting Bay and the Gulf of St. Lawrence. All 11 ducks wintering in Ohio used stopover sites in Lake St. Clair, Saginaw Bay, St. Mary's River and the Georgian Bay. Black Duck settled at inferred nesting areas in Newfoundland (*n* = 1), Labrador (*n* = 4), New Brunswick (*n* = 2), Quebec (*n* = 7), Nova Scotia (*n* = 1), Vermont (*n* = 1) and Ontario (*n* = 16). The two Black Duck that completed spring migrations in consecutive years returned to the same wetlands on inferred nesting areas despite different trajectories (Fig. 4).

Among all the PTT-tagged Black Duck (Table 4), departure date explained 18% and number of stopovers explained 44% of the variation in duration of stay on stopover sites, respectively. Total distance of migration

Table 2. Migratory variables (mean ± s.e.) of adult female American Black Duck by latitude during spring 2008 and 2009; levels not connected by the same letter within a row are significantly different.

	Latitude						
	North		**South**				
	n	$\bar{x}$ ± s.e.	n	$\bar{x}$ ± s.e.	F	d.f.	P
Departure date (s.e. in days)	16	12 Apr ± 3.6	16	21 Apr ± 5.5	1.75	1, 29	0.20
Departure time (s.e. in days)	16	1,806.3 ± 2.3	16	1,806.3 ± 1.7	0.00	1, 29	1.00
Arrival date (s.e. in days)	16	2 May ± 3.5 **B**	16	17 May ± 5.4 **A**	4.60	1, 29	**0.04**
Arrival time (s.e. in days)	16	1,444.8 ± 3.8	16	1,337.5 ± 3.6	0.11	1, 29	0.74
No. of stopovers	15	2.6 ± 0.4 **B**	16	4.1 ± 0.4 **A**	5.85	1, 28	**0.02**
Duration of stay (days)	41	7.41 ± 1.4	65	5.82 ± 0.9	1.02	1, 103	0.32
Total distance (km)	15	862.3 ± 76.0 **B**	16	1,373.5 ± 132.5 **A**	10.7	1, 28	**< 0.01**
Distance (leg; km)	58	239.0 ± 24.5	81	271.3 ± 19.3	1.09	1, 136	0.30
Rate of movement (km/h)	58	31.7 ± 3.0 **B**	81	41.5 ± 3.1 **A**	4.99	1, 136	**0.03**

explained 61% and 33% of the variation in number of stopovers and duration of stay on stopover sites, respectively. Duration of a migratory move explained 3% of the variation in length of stay on the next stopover.

A total of 13 PTTs (Ohio, $n = 6$; Virginia, $n = 3$; Delaware, $n = 2$; New York, $n = 2$) provided at least partial data during autumn migrations in either 2008 or 2009. Of those, five provided a full data set (Ohio, $n = 2$; Delaware, $n = 2$; New York, $n = 1$), whereas the others lost contact during migration ($n = 4$) or were lost due to hunter harvest ($n = 4$). Eighteen of the 31 migratory moves identified in our study needed adjustment to account for data gaps of > 1 day and < 10

Table 3. Migratory variables (mean ± s.e.) of adult female American Black Duck by longitude during spring 2008 and 2009; levels not connected by the same letter within a row are significantly different.

	Longitude						
	East		**West**				
	n	$\bar{x}$ ± s.e.	*n*	$\bar{x}$ ± s.e.	*F*	d.f.	*P*
Departure date (s.e. in days)	11	23 Apr ± 7.9	21	3 Apr ± 2.8	1.77	1, 29	0.19
Departure time (s.e. in days)	11	1,718.2 ± 3.0	21	1,852.4 ± 1.5	0.01	1, 29	0.94
Arrival date (s.e. in days)	11	23 May ± 7.2 **A**	21	2 May ± 2.6 **B**	7.76	1, 29	**0.01**
Arrival time (s.e. in days)	11	1,409.1 ± 4.6	21	1,381.0 ± 3.1	2.31	1, 29	0.14
No. of stopovers	11	4.0 ± 0.6	20	3.0 ± 0.4	0.01	1, 28	0.94
Duration of stay (days)	44	7.16 ± 1.4	62	5.93 ± 0.9	0.43	1, 103	0.51
Total distance (km)	11	1,284.4 ± 165.0	20	1,039.1 ± 102.9	3.68	1, 28	0.07
Distance (leg; km)	55	256.9 ± 22.5	84	258.4 ± 20.5	< 0.01	1, 136	0.96
Rate of movement (km/h)	55	39.7 ± 4.0	84	35.9 ± 2.6	0.98	1, 136	0.32

