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Long-term changes in the autumn migration phenology of dabbling ducks in southern Ontario and implications for waterfowl management

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Delays in waterfowl autumn migration have been widely reported by hunters and ornithologists throughout North America. The implications of such delays are vast, with potential effects on the efficacy of population management, reduced social and economic opportunities, and reduced resource availability by overuse and over-grazing in key staging areas. In this study, we tested for changes in autumn migration timing for six abundant species of dabbling ducks in southern Ontario, Canada. We applied generalized linear mixed models to test for effects of year and climate indices El Niño Southern Oscillation (ENSO) and North Atlantic Oscillation (NAO) on the Julian date of peak abundance as observed during aerial surveys conducted throughout the lower Great Lakes. Our analyses revealed delays of 11–18 days between 1968 and 2011 for four of six focal species: mallard, American black duck, American wigeon and gadwall. La Niña and El Niño events had no effect on migration timing for American black duck, American green-winged teal or American wigeon, while an increase in the annual NAO index resulted in a delayed migration for American wigeon. There was an NAO:ENSO interaction for mallard and gadwall migration; an increase in NAO advanced peak migration dates during La Niña events. However, an increase in NAO delayed migration for gadwall during the neutral phase of the ENSO and delayed migration for both species during El Niño events. Blue-winged teal and American green-winged teal showed no change in migration timing. Given that climate forecasts indicate continued positive-value phases, the autumn migrations for mallard, American black duck, gadwall and American wigeon may become increasingly delayed. Wildlife managers should use all available data, including from standardized aerial surveys, citizen science and climate models to inform and direct adaptive population management, hunting regulations, wildlife emergency response and habitat conservation.

Keywords: climate change, dabbling duck, lower Great Lakes, migration phenology, waterfowl

Climate change has yielded significant consequences for the migration phenologies of bird species across the globe (Visser and Both 2005, Knudsen et al. 2011). Many migratory species depart from their wintering grounds and arrive on the breeding grounds earlier in the year compared to historically (Murphy and Noon 1991, Murphy-Klassen et al. 2005, Knudsen et al. 2011, Travers et al. 2015). This trend has been observed among landbirds in Europe (Cotton 2003, Hüppop and Hüppop 2003, Jonzén et al. 2006), Australia (Chambers et al. 2014) and North America (Van Burskirk et al. 2009, Francoeur 2012, Hurlbert and Liang 2012, Barton and Sandercock 2017; but see Marra et al. 2005).

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Few studies, however, have focused on phenological shifts for waterfowl species, and even fewer during autumn migration in North America.

In North America, the spring arrival of lesser scaup *Aythya affinis* and greater scaup *A. marila* on the breeding grounds has been shown to be earlier and their migrations were more rapid in years with warmer temperatures and more precipitation (Austin et al. 2002, Finger et al. 2016). In autumn, migration has been occurring later for some European waterfowl species since the late 1970s (Lehikoinen and Jaatinen 2012). These results may be consistent with projected changes to migration timing and distance based on climate models in North America (Notaro et al. 2016). By 2050, seven species are expected to exhibit delays in their autumn migrations, with the greatest shift expected for mallard *Anas platyrhynchos* (Notaro et al. 2016). There is also evidence that the wintering populations for 21 of 44 waterfowl species monitored through the Christmas Bird Count

increased between 1966 and 2013 (Soykan et al. 2016). This increase may be due to a northward shift in wintering range that has been observed among mallard (Brook et al. 2009; but see Green and Krementz 2008), American black duck *A. rubripes* (Link et al. 2006, Brook et al. 2009, Robertson et al. 2017), and other diving and dabbling duck species (Petrie and Schummer 2002, La Sorte and Thompson 2007).

Conservation planning is dependent on accurate data related to the geographic distribution of a migratory species throughout its annual cycle (Kirby et al. 2008, Williams et al. 2014, Runge et al. 2015). These data enable wildlife managers to plan the protection of key habitats throughout the range of the species, which increases the likelihood that the energy needs of the species can be met (O'Neal et al. 2012, Williams et al. 2014). Delayed waterfowl migration in autumn could have important consequences under the current habitat conservation planning strategy of the North American Waterfowl Management Plan (NAWMP), which is based on bio-energetic models that aim to ensure that there are sufficient food resources during this critical period (Williams et al. 2014). Delayed autumn migration could also disrupt the efficacy of harvest regulations if there are discrepancies between open season timing and the presence of migratory waterfowl. Further, these shifts may have economic and social consequences for hunters, particularly in the southern USA. Along with ornithologists, hunters rely on predictable migration timing to plan their species-specific bird watching and hunting and have anecdotally described shifts in migration phenology since the 1960s (Glick 2005, Kaminski et al. 2005, Browne and Humburg 2010). A proper understanding of the mechanisms that drive migration phenology would help identify appropriate management strategies.

Local weather conditions such as air temperature and snow cover influence general migratory behaviour and may also affect timing of migration in autumn (Davis et al. 2014). For example, mallard were shown to winter further south during wetter and colder winters between 1950 and 1980 (Nichols et al. 1983). However, weather patterns in North America associated with dabbling duck migration have been less severe since the 1980s, and are correlated with abundance (Schummer et al. 2010, 2014) and may delay migration (Schummer et al. 2017).

Variation in climatic indices, such as the North Atlantic Oscillation Index (NAO) and the El Niño Southern Oscillation Index (ENSO), have been shown to predict spring arrival dates on the breeding grounds (Hüppop and Hüppop 2003, Francoeur 2012; but see Marra et al. 2005) and departure and transience probabilities at stopover sites during autumn migration among landbird species (Calvert et al. 2009). Waterfowl migration phenology may be similarly affected. Climate indices also predict waterfowl abundance on breeding (Sorenson et al. 1998, Flint 2012, Pöysä and Väänänen 2014, Ross et al. 2015) and wintering grounds (Sedinger et al. 2006) and have contributed to northward shifts in wintering range across bird species (Walther et al. 2002).

Quantifying the magnitude of change in autumn migration phenology may help guide harvest management policies if a more thorough understanding of potential discrepancies between open season timing and waterfowl presence during migration can be achieved. For example, this may

be of particular importance for the American black duck Adaptive Harvest Management Strategy, which seeks equity in harvest between Canada and the United States (Conroy and Peterson 2012). Understanding the climatic drivers will further support this effort, as this may help wildlife managers predict future changes in migration timing, abundance and distribution and inform habitat conservation strategies at the local, regional and flyway levels to ensure that targeted protected areas offer sufficient food resources to support migrating populations (Vonbank et al. 2016). In this study, we examined abundance data collected via the Great Lakes Migrant Waterfowl Survey (GLMWS), an aerial survey conducted from the late 1960s to 2011, to quantify the change in autumn migration phenology for waterfowl in southern Ontario. We defined autumn as the period between 15 August and 31 December; although this period overlaps with late summer and early winter, it aligns with the timing of the southbound migration between breeding and wintering territories for dabbling ducks in the Great Lakes region. We focused our analyses on six of the most common migrant dabbling duck species within the lower Great Lakes and tested whether two climatic indices were related to the timing of their peak abundances during autumn.

