Atmospheric teleconnections and Eurasian snow cover as predictors of a weather severity index in relation to Mallard *Anas platyrhynchos* autumn–winter migration

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Abstract

Research on long-term trends in annual weather severity known to influence migration and winter distributions of Mallard *Anas platyrhynchos* and other migratory birds is needed to predict effects of changing climate on: 1) annual distributions and vital rates of these birds, 2) timing of habitat use by migratory birds, and 3) demographics of the hunters of these species. Weather severity thresholds developed previously for Mallard were used to calculate weather severity and spatially-depicted Weather Severity Index Anomalies (± km^2, WSIA), in comparison with normal conditions, for Mallard in eastern North America from November–January 1950–2008. We determined whether WSIA differed among decades and analysed the effects of atmospheric teleconnections and Eurasian snow cover on annual variation in WSIA. Weather severity was mildest (+ WSIA) during the 2000s compared to other decades and differed substantially from the 1960s and 1970s (– WSIA). The Arctic Oscillation Index explained substantial variation in WSIA during El Niño and La Niña episodes, but not when the Oceanic Niño Index was neutral. Eurasian snow cover models accurately predicted if the WSIA would be greater or less than normal for 75% of the years studied. Our results may provide a partial explanation for recent observations of interrupted or reduced migration to southern latitudes by Mallard and other migratory birds during autumn–winter. Our models also provide ecologists with teleconnection models to help predict future distributions of Mallard and potentially other migratory birds in eastern North America. Future investigations could include testing the influence of WSIA on Mallard survival and on annual movements and distributions for other migratory birds, to provide a better understanding of the influences of climate and changes in climate on population dynamics and the need to conserve particular habitats.

Key words: Arctic Oscillation, climate, El Niño, migration, waterfowl, weather, winter.

The winter distribution of migratory birds is influenced by a range of variables including food and habitat availability, weather, evolutionary and ecological mechanisms, body condition and anthropogenic factors (Miller *et al.* 2005; Newton 2007, 2008; Schummer *et al.* 2010). Evidence suggests that global climate change has lengthened growing seasons, increased winter temperatures and decreased snow accumulation at many locations worldwide (Field *et al.* 2007). Concurrently, delays in autumn migration and changes in the birds' winter distributions have been documented in North America and Eurasia (Sokolov *et al.* 1999; Cotton 2003; La Sorte & Thompson 2007; Brook *et al.* 2009; Sauter *et al.* 2010). Many migratory birds distribute annually along a latitudinal gradient as a function of physiological tolerances to the severity of winter weather (Root & Schneider 1995). Although food and habitat availability, refugia, flooding and other exogenous factors can mitigate influences of weather severity on bird energy budgets, climate remains a primary determinant of winter distributions of many species (Root 1988). Thus, climate warming is often cited as the mechanism underlying a shift in range towards the pole (Crick 2004; Gordo 2007; La Sorte & Thompson 2007; Nevin *et al.* 2010).

Northward shifts in winter range and changes in autumn migration phenology can arise from changes in weather severity, food and habitat availability, or a combination of these (Gordo 2007; Newton 2008; Schummer *et al.* 2010). Concurrent with milder weather during winter, habitat has become increasingly available to waterfowl through wetland conservation programmes in northern and mid-latitude regions of North America (NAWMP 2004; Dahl 2006). This has led to considerable debate regarding the mechanism(s) determining current winter distributions of Nearctic waterfowl (National Flyway Council and Wildlife Management Institute 2006, Greene and Krementz 2008; Brook *et al.* 2009). Research into the long-term changes in weather conditions known to elicit southerly migrations by waterfowl therefore is needed to understand influences of weather severity and habitat availability on the birds' winter distribution and migration phenology (*e.g.* Schummer *et al.* 2010). Further, success of wetland restoration is often measured by monitoring the recolonisation and use of habitats by wildlife (Jordan *et al.* 1987; Scodari 1997), though confirming the outcome of restoration efforts is difficult without concurrent quantification of the weather factors that influence distribution.