days. In total, Black Duck departed their inferred nesting or moulting areas during 5 October–1 December ($\bar{x}$ = 24 October ± 4.3 days), averaged 2.0 ± 0.3 stopovers (range = 1–4 stopovers), spent 12.6 ± 3.5 days at stopover sites (range = 0.25–41 days), migrated 993 ± 202.9 km (range = 277–1,485 km) and arrived at wintering areas during 18 November–18 December ($\bar{x}$ = 1 December ± 5.8 days). Eight Black Duck returned to wintering areas or reappeared there after prolonged PTT inactivity, four of which settled into the same location where they had been caught the previous winter (Prime Hook NWR, *n* = 2; Ottawa NWR, *n* = 1; Castalia, OH, *n* = 1). Black Duck that

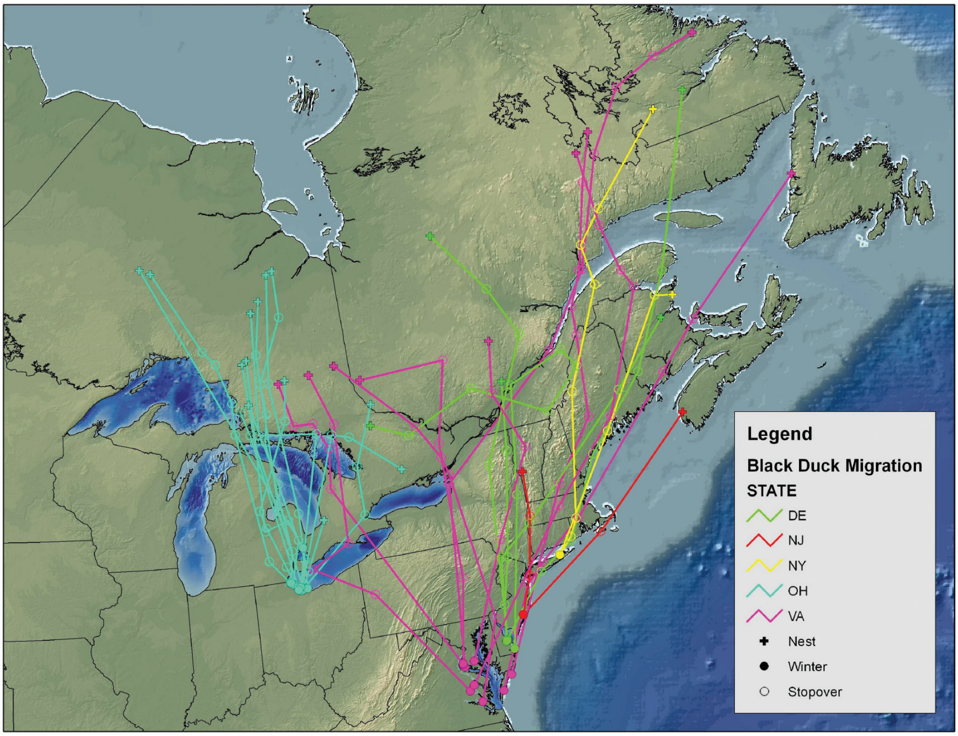

Figure 3. Spring migration routes of adult female American Black Duck PTT-tagged in New Jersey, Ohio, Virginia, Delaware and New York, USA during winters 2007/08 and 2008/09.

completed either full or partial autumn migrations largely followed different routes than their spring trajectories. Additionally, PTTs on two Ohio Black Duck continued transmitting data over winter, during which they spent an average of 157.5 ± 7.5 days.

Discussion

Transmitter weight, attachment methodologies and limited sample size (*i.e.* $n < 30$) have the potential to bias results in satellite tracking studies of migratory animals (Webster *et al.* 2002; Miller *et al.* 2005a; Lindbergh & Walker 2007; Barron *et al.* 2010; Lameris & Kleyheeg 2017; Lameris *et al.* 2018). In our study, 68 Black Duck were affixed with PTTs. They were caught on wintering areas that accounted for 67% of all Black Duck counted during the 2008 mid-winter waterfowl survey (USFWS 2012). Although the geographic distribution of PTT-tagged ducks is not entirely representative of the proportion of Black Duck within and between flyways, our goal was to collect information from across their entire range, subject to cost and logistical constraints. In the future, more samples from these and other Black Duck wintering concentrations and reduced gaps between programmed daily fixes would provide