Methods

Survey area

The lower Great Lakes falls within Bird Conservation Region 13, lower Great Lakes/St. Lawrence Plain, in the North American Bird Conservation Initiative. The landscape is predominantly agricultural, with interspersed portions of mixed, coniferous and deciduous forests, wetlands and urban areas (EC 2014). The shores of the lower Great Lakes and St. Lawrence River are conservation priority areas identified by the Eastern Habitat Joint Venture (EHJV; EHJV 2017) and provide critical habitat to hundreds of wildlife and plant species, including diving and dabbling ducks. Specifically, the lower Great Lakes represent continentally important staging habitat for migrating waterfowl (Bookhout et al. 1989).

Data collection

The Canadian Wildlife Service of Environment and Climate Change Canada periodically surveys the coastlines and associated wetlands of the Great Lakes to determine seasonal waterfowl abundance and habitat use throughout the non-breeding periods, primarily spring and autumn, of the annual cycle. Visually estimated counts of individual waterfowl observed from fixed-wing aircraft by two biologists were recorded within a series of survey sectors that were distributed throughout the St. Lawrence River, Lake Ontario, Lake Huron/Georgian Bay, Lake Superior, Lake Erie and Lake St. Clair. Individual survey sectors spanned variable lengths of shoreline and are based on geographic landforms or other distinct features such as points of land, bays, river or stream outflows, and roads. Counts were recorded by species or species group when species were difficult to distinguish (e.g. unidentified teal species, large dabbling duck) and were organized by waterbody, survey sector and date. The autumn

GLMWS was conducted during 15 August–31 December every two weeks in a survey year, resulting in $n=4\text{--}11$ surveys per sector per year. The GLMWS was carried out periodically between 1968 and 2011, with variation in survey frequency among sectors. Much or all of the study area has been surveyed at an approximate interval of 10 years. Ross (1989) provides additional details regarding the survey history and methodology. All GLMWS data were downloaded from a publicly available online database (ECCC 2018).

We compiled autumn GLMWS data from survey sectors that were sampled in three or more years between 1968 and 2011. This resulted in a dataset representing 90 survey sectors distributed throughout the lower Great Lakes, including the St. Lawrence River, Lake Ontario, Niagara River, Lake Erie, Detroit River and Lake St. Clair (Fig. 1), shoreline that spans ~800 km from east to west.

Focal species

We focused our analyses on six species of dabbling ducks that are commonly observed in large portions of Canada and the USA: mallard, American black duck, gadwall *Mareca strepera*, American wigeon *M. americana*, American green-winged teal *Anas crecca carolinensis* and blue-winged teal *A. discors*. We included all autumn GLMWS survey data for the focal species and excluded records from ambiguous species groups, e.g. unidentified teal species. Each species is migratory, among the most harvested species throughout Canada and the USA (Gendron and Smith 2017, Raftovich et al. 2019), and commonly observed in varying abundances during the GLMWS. The NAWMP has identified each of these species as priorities for management and conservation (NAWMP 2018). The mallard, American black duck and American green-winged teal are priorities species of the EHJV (EHJV 2017).

Climate data

There are several climatic teleconnections active throughout North America and the most common indices to track

these climatic anomalies include the ENSO, the NAO, the Pacific North America (PNA) and the Arctic Oscillation (AO); such indices represent causal connections between meteorological phenomena that occur over large distances. The NAO climatic index represents the pressure differential between Iceland and the Azores. Its impact on winter climate is evident from Greenland to Florida (Visbeck et al. 2001, Stenseth et al. 2003), which includes the breeding and wintering grounds for many temperate migrants. Overall temperature warming in North America has been correlated with sustained positive phase NAO (Hurrell and Deser 2010) and weather conditions are generally warm but wet in the southern USA and cool and dry in eastern Canada when NAO is positive (Visbeck et al. 2001, Stenseth et al. 2003). The ENSO is a coupled ocean–atmosphere phenomenon that causes global climate variability on inter-annual time scales. Sustained positive ENSO indices (i.e. >5 consecutive months) are associated with El Niño, or warming, while sustained negative ENSO indices are associated with La Niña, or cooling, in Central and South America (Stenseth et al. 2003, NOAA 2018). In the Great Lakes region, there is a positive correlation between ENSO and winter weather severity during El Niño years (Rodionov and Assel 2003). The ENSO and NAO indices have been linked to migration timing for North American landbirds in spring and autumn (Calvert et al. 2009, Van Buskirk et al. 2009, Francoeur 2012) and are important climate indicators throughout the geographic ranges of our study species. We used the Oceanic Niño Index (ONI) as an indicator of the ENSO and reclassified the ONI as a categorical variable to better capture La Niña and El Niño events (Schummer et al. 2014). Each year in which there were five consecutive overlapping three month seasons with an ONI ≥ 0.5 between June–August–September and January–February–March was categorized as an El Niño event, while years with an ONI ≤ -0.5 was categorized as a La Niña event (NOAA 2018). Years that did not meet either definition were categorized as neutral. We downloaded climate data from the National Oceanic and Atmospheric Administration (NOAA 2018).



Figure 1. Map of the Great Lakes Migrant Waterfowl Survey area throughout the lower Great Lakes of southern Ontario. Each polygon represents a survey sector for which peak migration dates were determined using dabbling duck abundance data collected during aerial surveys between 1968 and 2011. Surveyed waterbodies include the St. Lawrence River, Lake Ontario, Niagara River, Lake Erie, Detroit River and Lake St. Clair.

Hypotheses and data analysis

We predicted that the timing of autumn migration for five of our target species (all except blue-winged teal) has changed, such that the date of peak abundance has become later through time, from the late 1960s to 2011. We predicted that La Niña events would have a negative relationship with the date of peak abundance because negative ENSO conditions have been linked to lower transience and departure probabilities among landbirds at autumn stopover sites (Calvert et al. 2009). We predicted a negative relationship between the annual index for NAO and peak migration date because NAO variation has been associated with local weather factors that affect mallard abundance during autumn migration (Schummer et al. 2014). There is evidence that the effect of NAO on mallard migration in the autumn is mediated by ENSO conditions (Schummer et al. 2014), so we included an interaction between the two climatic indices in our candidate models. For blue-winged teal, we hypothesized that migration timing would be unchanged through time, as photoperiod has been shown to be a more informative predictor of abundance in autumn than are weather conditions (Van Den Elsen 2016).

For species or populations that exhibit a change in migration phenology through time, the magnitude of change varies according to the phenological measure (Van Buskirk et al. 2009, Francoeur 2012, Barton and Sandercock 2017). Studies often describe phenology by comparing first arrival dates, although simulation-based analyses suggest this metric can be inaccurate and biased (Moussus et al. 2010, Knudsen et al. 2011). Mean passage date, however, is representative of the timing of the broader population and provides unbiased results in comparative studies (Moussus et al. 2010). We opted to describe migration timing using the Julian date of peak abundance in each year because the number of GLMWS surveys completed per year were limited in some sectors ($n = 4\text{--}11$). As the temporal distributions of abundance were unimodal across species and years, we assumed that this metric was an acceptable substitute for mean passage date.

We used generalized linear mixed-effects models (GLMM) with a normally distributed error structure to test for variation in autumn migration phenology. We constructed 10 a priori models to test our hypotheses of the effects of climate and year. For each model, Julian date of peak abundance was the response variable and survey sector was included as a random effect to account for geographic variation in migration phenology (Table 1). The full model included year, annual indices for NAO, the ONI categorical variable to represent ENSO, and the interaction between NAO and ENSO as

Table 1. A priori candidate models to explain the variation in phenology for six species of dabbling ducks during autumn migration (15 August–31 December) between 1968 and 2011 throughout the lower Great Lakes in southern Ontario.

Model	No. of fixed parameters	Fixed parameters
M1	1	Intercept only
M2	2	NAO
M3	3	ENSO
M4	4	NAO + ENSO
M5	6	NAO + ENSO + NAO \times ENSO
M6	2	Year
M7	3	Year + NAO
M8	4	Year + ENSO
M9	5	Year + NAO + ENSO
M10	7	Year + NAO + ENSO + NAO \times ENSO

predictor variables. Predictor variables for NAO and year were centered before the analysis to facilitate model convergence. We used the Neutral phase of the ENSO as the reference class in all analyses. To account for the fact that the timing of the GLMWS is not always optimally aligned with the migration period, we included the mean survey date in each year as an offset. The intercept in the models therefore represented the difference between the date of peak abundance and the mean survey date in days. Including the offset for mean survey date affected the intercepts but did not affect the slope of the regressors. Model fit was visually assessed by plotting residuals versus fitted values and we visually assessed the normality of the scaled residuals of the best fitting models. Data for each focal species were modelled separately.

For blue-winged teal and American green-winged teal, the GLMMs provided a singular fit (i.e. the variance parameter was estimated as zero), which indicated that survey sector had a limited effect on the Julian peak of abundance. We therefore refit the model set for this species using a series of simplified generalized linear models (GLMs) with the same predictor variables indicated in Table 1 and excluded the random effect for survey sector (Matuschek et al. 2017).

We used Akaike's information criterion corrected for small sample sizes (AICc) to assess support among candidate models (Hurvich and Tsai 1989). The most parsimonious model was the one with the lowest AICc but models within two AICc units were considered competitive (Burnham and Anderson 2002). We averaged across models to calculate parameter estimates and 95% confidence intervals (CIs). Parameters were considered significant if the 95% CIs did not overlap zero. All statistical analyses were conducted in R ver. 3.5.2 using packages lme4 to fit GLMMs (Bates et al. 2015) and AICcmodavg to conduct model selection and model averaging (Mazerolle 2019).

Table 2. Detection summaries of six species of dabbling ducks surveyed during autumn migration (15 August–31 December) throughout the lower Great Lakes in southern Ontario between 1968 and 2011.

Species	No. of years observed	n year ⁻¹ (SD)	Average no. surveys observed/year	Average peak abundance
Mallard	35	33 156 (32 036)	45	7171
American black duck	35	15 846 (14 088)	41	4413
American green-winged teal	32	2711 (3460)	10	1042
Gadwall	34	763 (1396)	10	362
Blue-winged teal	29	1196 (1526)	7	643
American wigeon	35	11 006 (12 377)	13	4666

Results

An average of 33 sectors were surveyed in each year that the GLMWS was completed, with a minimum of three in 1968 and a maximum of 68 in 2000. A total of 1204 surveys were completed in the 43 year history of the GLMWS. Overall, mallard was the most abundant species, with an average annual peak abundance of >7000 individuals (Table 2). American black duck and American wigeon were observed in similar numbers and gadwall was the least common. While the most abundant species were detected in every year that surveys were completed (n = 35 years), blue-winged teal was observed in just 29 years. There was considerable annual variation in abundance across species (Table 2).

In the survey area, blue-winged teal migration was the earliest, with a predicted date of peak abundance in early September followed by American green-winged teal and American wigeon in mid-October (Table 3). Predicted gadwall and mallard abundances peaked in late October, while American black duck abundance peaked in early November (Table 3). The most parsimonious model varied among species (Table 4). Models with the NAO:ENSO interaction were not among the best fitting (i.e. $\Delta AIC_c \leq 2$) for American black duck, American green-winged teal and American wigeon, and had low AICc weights (<0.10). Since the interpretation of the main effects differ when they also appear in an interaction, we excluded the models with an interaction term from the candidate set for model averaging purpose for these three species. Conversely, models with the NAO:ENSO interaction were in the best fitting models and had a cumulative weight ≥ 0.50 for mallard, blue-winged teal and gadwall. We therefore restricted the model averaging to include these models for mallard, blue-winged teal and gadwall.

Model averaged predictions indicated a strong positive effect of year on four of six species (Table 3, Fig. 2). Over the 43 year study, peak migration occurred 14 ± 7 days (mean \pm 95% CIs) later for mallard, 18 ± 6 days for American black duck, 11 ± 11 days for gadwall, and 13 ± 11 days for American wigeon (Fig. 2). La Niña and El Niño events had no discernible effect on the peak migration date for American black duck, American green-winged teal or American wigeon but an increase in NAO resulted in a delayed migration for American wigeon (Table 3, Fig. 3). The effect of NAO depended on ENSO phase for mallard and gadwall, such that an increase in NAO advanced the peak migration date during La Niña events (Table 3, Fig. 4). However, an increase in NAO delayed the peak migration date for gadwall during neutral phase of the ENSO, and delayed the migration of mallard and gadwall during El Niño events.

Discussion

Changes in winter distributions of dabbling duck species have been well documented in eastern North America (Petrie and Schummer 2002, Link et al. 2006, Brook et al. 2009, Robertson et al. 20107), as has the impact of climate on waterfowl movement during migration (Schummer et al. 2014, 2017, Notaro et al. 2016). However, our study is the

Table 3. Model averaged parameter estimates (β) and 95% confidence intervals (CIs) to explain variation in the Julian date of peak abundance of six species of dabbling ducks during autumn migration (15 August–31 December) to year and climate variables throughout the lower Great Lakes in southern Ontario between 1968 and 2011. Parameters with significant effects are indicated in bold font.