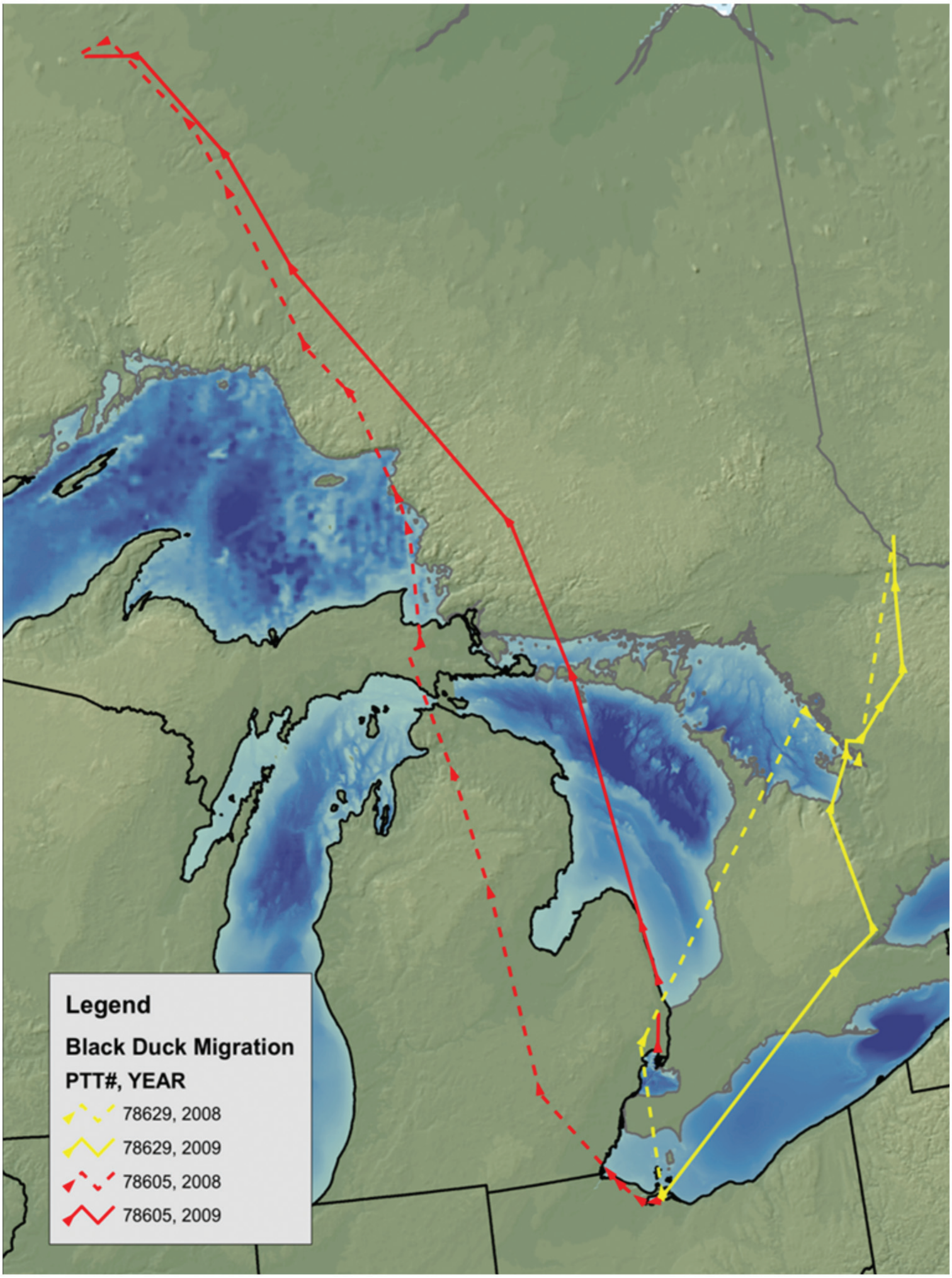

Figure 4. Spring migration routes and inferred nesting locations of 2 adult female American Black Duck PTT-tagged in Ohio during winter 2007/08.

Table 4. Relationships between migratory variables of adult female American Black Duck in eastern North America during spring 2008 and 2009.