Species	Intercept	Year	NAO	La Niña	El Niño	NAO: La Niña	NAO: El Niño
Mallard	303 (299–308)	0.34 (0.17–0.51)	5.26 (–4.51 to 15.04)	–1.01 (–5.62 to 3.6)	–0.89 (–5.73 to 3.94)	–24.72 (–36.45 to –12.98)	3.32 (–10.93 to 17.58)
American black duck	312 (309–314)	0.41 (0.25–0.57)	1.48 (–3.06 to 6.03)	–1.88 (–6.32 to 2.56)	–0.15 (–4.72 to 4.42)	NA	NA
American green-winged teal	292 (287–296)	0.19 (–0.05 to 0.43)	3.64 (–4.92 to 12.2)	0.06 (–7.8 to 7.93)	5.72 (–2.7 to 14.14)	NA	NA
Gadwall	297 (290–303)	0.33 (0.04–0.63)	31.34 (13.56–49.12)	4.86 (–3.11 to 12.84)	3.6 (–4.39 to 11.6)	–42.65 (–65.07 to –20.22)	–27.33 (–50.32 to –4.34)
Blue-winged teal	256 (250–261)	–0.03 (–0.25 to 0.19)	–3.88 (–20.34 to 12.57)	6.89 (–0.15 to 13.92)	4.9 (–2.67 to 12.48)	–17.55 (–38.72 to 3.61)	6.48 (–14.07 to 27.03)
American wigeon	296 (290–301)	0.32 (0.1–0.53)	7.83 (1.26–14.39)	–5.97 (–12.35 to 0.4)	–4.12 (–10.35 to 2.1)	NA	NA

Table 4. Akaike's information criterion corrected for small sample sizes and model weight for each candidate models to explain the variation in phenology for six species of dabbling ducks during autumn migration (15 August–31 December) throughout the lower Great Lakes in Ontario between 1968 and 2011. Best model for each species is indicated in bold font.

	Mallard		American black duck		American green-winged teal		Gadwall		Blue-winged teal		American wigeon	
	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i
M1	42.30	0.00	23.56	0.00	0.62	0.16	7.17	0.02	3.83	0.06	8.12	0.01
M2	33.28	0.00	25.59	0.00	1.78	0.09	8.34	0.01	2.35	0.12	6.56	0.02
M3	46.16	0.00	27.00	0.00	1.68	0.10	10.19	0.00	4.20	0.05	8.16	0.01
M4	37.34	0.00	29.00	0.00	3.21	0.05	11.32	0.00	2.88	0.09	7.40	0.01
M5	12.93	0.00	30.97	0.00	3.20	0.05	2.58	0.18	0.00	0.38	9.79	0.00
M6	25.13	0.00	0.00	0.57	0.00	0.22	4.28	0.08	3.82	0.06	3.82	0.07
M7	20.23	0.00	1.59	0.26	1.39	0.11	5.24	0.05	3.31	0.07	0.00	0.45
M8	29.13	0.00	3.12	0.12	1.50	0.11	7.86	0.01	5.33	0.03	3.74	0.07
M9	24.25	0.00	4.94	0.05	3.17	0.05	8.89	0.01	4.68	0.04	0.98	0.28
M10	0.00	1.00	7.94	0.01	2.46	0.07	0.00	0.65	2.23	0.12	3.23	0.09

first to directly measure a temporal shift in the timing of autumn migration among dabbling ducks in North America.

Between 1968 and 2011, we found that peak autumn migration occurred 11–18 days later for four of six focal species, the equivalent of 3–5 days/decade. These results are consistent with those from Lehtikoinen and Jaatinen (2012) who documented delays in the timing of autumn migration

among European waterfowl species. Weather severity and habitat conditions are thought to be important factors that influence autumn migration among waterfowl (Nichols et al. 1983, Schummer et al. 2010, O’Neal et al. 2012, Baldassarre 2014). In North America, there has been a continental increase in winter temperature and a decrease in snow cover since 1955 (Field et al. 2007), which may help explain

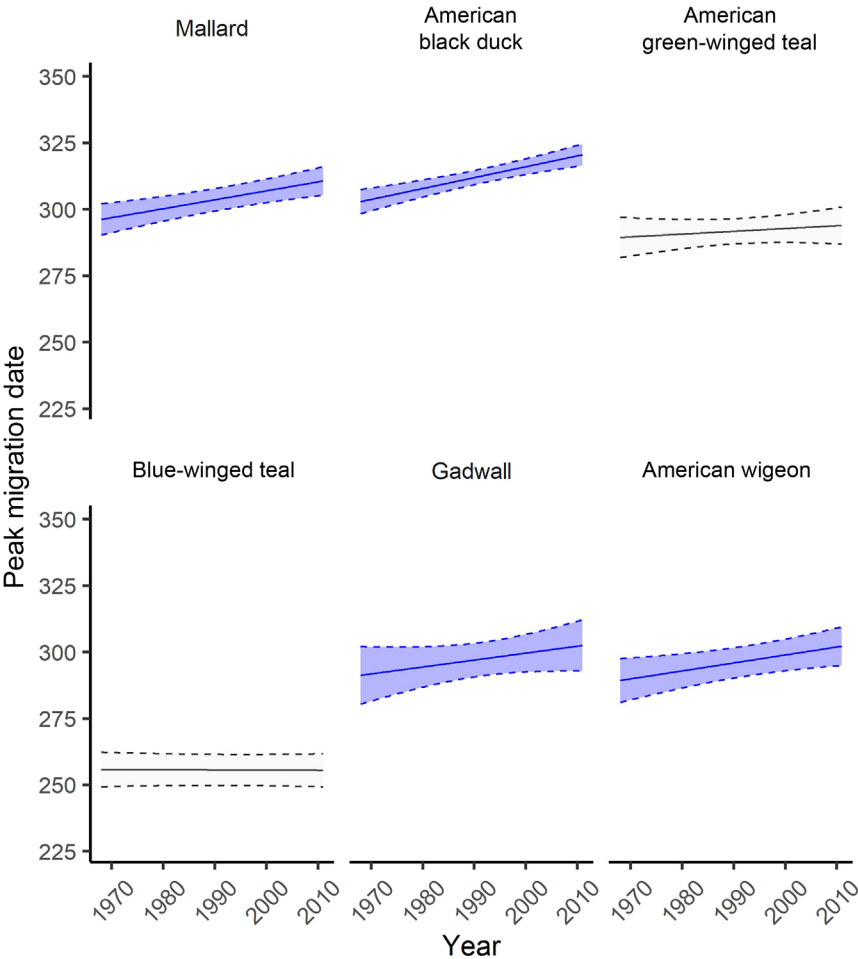


Figure 2. Model averaged Julian date of peak abundance during autumn migration (15 August–31 December) throughout the lower Great Lakes in southern Ontario versus Year for six species of dabbling ducks. Shaded areas represent 95% confidence intervals. Parameters significant at the 95% level are identified in blue.

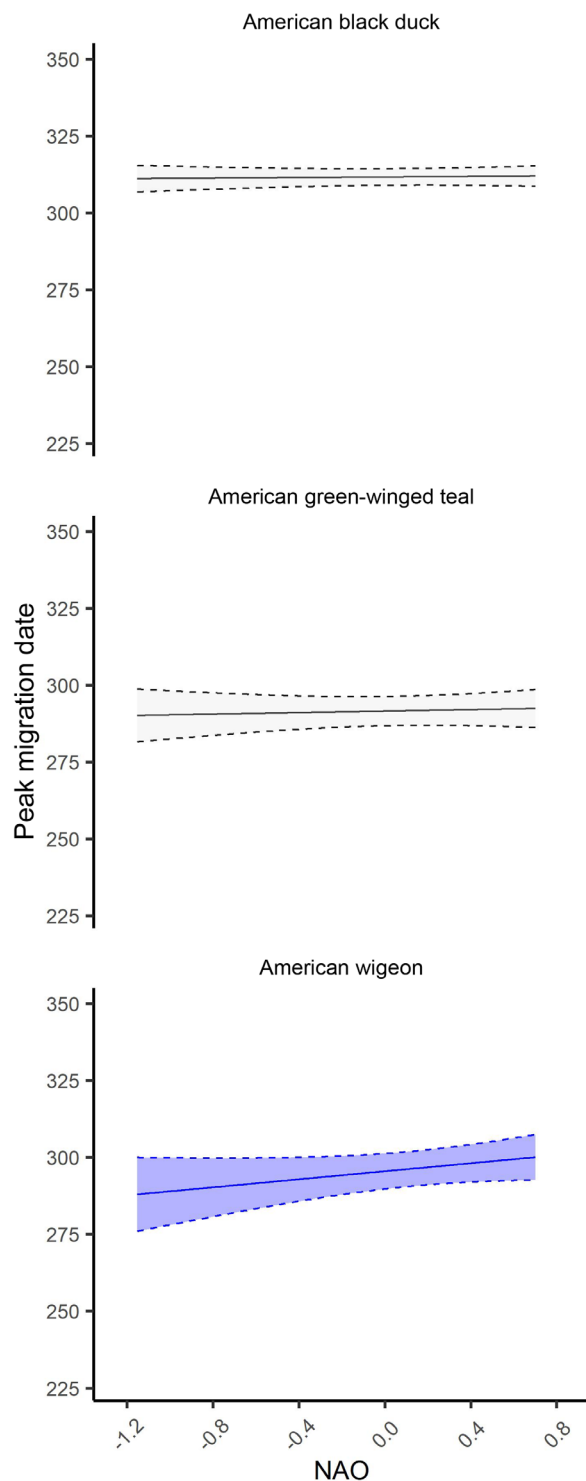


Figure 3. Model averaged Julian date of peak abundance during autumn migration (15 August–31 December) throughout the lower Great Lakes in southern Ontario versus NAO index for three species of dabbling ducks. Shaded areas represent 95% confidence intervals. Parameters significant at the 95% level are identified in blue.

the observed delays in migration (this study) and northward shifts in winter distributions reported elsewhere from the 1970s and onward (Petrie and Schummer 2002, Link et al. 2006, Brook et al. 2009, Robertson et al. 2017). Additional

factors that could explain the later migration include, but are not limited to, increased food availability from agricultural resources such as waste grain and corn (Stafford et al. 2010, Pearse et al. 2012), the introduction of exotic species as an abundant food source like the zebra mussel *Dreissena polymorpha* in the Great Lakes (Petrie and Schummer 2002), and supplemental feeding in wildlife refuges (Palumbo et al. 2019) near breeding territories or at staging sites.

In our tests of the effects of climate on migration phenology, we included the annual index for NAO and a categorical representation of the ENSO to represent the variable conditions to which birds are exposed throughout their geographic range (Ahola et al. 2004), regardless of their migration timing. In the Great Lakes, there is a positive correlation between ENSO and the winter weather severity, such that warm winters and reduced ice coverage are correlated with a warm phase of the ENSO (i.e. El Niño events; Assel 1998, Rodionov and Assel 2003). The observed correlations between mallard, American wigeon and gadwall migrations and ENSO and NAO indices indicate that these species are prone to migrate earlier in years with harsh conditions in the autumn and migrate later in years when conditions are less severe. Our observations are consistent with previous research done on the impact of a 'weather severity index' (WSI), an index that summarizes the impact of temperature and snow cover, on autumn migration phenology among waterfowl species in eastern North America (Schummer et al. 2014, 2017, Notaro et al. 2016). Overall, the climatic indices had a positive effect on the timing of peak migration. Given that climate models forecast that both indices will be in positive-value phases in the future (Timmermann et al. 1999, Visbeck et al. 2001), wildlife managers should expect that migrations for mallard, American black duck, gadwall and American wigeon will become increasingly delayed with time. There was, however, considerable variation among species in their response to climate variation, and more targeted species-specific analyses will help managers refine their future waterfowl management plans.

There was no evidence of a phenological shift for the blue-winged teal or the American green-winged teal. Likewise, the annual climate indices were poor predictors of migration timing for both species in our study. That there was no evidence of a change in migration phenology for the blue-winged teal is consistent with other research that concluded that photoperiod was a better predictor of blue-winged teal abundance during autumn migration compared to weather or climate variables (Notaro et al. 2016, Van Den Elsen 2016). The blue-winged teal is a long distance migrant, and is among the last duck species to migrate north in spring and among the earliest to migrate south in autumn (Rohwer et al. 2002). The timing of its migration creates a short breeding season with little opportunity to initiate an earlier or later autumn migration based on weather. For the American green-winged teal, other research has established a link between its migration timing and a WSI in North America (Schummer et al. 2014, 2017, Notaro et al. 2016) while the autumn migration for Eurasian teal in Europe was delayed between 1979 and 2009 (Lehikoinen and Jaatinen 2012). However, American green-winged teal migration was relatively insensitive to the WSI in autumn (i.e. between October and January) and was more strongly correlated with