Independent Variable	**Dependent Variable**	***F***	**d.f.**	***P***	***R*²**	**β**
Departure date	No. of stopovers	2.21	1, 29	0.15	0.07	–0.03
Departure date	Duration of stay on stopovers (h)	6.15	1, 29	0.02	0.18	–8.50
Departure date	Distance of migration (total; km)	1.30	1, 29	0.26	0.04	–5.44
No. of stopovers	Duration of stay on stopovers (h)	23.20	1, 29	< 0.01	0.44	142.70
Distance of migration (total; km)	# of stopovers	45.60	1, 29	< 0.01	0.61	0.003
Distance of migration (total; km)	Duration of stay on stopovers (h)	14.40	1, 29	< 0.01	0.33	0.45
Distance of migration (leg; km)	Duration of stay on next stopover (h)	0.02	1, 104	0.90	< 0.01	–0.01
Duration of migration (leg; h)	Duration of stay on next stopover (h)	2.87	1, 104	0.09	0.03	5.06
Duration of stay on stopovers (h)	Distance of next migration (leg; km)	0.63	1, 104	0.43	< 0.01	0.06
Duration of stay on stopovers (h)	Duration of next migration (leg; h)	0.04	1, 104	0.84	< 0.01	–0.001

additional insight. Therefore, inference is restricted to PTT-tagged Black Duck and the data collected during the two years of our study.

Our PTT-derived data corroborate documented spring migration routes (Addy 1953; Bellrose 1980), stopovers (Bookhout *et al.* 1989; Jorde *et al.* 1989; Belanger & Lehoux 1994) and band recovery associations, especially for Black Ducks wintering in the Mississippi and South Atlantic Flyways migrating to breeding areas in western Quebec and Ontario (Zimpfer & Conroy 2006; Robinson *et al.* 2016a). All 14 Black Duck wintering in Ohio remained in the Mississippi Flyway during spring migrations, where they were joined by four from the South Atlantic Flyway (three from western Virginia; one from Delaware). All other Black Duck wintering in Delaware or on the eastern shore of Virginia progressed into the eastern breeding range. Contrary to Addy (1953), western Virginia Black Duck displayed no apparent aversion to crossing the Chesapeake Bay, as three of seven did so at the onset of migration.

Waterfowl migration may span several months each year, though migration chronology varies by season (Wege & Raveling 1983; Petrie & Wilcox 2003), year (Wege & Raveling 1983; Murphy-Klassen *et al.* 2005), origin (Haukos *et al.* 2006) and destination (Miller *et al.* 2005a). We failed to detect a difference in the onset of migration, with Black Duck from different regions, latitudes and longitudes departing their wintering areas at approximately the same time in both years.

Given that departure date was a non-factor in group-wise comparisons, delayed arrival at inferred nesting areas among South Atlantic Flyway Black Duck was likely a result of the positive relationship between total distance of migration and both the number of and duration of stay at stopover sites. In our study, South Atlantic Flyway Black Duck migrated farther, took more stopovers, spent a greater amount of time on stopovers and, despite travelling faster, arrived several weeks later at inferred nesting areas. Their behaviour is consistent with the increased energetic demand of longer migrations (Arzel *et al.* 2006; Newton 2006), but has the potential to have an adverse effect on reproductive success, recruitment and survival (Heitmeyer & Fredrickson 1981; Krapu 1981; Kaminski & Gluesing 1987; Raveling & Heitmeyer 1989; Alisauskas & Ankney 1992; Rohwer 1992; Dubovsky & Kaminski 1994; Arnold *et al.* 2002; Devries *et al.* 2008). Black Duck from their southern wintering and western breeding ranges have experienced disproportionate declines (Rogers & Patterson 1984; Petrie 1998; Zimpfer & Conroy 2006). Although our study does not provide any direct evidence linking delayed arrival at inferred nesting areas with population declines among South Atlantic Flyway Black Duck, the potential for causality warrants further consideration.

To develop habitat conservation goals using energetics models, planners must estimate the length of time that migrating waterfowl stay at their stopover sites. The UMRGLRJV assumed that Black Duck on average occupy the region for 45 days during spring migration and 90 days over winter, giving an estimated total of 135 days in the UMRGLR (Soulliere *et al.* 2007). In our study, Mississippi Flyway (*i.e.* Ohio) Black Duck averaged only 7.22 ± 2.0 days (range = 0.08–23.2 days) in the UMRGLR during spring migration and 157.5 ± 7.5 days over winter, giving an estimated total of 164.7 days in the UMRGLR during spring migration and winter combined.

The UMRGLRJV established its Black Duck population goal as a product of the NAWMP goal and the proportion of Black Duck harvested in the UMRGLR (Soulliere *et al.* 2007). The JV population goal was multiplied by the estimated duration of stay to determine duck-use days, which in turn was multiplied by daily energy requirements (kJ/bird/day) to calculate the total energetic requirements of Black Duck, later converted to habitat required to meet the JV population goal. The habitat requirements calculated using our duration of stay estimates for the spring and winter periods combined was 58,005 ha (95% CI = 51,488–64,562 ha) compared to the UMRGLRJV estimate of 47,539 ha. This suggests the UMRGLRJV underestimated the non-breeding habitat objectives for Black Duck in the UMRGLR by 10,466 ha, or approximately 18%.

Our data on migration routes, wintering, stopover and inferred nesting locations, and estimates of duration of stay will be useful in Black Duck conservation efforts. Wintering, spring and autumn stopover, and inferred nesting locations identified in our study represent important targets for population monitoring and conservation efforts aimed at Black Duck recovery. In addition, our estimates of duration of stay provide valuable information for developing energetics models to predict habitat goals to support Black Duck during the non-breeding period. Thus, we suggest that the UMRGLRJV and others consider combining satellite telemetry data with waterfowl counts (Petrie *et al.* 2011), food availability sampling (Brasher *et al.* 2007; Straub *et al.* 2012) and band returns when recalibrating models and management strategies.

Acknowledgements

We would like to thank the following contributors for their support of this study: A. Aiken, L. Allison, J. Anderson, BDJV, T. Brown, Camp Fire Conservation Fund, Cape May NWR, P. Castelli, T. Chappell, Chincoteague NWR, G. Costanzo, D. Cramer, R. Dalio, W. D'Alonzo, Delaware Division of Fish and Wildlife, M. DiBona, Herbert H. and Grace A. Dow Foundation, Edwin B. Forsythe NWR, B. Gunter, K. Jarman, B. Jennings, J. Kanas, C. Kessler, J. Konkel, M. Lamberth, B. Lewis, New Jersey Division of Fish and Wildlife, New York State Department of Environmental Conservation, Moses D. Nunnally, Jr. Charitable Lead Trust, T. O'Connor, Ohio Division of Wildlife, Ottawa NWR, J. Ottley, J. Pike, Prime Hook NWR, J. Rogerson, D. Sherman, Suffolk County Department of Parks, The Nature Conservancy, L. Tymkiw, N. Troyan, University of Delaware, UMRGLRJV, Virginia Department of Game and Inland Fisheries, Waterfowl Research Foundation, Inc., D. Welles, Winous Point Marsh Conservancy, E. Wright and a host of private donors. We also thank M. Schummer for constructive comments on an earlier version of the manuscript.

References

Addy, C.E. 1953. *Fall Migration of the Black Duck*. Special Scientific Report: Wildlife No. 19. United Fish and Wildlife Service, Washington D.C., USA.

Afton, A.D. 2008. Chronology and rates of migratory movements, migration corridors, and habitats used throughout the annual life cycle by female lesser scaup radio-marked on Pool 19 of the Mississippi River. Progress report to the Upper Mississippi River and Great Lakes Region Joint Venture, Bloomington, Minnesota, USA.

Alisauskas, R.T. & Ankney, C.D. 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl. *In* B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec & G.L. Krapu (eds.), *Ecology and Management of Breeding Waterfowl*, pp. 30–61. University of Minnesota Press, Minneapolis, USA.

Argos. 2011. *Argos User's Manual*. Argos (satellite system), CLS/Argos, Toulouse, France. Available at https://www.argos-system.org/manual/ (last accessed 3 March 2009).

Arnold, T.W., Howerter, D.W., Devries, J.H., Joynt, B.L., Emery, R.B. & Anderson, M.G. 2002. Continuous laying and clutch-size limitation in Mallards. *Auk* 119: 261–266.

Arzel, C., Elmberg, J. & Guillemain, M. 2006. Ecology of spring-migrating Anatidae: a review. *Journal of Ornithology* 147: 167–184.

Ashley, E.P., North, N.R., Petrie, S.A. & Bailey, R.C. 2006. Age determination of American Black Ducks in winter and spring. *Wildlife Society Bulletin* 34: 1401–1410.

Barron, D.G., Brawn, J.D. & Weatherhead, P.J. 2010. Meta-analysis of transmitter effects on avian behavior and ecology. *Methods in Ecology and Evolution* 1: 180–187.

Belanger, L. & Lehoux, D. 1994. Use of a tidal saltmarsh and coastal impoundments by sympatric breeding and staging American Black Ducks *Anas rubripes* and Mallards *A. platyrynchos*. *Canadian Field Naturalist* 108: 311–317.

Bellrose, F.C. 1980. *Ducks, Geese, and Swans of North America. 3rd Edition*. Stackpole, Mechanicsburg, USA.