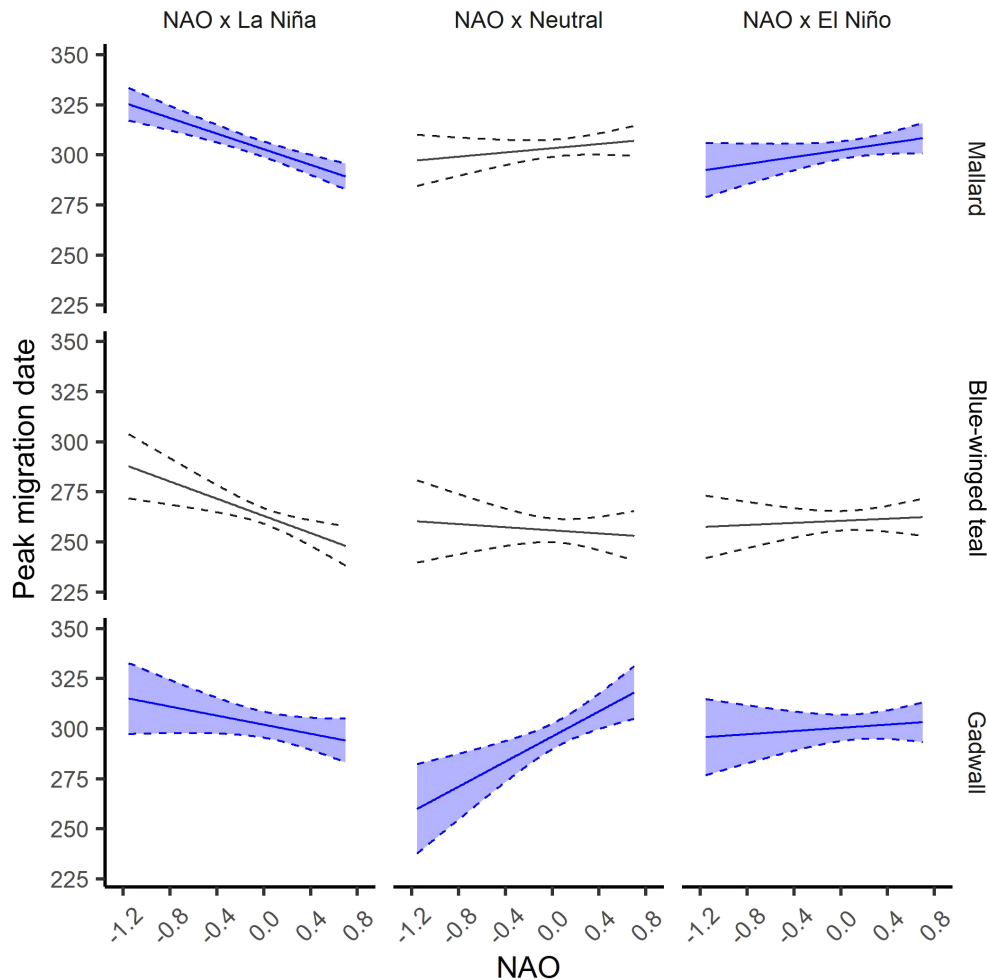


Figure 4. Model averaged Julian date of peak abundance during autumn migration (15 August–31 December) throughout the lower Great Lakes in southern Ontario versus NAO index and phase of the Oceanic Niño Index (La Niña, Neutral and El Niño) for three species of dabbling ducks. Shaded areas represent 95% confidence intervals. Parameters significant at the 95% level are identified in blue.

the index in the spring, February–April (Schummer et al. 2017). Our results reflect that of Schummer et al. (2017), such that American green-winged teal autumn migration timing was consistent between 1968 and 2011.

A limitation of our study was the survey dates for the GLMWS, 15 August–31 December. Given that male blue-winged teal depart from the breeding grounds earlier than females, often in late July to early August (Rohwer et al. 2002), a portion of the population that migrated through the Great Lakes may have been missed in autumn surveys in some years. Summer surveys of the Great Lakes were periodically undertaken between 1968 and 2002, but at a smaller scale and on a less frequent basis than the GLMWS (ECCC 2018). Data collected during summer surveys, therefore, could not be used to understand the early phases of autumn migration for the blue-winged teal. For later migrating species, we cannot be sure that all individuals had passed through the Great Lakes prior to 31 December in all years. For example, gadwall have been shown to arrive on the wintering grounds on the Chesapeake Bay as late as 8 January (Reese and Weterings 2018). Given that Chesapeake Bay is south of our study area, autumn migration would therefore be observed comparatively later in the year. However, midwinter survey data collected in January have shown

that relatively few American green-winged teal, gadwall and American wigeon remain in the lower Great Lakes (Fronscak 2012), suggesting that while temporal coverage for these species might be truncated at the end of the season, peak migration should be well captured by the GLMWS.

The general shift towards a later autumn migration among some waterfowl species may yield negative economic, social and ecological consequences. Annually, waterfowl hunting generates millions of dollars in revenue for recreation, tourism and conservation initiatives throughout North America (Grado et al. 2011, Heffelfinger et al. 2013, Henderson et al. 2014, Cooper et al. 2015). Hunting is also a key tool used by wildlife managers to manage some species populations at acceptable levels (Heffelfinger et al. 2013). Should a changing migration phenology create a timing mismatch between open hunting season dates and the presence of waterfowl, there will be fewer opportunities to harvest waterfowl, which could result in an inability to manage a specific species at an acceptable population level or contribute to dissatisfaction among hunters and a decline in economics revenues for management agencies (Green and Kremenetz 2008, Vrtiska et al. 2013). That the migration phenologies of dabbling ducks in the lower Great Lakes will continue to change is corroborated by Notaro et al. (2016), who projected increased delays

of 12–19 days by 2050, such that American black duck and mallard may overwinter in the region by 2100. Jurisdiction-level adjustments to hunting regulations that reflect current migratory timing for key species of waterfowl could help mitigate hunter dissatisfaction, maintain social engagement and stabilize economic opportunities.

Our study looked at the timing of peak migration but did not address change in residency time. However, the change in autumn migration phenology that we detected is also coincident with a northward shift in the wintering distribution for mallard, American black duck and other species of diving and dabbling ducks (Petrie and Schummer 2002, Link et al. 2006, Brook et al. 2009, Robertson et al. 2017), which may compound resource depletion in some habitats in the future. Areas that are occupied by an increasing number of wintering waterfowl may be subjected to limiting food resources via over-exploitation (Hagy and Kaminski 2015), which could then affect the broader ecosystem health and its carrying capacity (Abraham et al. 2005). In the lower Great Lakes, Churchill et al. (2016) found that Lake Erie dreissenid mussel and submerged aquatic vegetation densities declined from 1992 to 2009, thus diminishing the overall carrying capacity for both diving ducks and dabbling ducks. The potential for increased usage of wetlands in the Great Lakes throughout the annual cycle highlights the need for accurate estimates of carrying capacity (Hagy et al. 2014) that can be used to inform habitat management and conservation through Habitat joint ventures and cross-border partnerships.

Conclusion

Our study revealed notable temporal trends in migration timing in which four dabbling duck species delayed their autumn migration through the lower Great Lakes in Ontario between 1968 and 2011. Our results indicate that the reported declines in waterfowl abundance observed during the hunting season in the southern USA (Glick 2005, Kaminski et al. 2005, Browne and Humburg 2010) are potentially due to shifts in the timing of autumn migration. The delay ranged 11–18 days for mallard, American black duck, gadwall and American wigeon; such a magnitude may have direct implications for harvest opportunities for these species, and suggests that wetland habitat in the lower Great Lakes may face increased pressure by waterfowl throughout the annual cycle in the future. Declining population sizes could further compound the effect of a changing migration phenology for hunters in the southern USA, although this was not addressed in our study. Future research should examine waterfowl migration timing with a broader geographic lens to enable adaptive, cross-border harvest management policies that are species specific. Such studies will allow managers to gauge the impacts to regional hunting opportunities throughout each of the major migratory flyways and will guide habitat procurement, conservation and protection to support current and future habitat use by migrant waterfowl. This research should be undertaken using all relevant sources of information, including citizen science data, in order to better understand the variable effects of climate change on

waterfowl migration timing, abundance and distribution and to inform management and conservation plans at local, regional and continental scales.