Black Duck Joint Venture. 2008. *Black Duck Joint Venture Strategic Plan 2008–2013*. U.S. Fish & Wildlife Service, Laurel, USA and Canadian Wildlife Service, Ottawa, Canada. Available at http://nawmp.wetlandnetwork.ca/Media/Content/files/BDJV%20Strategic%20Plan%202008_2013.pdf (last accessed 12 December 2012).

Bookhout, T.A., Bednarick, K.E. & Kroll, R.W. 1989. The Great Lakes marshes. *In* L.M. Smith, R.L. Pederson & R.M. Kaminski (eds.), *Habitat Management for Migrating and Wintering Waterfowl in North America*, pp. 131–156. Texas Tech University Press, Lubbock, USA.

Bowman, T.D. & Brown, P.W. 1992. Site fidelity of male Black Ducks to a moulting area in Labrador. *Journal of Field Ornithology* 63: 32–34.

Brasher, M.G., Steckel, J.D. & Gates, R.J. 2007. Energetic carrying capacity of actively and passively managed wetlands for migrating ducks in Ohio. *Journal of Wildlife Management* 71: 2532–2541.

Brook, R.W., Ross, R.K., Abraham, K.F., Fronczak, D.L. & Davies, J.C. 2007. Evidence for black duck winter distribution change. *Journal of Wildlife Management* 73: 98–103.

Chaulk, K.G. & Turner, B. 2007. The timing of waterfowl arrival and dispersion during spring migration in Labrador. *Northeastern Naturalist* 14: 375–386.

Conroy, M.J., Miller, M.W. & Hines, J.E. 2002. Identification and synthetic modeling of factors affecting American Black Duck populations. *Wildlife Monographs* 150: 1–64.

Cox, R.R. Jr. & Afton, A.D. 1998. Effects of capture and handling on survival of female Northern Pintails. *Journal of Field Ornithology* 69: 276–287.

Cramer, D.M., Castelli, P.M., Yerkes, T. & Williams, C.K. 2012. Food resource availability for American Black Ducks wintering in southern New Jersey. *Journal of Wildlife Management* 76: 214 –219.

Devries, J.H., Brook, R.W., Howerter, D.W. & Anderson, M.G. 2008. Effects of spring body condition and age on reproduction in Mallards *Anas platyrhynchos*. *Auk* 125: 618–628.

Dubovsky, J.A. & Kaminski, R.M. 1994. Potential reproductive consequences of winter-diet restriction in Mallards. *Journal of Wildlife Management* 58: 780–786.

Fair, J., Paul, E. & Jones, J. (eds.). 2010. Guidelines to the use of wild birds in research. Ornithological Council, Washington D.C., USA. Available at http://www.ebd.csic.es/documents/240051/0/Guidelines_to_the_use_of_wild_birds_in_research.pdf/4080feb3-01f7-48a3-9712-be5c95e9f8e5 (last accessed 12 December 2012).

Haukos, D.A., Miller, M.R., Orthmeyer, D.L., Takekawa, J.Y., Fleskes, J.P., Casazza, M.L., Perry, W.M. & Moon, J.A. 2006. Spring migration of Northern Pintails from Texas and New Mexico, USA. *Waterbirds* 29: 127–136.

Heitmeyer, M.E. & Fredrickson, L.H. 1981. Do wetland conditions in the Mississippi Delta hardwoods influence Mallard recruitment? *Transactions of the 46th North American Wildlife and Natural Resources Conference* 46: 44–57.

Jorde, D.G., Longcore, J.R. & Brown, P.W. 1989. Tidal and non-tidal wetlands of the northern Atlantic states. *In* L.M. Smith, R.L. Pederson & R.M. Kaminski (eds.), *Habitat Management for Migrating and Wintering Waterfowl in North America*, pp. 1–26. Texas Tech University Press, Lubbock, USA.

Kaminski, R.M. & Gluesing, E.A. 1987. Density and habitat related recruitment in Mallards. *Journal of Wildlife Management* 51: 141–148.

Krapu, G.L. 1981. The role of nutrient reserves in Mallard reproduction. *Auk* 98: 29–38.

Krementz, D.G., Asante, K. & Naylor, L.W. 2011. Spring migration of Mallards from Arkansas as determined by satellite telemetry. *Journal of Fish and Wildlife Management* 2: 156–168.

Lameris, T.K. & Kleyheeg, E. 2017. Reduction in adverse effects of tracking devices on waterfowl requires better measuring and reporting. *Animal Biotelemetry* 5: 24.

Lameris, T.K., Müskens, G.J.D.M., Kölzsch, A., Dokter, A.M., Van der Jeugd, H.P. & Nolet, B.A. 2018. Effects of harness-attached tracking devices on survival, migration, and reproduction in three species of migratory waterfowl. *Animal Biotelemetry* 6: 7.