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References

- Abraham, K. F. et al. 2005. Goose-induced changes in vegetation and land cover between 1976 and 1997 in an Arctic Coastal Marsh. – *Arct. Antarc. Alp. Res.* 37: 269–275.
- Ahola, M. et al. 2004. Variation in climate warming along the migration route uncouples arrival and breeding dates. – *Global Change Biol.* 10: 1610–1617.
- Assel, R. A. 1998. The 1997 ENSO event and implication for North American Laurentian Great Lakes winter severity and ice cover. – *Geophys. Res. Lett.* 25: 1031–1033.
- Austin, J. E. et al. 2002. Scaup migration patterns in North Dakota relative to temperatures and water conditions. – *J. Wildl. Manage.* 66: 874–882.
- Baldassarre, G. A. 2014. Ducks, geese and swans of North America. – Univ. Press.
- Barton, G. G. and Sandercock, B. K. 2017. Long-term changes in the seasonal timing of landbird migration on the Pacific Flyway. *Cambios a largo plazo en la fecha estacional de migración de las aves canoras en el corredor de vuelo del Pacífico*. Migration timing of western landbirds. – *Condor* 120: 30–46.
- Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. – *J. Stat. Softw.* 67: 1–48.
- Bookhout, T. A. et al. 1989. The Great Lakes marshes. – In: Smith, L. M. et al. (eds), *Habitat management for migration and wintering waterfowl in North America*. Texas Tech. Univ. Press, pp. 131–156.
- Brook, R. W. et al. 2009. Evidence for black duck winter distribution change. – *J. Wildl. Manage.* 73: 98–103.
- Browne, D. M. and Humburg, D. D. 2010. Confronting the challenges of climate change for waterfowl and wetlands. – Ducks Unlimited Inc., Memphis, TN.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. – Springer.
- Calvert, A. M. et al. 2009. Cross-scale environmental influences on migratory stopover behaviour. – *Global Change Biol.* 15: 744–759.
- Chambers, L. E. et al. 2014. Continental scale analysis of bird migration timing: influences of climate and life history traits – a generalized mixture model clustering and discriminant approach. – *Int. J. Biometeorol.* 58: 1147–1162.
- Churchill, R. T. J. et al. 2016. Long-term changes in distribution and abundance of submerged aquatic vegetation and dreissenid mussels in Long Point Bay, Lake Erie. – *J. Great Lakes Res.* 42: 1060–1069.
- Conroy, M. J. and Peterson, J. T. 2012. Decision making in natural resource management: a structured, adaptive approach. – Wiley-Blackwell.

- Cooper, C. et al. 2015. Are wildlife recreationists conservationists? Linking hunting, birdwatching and pro-environmental behavior. – *J. Wildl. Manage.* 79: 446–457.
- Cotton, P. A. 2003. Avian migration phenology and global climate change. – *Proc. Natl Acad. Sci. USA* 100: 12219–12222.
- Davis, J. B. et al. 2014. Habitat and resource use by waterfowl in the northern hemisphere in autumn and winter. – *Wildfowl Spec. Issue* 4: 17–69.
- Eastern Habitat Joint Venture 2017. Eastern Habitat Joint Venture North American Waterfowl Management Plan Implementation Plan 2015–2020. Report of the Eastern Habitat Joint Venture. – Environment and Climate Change Canada.
- Environment Canada 2014. Bird conservation strategy for bird conservation region 13 in Ontario region: Lower Great Lakes/St. Lawrence Plain. Abridged Version. – Environment Canada.
- Environment and Climate Change Canada 2018. Data from: Great Lakes Migrant Waterfowl Survey. – <<http://data.ec.gc.ca/data/species/assess/great-lakes-migrant-waterfowl-survey/>>
- Field, C. B. et al. 2007. North America. Climate Change 2007: impacts, adaptation and vulnerability. – In: Parry, M. L. et al. (eds), Contribution of working group II to the fourth assessment report of the intergovernmental panel on climate change. Cambridge Univ. Press, pp. 617–652.
- Finger, T. A. et al. 2016. Environmental factors influence lesser scaup migration chronology and population monitoring. – *J. Wildl. Manage.* 80: 1437–1449.
- Flint, P. L. 2012. Changes in size and trends of North American sea duck populations associated with North Pacific oceanic regime shifts. – *Mar. Biol.* 160: 59–65.
- Francoeur, X. W. 2012. Effets des changements climatiques sur la phénologie printanière de l'avifaune du Québec. – Dépt de biologie, chimie et géographie. Univ. du Québec à Rimouski.
- Fronscak, D. 2012. Midwinter waterfowl survey, Mississippi Flyway. – United States Fish and Wildlife Service.
- Gendron, M. H. and Smith, A. C. 2017. Data from: National harvest survey web site. – <<https://wildlife-species.canada.ca/harvest-survey/>>
- Glick, P. 2005. The Waterfowlers' guide to global warming. – National Wildlife Federation, Washington, DC.
- Grado, S. C. et al. 2011. Economic impacts of waterfowl hunting in Mississippi derived from a state-based mail survey. – *Hum. Dimens. Wildl.* 16: 100–113.
- Green, A. W. and Kremetz, D. G. 2008. Mallard harvest distributions in the Mississippi and Central Flyways. – *J. Wildl. Manage.* 72: 1328–1334.
- Hagy, H. M. and Kaminski, R. M. 2015. Determination of foraging thresholds and effects of application on energetic carrying capacity for waterfowl. – *PLoS One* 10: e0118349.
- Hagy, H. M. et al. 2014. Annual variation in food densities and factors affecting wetland use by waterfowl in the Mississippi Alluvial Valley. – *Wildfowl Spec. Issue* 4: 436–450.
- Heffelfinger, J. R. et al. 2013. The role of hunting in North American wildlife conservation. – *Int. J. Environ. Stud.* 70: 399–413.
- Henderson, E. B. et al. 2014. Species distribution modelling for plant communities: stacked single species or multivariate modelling approaches? – *Appl. Veg. Sci.* 17: 516–527.
- Hüppop, O. and Hüppop, K. 2003. North Atlantic Oscillation and timing of spring migration in birds. – *Proc. R. Soc. Biol. Sci. Ser. B* 270: 233–240.
- Hurlbert, A. H. and Liang, Z. 2012. Spatiotemporal variation in avian migration phenology: citizen science reveals effects of climate change. – *PLoS One* 7: e31662.
- Hurrell, J. W. and Deser, C. 2010. North Atlantic climate variability: the role of the North Atlantic Oscillation. – *J. Mar. Syst.* 79: 231–244.
- Hurvich, C. M. and Tsai, C.-L. 1989. Regression and time series model selection in small samples. – *Biometrika* 76: 297–307.
- Jonzén, N. et al. 2006. Rapid advance of spring arrival dates in long-distance migratory birds. – *Science* 312: 1959–1961.
- Kaminski, R. et al. 2005. Where have all the mallards gone. – *Delta Wildl.* 13: 23–26.
- Kirby, J. S. et al. 2008. Key conservation issues for migratory land- and waterbird species on the world's major flyways. – *Bird Conserv. Int.* 18: 49–73.
- Knudsen, E. et al. 2011. Challenging claims in the study of migratory birds and climate change. – *Biol. Rev.* 86: 928–946.
- La Sorte, F. A. and Thompson 3rd, F. R. 2007. Poleward shifts in winter ranges of North American birds. – *Ecology* 88: 1803–1812.
- Lehikoinen, A. and Jaatinen, K. 2012. Delayed autumn migration in northern European waterfowl. – *J. Ornithol.* 153: 563–570.
- Link, W. A. et al. 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.
- Marra, P. P. et al. 2005. The influence of climate on the timing and rate of spring bird migration. – *Oecologia* 142: 307–315.
- Matuschek, H. et al. 2017. Balancing type I error and power in linear mixed models. – *J. Memory Language* 94: 305–315.
- Mazerolle, M. J. 2019. AICcmodavg: model selection and multi-model inference based on (Q)AIC(c). – R package ver. 2.2. <<https://cran.r-project.org/package=AICcmodavg>>
- Moussus, J.-P. et al. 2010. Featuring 10 phenological estimators using simulated data. – *Methods Ecol. Evol.* 1: 140–150.
- Murphy, D. D. and Noon, B. D. 1991. Coping with uncertainty in wildlife biology. – *J. Wildl. Manage.* 55: 773–782.
- Murphy-Klassen, H. M. et al. 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 2018. Data from: Climate indices: monthly atmospheric and ocean time-series. – <<https://www.esrl.noaa.gov/psd/data/climateindices/list/>>
- Nichols, J. D. et al. 1983. Factors affecting the distribution of mallards wintering in the Mississippi alluvial valley. – *Auk* 100: 932–946.
- North American Waterfowl Management Plan 2018. North American Waterfowl management plan (NAWMP) update: connecting people, waterfowl and wetland. <https://nawmp.org/sites/default/files/2018-12/6056%202018%20NAWMP%20Update_EN16.pdf>
- Notaro, M. et al. 2016. Projected influences of changes in weather severity on autumn–winter distributions of dabbling ducks in the mississippi and atlantic flyways during the twenty-first century. – *PLoS One* 11: e0167506.
- O'Neal, B. J. et al. 2012. Stopover duration of fall-migrating dabbling ducks. – *J. Wildl. Manage.* 76: 285–293.
- Palumbo, M. D. et al. 2019. Mallard resource selection trade-offs in a heterogeneous environment during autumn and winter. – *Ecol. Evol.* 9: 1798–1808.
- Pearse, A. T. et al. 2012. Local and landscape associations between wintering dabbling ducks and wetland complexes in Mississippi. – *Wetlands* 32: 859–869.
- Petrie, S. A. and Schummer, M. L. 2002. Waterfowl response to zebra mussels on the lower Great Lakes. – *Birding* 34: 346–351.
- Pöysä, H. and Väänänen, V.-M. 2014. Drivers of breeding numbers in a long-distance migrant, the garganey (*Anas querquedula*): effects of climate and hunting pressure. – *J. Ornithol.* 155: 679–687.
- Raftovich, R. V. et al. 2019. Migratory bird hunting activity and harvest during the 2017–18 and 2018–19 hunting seasons. – U.S. Fish and Wildlife Service.
- Reese, J. G. and Weterings, R. 2018. Waterfowl migration chronologies in central Chesapeake Bay during 2002–2013. – *Wilson J. Ornithol.* 130: 52–69.

- Robertson, G. J. et al. 2017. Increases in the number of American black ducks wintering in Nova Scotia, 1970–2015. – J. Fish Wildl. Manage. 8: 669–675.
- Rodionov, S. and Assel, R. A. 2003. Winter severity in the Great Lakes region: a tale of two oscillations. – Clim. Res. 24: 19–31.
- Rohwer, F. C. et al. 2002. Blue-winged teal (*Spatula discors*), ver. 2.0. – In: Poole, A. F. and Gill, F. B. (eds), The birds of North America. Cornell Lab of Ornithology.
- Ross, R. K. 1989. A re-survey of migrant waterfowl use of the Ontario St. Lawrence River and northeastern Lake Ontario. – Can. Wildl. Service Occas. Paper 52, Ottawa.
- Ross, B. E. et al. 2015. Combined effects of climate, predation and density dependence on scaup population dynamics. – Ecol. Appl. 25: 1606–1617.
- Runge, C. A. et al. 2015. Protected areas and global conservation of migratory birds. – Science 350: 1255–1258.
- Schummer, M. L. et al. 2010. Weather-related indices of autumn–winter dabbling duck abundance in middle North America. – J. Wildl. Manage. 74: 94–101.
- Schummer, M. L. et al. 2014. Atmospheric teleconnections and Eurasian snow cover as predictors of a weather severity index in relation to mallard *Anas platyrhynchos* autumn–winter migration. – Wildfowl Spec. Issue 4: 451–469.
- Schummer, M. L. et al. 2017. Long-term trends in weather severity indices for dabbling ducks in eastern North America. – Wildl. Soc. Bull. 41: 615–623.
- Sedinger, J. S. et al. 2006. Effects of El Niño on distribution and reproductive performance of black brant. – Ecology 87: 151–159.
- Sorenson, L. G. et al. 1998. Potential effects of global warming on waterfowl populations breeding in the northern Great Plains. – Clim. Change 40: 343–369.
- Soykan, C. U. et al. 2016. Population trends for North American winter birds based on hierarchical models. – Ecosphere 7: e01351.
- Stafford, J. D. et al. 2010. Avian foods, foraging and habitat conservation in world rice fields. – Waterbirds 33: 133–150.
- Stenseth, N. C. et al. 2003. Review article. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. – Proc. R. Soc. Biol. Sci. Ser. B 270: 2087–2096.
- Timmermann, A. et al. 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. – Nature 398: 694–697.
- Travers, S. E. et al. 2015. Climate change and shifting arrival date of migratory birds over a century in the northern Great Plains. – Wilson J. Ornithol. 127: 43–51.
- Van Buskirk, J. et al. 2009. Variable shifts in spring and autumn migration phenology in North American songbirds associated with climate change. – Global Change Biol. 15: 760–771.
- Van Den Elsen, L. M. 2016. Weather and photoperiod indices of autumn and winter dabbling duck abundance in the Mississippi and Atlantic Flyways of North America. Biology. – Univ. of Western Ontario.
- Visbeck, M. H. et al. 2001. The North Atlantic Oscillation: past, present and future. – Proc. Natl Acad. Sci. USA 98: 12876–12877.
- Visser, M. E. and Both, C. 2005. Shifts in phenology due to global climate change: the need for a yardstick. – Proc. R. Soc. Biol. Sci. Ser. B 272: 2561–2569.
- Vonbank, J. A. et al. 2016. Energetic carrying capacity of riverine and connected wetlands of the Upper Illinois River for fall-migrating waterfowl. – Am. Midl. Nat. 176: 210–221.
- Vrtiska, M. P. et al. 2013. Economic and conservation ramifications from the decline of waterfowl hunters. – Wildl. Soc. Bull. 37: 380–388.
- Walther, G.-R. et al. 2002. Ecological responses to recent climate change. – Nature 416: 389–395.
- Williams, C. K. et al. 2014. Estimating habitat carrying capacity for migrating and wintering waterfowl: considerations, pitfalls and improvements. – Wildfowl 4: 407–435.