Lindberg, M.S. & Walker, J. 2007. Satellite telemetry in avian research and management: sample size considerations. *Journal of Wildlife Management* 71: 1002–1009.

Link, W. A. & Sauer, J.R. 2006. A hierarchical model for regional analysis of population change using Christmas bird count data, with application to the American Black Duck. *Condor* 108: 13–24.

Longcore, J.R., McAuley, D.G., Hepp, G.R. & Rhymer, J.M. 2000. American Black Duck *Anas rubripes*, Version 1.0. *In* A.F. Poole & F.B. Gill (eds.), *Birds of the World*. Cornell Lab of Ornithology, Ithaca, USA. Available at https://birdsoftheworld.org/bow/species/ambduc/cur/introduction (last accessed 10 October 2008).

Maisonneuve, C., Belanger, L., Bordage, D., Jobin, B., Grenier, M., Beaulieu, J., Gabor, S. & Filion, B. 2006. American Black Duck and Mallard breeding distribution and habitat relationships along a forest-agriculture gradient in southern Quebec. *Journal of Wildlife Management* 70: 450–459.

Malecki, R., Sheaffer, S., Howell, D. & Strange, T. 2006. Northern Pintails in eastern North America: their seasonal distribution, movement patterns, and habitat affiliations. Final report to the Atlantic Flyway Council, Laurel, USA. Available at http://www.ncwildlife.org/Portals/0/Hunting/Documents/northern_pintail_final_report.pdf (last accessed 3 March 2009).

Malecki, R.A., Batt, B.D.J. & Sheaffer, S.E. 2001. Spatial and temporal distribution of Atlantic Population Canada Geese. *Journal of Wildlife Management* 65: 242–247.

McAuley, D.G., Clugston, D.A. & Longcore, J.R. 2004. Dynamic use of wetlands by Black Ducks and Mallards: evidence against competitive exclusion. *Wildlife Society Bulletin* 32: 465–473.

Merendino, M.T. & Ankney, C.D. 1994. Habitat use by Mallards and American Black Ducks breeding in Central Ontario. *Condor* 96: 411–421.

Miller, M.R., Takekawa, J.Y., Fleskes, J.P., Orthmeyer, D.L., Casazza, M.L. & Perry, W.M. 2005a. Spring migration of Northern Pintails from California's Central Valley wintering area tracked with satellite telemetry: routes, timing, and destinations. *Canadian Journal of Zoology* 83: 1314–1332.

Miller, M.R., Takekawa, J.Y., Fleskes, J.P., Orthmeyer, D.L., Casazza, M.L., Haukos, D.A. & Perry, W.M. 2005b. Flight speeds of Northern Pintails during migration determined using satellite telemetry. *Wilson Bulletin* 117: 364–374.

Morton, J.M., Fowler, A.C. & Kirkpatrick, R.L. 1989. Time and energy budgets of American Black Ducks in winter. *Journal of Wildlife Management* 53: 401–410.

Murphy-Klassen, H.M., Underwood, T.J., Sealy, S.G. & Czyrnyj, A.A. 2005. Long-term trends in spring arrival dates of migrant birds at Delta Marsh, Manitoba, in relation to climate change. *Auk* 122: 1130–1148.

National Oceanic and Atmospheric Administration. 2013. *National Centers for Environmental Information: Climate at a Glance*. NOAA, U.S. Department of Commerce, Washington DC, USA. Available at http://www.ncdc.noaa.gov/cag/ (last accessed 3 March 2013).

Newcomb, K.A., Davis, J.B., Kaminski, R.M. & Gray, M.J. 2016. Winter survival of American Black Ducks in Tennessee, USA. *Condor* 118: 33–45.

Newton, I. 2006. Can conditions experienced during migration limit the population levels of birds? *Journal of Ornithology* 147: 146–166.

North American Waterfowl Management Plan. 1986. *North American Waterfowl Management Plan: a Strategy for Cooperation*. U.S. Department of the Interior, Washington D.C., USA and Environment Canada, Ottawa, Canada. Available at https://nawmp.org/sites/default/files/2018-01/1986%20OriginalNAWMP.pdf (last accessed 3 March 2009).

Parker, G.R. 1991. Survival of juvenile American Black Ducks on a managed wetland in New Brunswick. *Journal of Wildlife Management* 55: 466–470.

Petrie, M.J. 1998. The role of interspecific competition in the decline of the Black Duck. Ph.D. thesis, University of Missouri, Columbia, USA.

Petrie, M.J., Brasher, M.G., Soulliere, G.J., Tirpak, J.M., Pool, D.B. & Reker, R.R. 2011. *Guidelines for Establishing Joint Venture Waterfowl Population Abundance Objectives*. North American Waterfowl Management Plan Science Support Team Technical Report No. 2011-1. U.S. Fish and Wildlife Service, Washington D.C., USA.

Petrie, S.A. & Wilcox, K.L. 2003. Migration chronology of Eastern Population Tundra

Swans. *Canadian Journal of Zoology* 81: 861–870.

Plattner, D.M., Eichholz, M.W. & Yerkes, T. 2010. Food resources for wintering and spring staging Black Ducks. *Journal of Wildlife Management* 74: 1554–1558.

Raveling, D.G. & Heitmeyer, M.E. 1989. Relationships of population size and recruitment of Pintails to habitat conditions and harvest. *Journal of Wildlife Management* 53: 1088–1103.

Reed, A. 1975. Reproductive output of Black Ducks in the St. Lawrence estuary. *Journal of Wildlife Management* 39: 243–255.

Robinson, O.J., McGowan, C.P. & Devers, P.K. 2016a. Updating movement estimates for American Black Ducks (*Anas rubripes*). *PeerJ* 4: e1787.

Robinson, O.J., McGowan, C.P. & Devers, P.K. 2016b. Disentangling density-dependent dynamics using full annual cycle models and Bayesian model weight updating. *Journal of Applied Ecology* 54: 670–678.

Robinson, O.J., McGowan, C.P., Devers, P.K., Brook, R.W., Huang, M., Jones, M., McAuley, D.G. & Zimmerman, G. 2016c. A full annual cycle modeling framework for American Black Ducks. *Natural Resource Modeling* 29: 159–174.

Rogers, J.P. & Patterson, J.H. 1984. The Black Duck population and its management. *Transactions of the North American Wildlife and Natural Resources Conference* 49: 527–534.

Rohwer, F.C. 1992. The evolution of reproductive patterns in waterfowl. *In* B.D.J. Batt, A.D. Afton, M.G. Anderson, C.C. Ankney, D.H. Johnson, J.A. Kadlec & G.L. Krapu (eds.), *Ecology and Management of Breeding Waterfowl*, pp. 486–539. University of Minnesota Press, Minneapolis, USA.

Rusch, D.H., Ankney, C.D., Boyd, H., Longcore, J.R., Montalbano, F. III, Ringelman, J.K. & Stotts, V.D. 1989. Population ecology and harvest of the American Black Duck: a review. *Wildlife Society Bulletin* 17: 379–406.

Seymour, N.R. 1991. Philopatry in male and female American Black Ducks. *Condor* 93: 189–191.

Soulliere, G.J., Potter, B.A., Coluccy, J.M., Gatti, R.C., Roy, C.L., Luukkonen, D.R., Brown, P.W. & Eichholz, M.W. 2007. *Upper Mississippi River and Great Lakes Region Joint Venture Waterfowl Habitat Conservation Strategy*. U.S. Fish & Wildlife Service, Fort Snelling, USA. Available at http://www.uppermissgreatlakesjv.org/docs/UMRGLR_JV_WaterfowlHCS.pdf (last accessed 3 March 2009).

Straub, J.N., Gates, R.J., Schultheis, R.D., Yerkes, T., Coluccy, J.M. & Stafford, J.D. 2012. Wetland food resources for spring-migrating ducks in the Upper Mississippi River and Great Lakes Region. *Journal of Wildlife Management* 76: 768–777.

U.S. Fish and Wildlife Service. 2012. Mid-Winter Waterfowl Survey. U.S. Fish and Wildlife Service, Laurel, USA. Available at: http://mbdcapps.fws.gov/ (last accessed 6 June 2012).

Webster, M.S., Marra, P.P., Haig, S.M., Bensch, S. & Holmes, R.T. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology and Evolution* 17: 76–83.

Wege, M.L. & Raveling, D.G. 1983. Factors influencing the timing, distance, and path of migrations of Canada Geese. *Wilson Bulletin* 95: 209–221.

Zimmerman, G., Sauer, J.R., Link, W.A. & Otto, M. 2011. Composite analysis of Black Duck breeding population surveys in eastern North America. *Journal of Wildlife Management* 76: 1165–1176.

Zimpfer, N.L. & Conroy, M.J. 2006. Modeling movement and fidelity of American Black Ducks. *Journal of Wildlife Management* 70: 1770–1777.