Increasingly, studies are identifying changes in the frequency and amplitude of atmospheric teleconnections as influencing temporal and spatial distributions of populations and species (Stenseth *et al.* 2003; Wang & Schimel 2003). Atmospheric teleconnnections are defined as recurring, persistent, large-scale patterns of atmospheric pressure, circulation and temperature anomalies occurring over thousands of square kilometres (Bridgman & Oliver 2006). Prominent teleconnections dominant in the North American sector include the El Niño Southern Oscillation (ENSO), the Pacific North America teleconnection pattern (PNA), the Arctic Oscillation (AO) and the North Atlantic Oscillation (NAO; Bridgman & Oliver 2006). A substantial portion of the warming trends in North America over the past 20 years have been attributed to sustained positive phases in atmospheric oscillations (Serreze & Barry 2005; Hurrell & Deser 2009). Further, some models indicate increased frequency and amplitude of positive AO and NAO phases as a result of global climate change (Corti *et al.* 1999; Gillet *et al.* 2003). Positive phase teleconnections may result in increased frequency of mild winters and changes in winter distributions and migration phenology of birds (Cotton 2003). The AO and NAO can only be forecast accurately *c.* 7 days in advance; thus we sought additional indices of winter weather used to produce long-term seasonal forecasts for eastern North America (see Fig. 1). Cohen and Jones (2011) detected a strong correlation between the advance of Eurasian snow cover during October and the winter AO, which influences winter temperatures in eastern North America (*i.e.* the Snow Advance Index; SAI). Thus, we reasoned that the SAI may predict severe winter weather months in advance of traditional atmospheric teleconnections and provide seasonal forecasts of waterfowl migration timing and intensity.

Using temperature and snow data, Schummer *et al.* (2010) developed several competing models to explain rates of change in relative abundance of Mallard *Anas platyrhynchos* at mid-latitude staging areas in North America (*i.e.* Missouri) during autumn–winter. The model which best explained annual variation in the rate of change in Mallard abundance was calculated daily for November–January inclusive as the mean daily temperature –(°C)+ the number of consecutive days where the mean temperature was ≤ 0°C + snow depth + the number of consecutive days with snow cover (*i.e.* the Weather Severity Index, WSI; Schummer *et al.* 2010). Temperatures of < 0°C were given a positive algebraic sign (*i.e.* indicating more severe weather and accumulating positively when added to other variables in the model), and temperatures > 0°C were given a negative sign. Here we use the WSI to rank severity of winter weather for nearly six decades and determine differences in mean decadal rank for the winters 1950/51–2008/09 (hereafter 1950–2008) in eastern North America (see Fig. 1). Eastern North America was selected because it corresponded with the geographic area in which the WSI was developed (Schummer *et al.* 2010) and ecoregions used in conservation planning for Nearctic waterfowl (*i.e.* Mississippi and Atlantic Flyways: Bellrose 1980; NAWMP

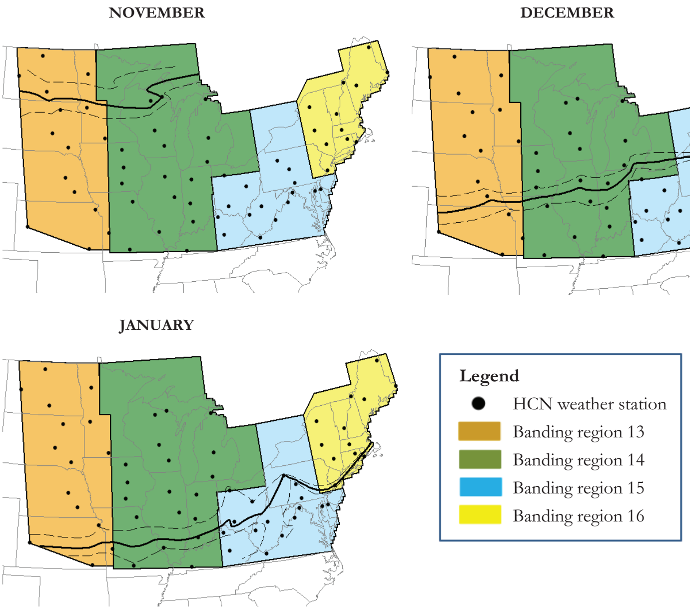

Figure 1. Long-term mean location (solid line) ± 95% C.I. (dashed line) of the threshold weather severity index (WSI = 8) for Mallard in the Mississippi Flyway (USFWS banding regions 13–14) and the Atlantic Flyway (USFWS banding regions 15–16), for winters 1950–2008, calculated using Historical Climatology Network (HCN) data (black dots).

2012). The period 1950–2008 was used because monitoring long-term metrics of Mallard breeding population and habitat dynamics (*i.e.* the Breeding Waterfowl and Habitat Survey: Baldassarre & Bolen 2006) commenced during the 1950s. We used data through to 2008, which was the end of the initial funding period for data compilation and analysis (Zimmerman 2009). As the overall aim of the study was to investigate if indices used to forecast winter weather (*sensu* Cohen & Jones 2011) could be used to predict WSI and potentially provide longer-term projections of Mallard distributions associated with climate change, we conclude by relating our findings to global climate and climate change models.

Methods

Weather data

Sixty two weather stations in the United States Historical Climatology Network (HCN) at *c.* ≥ 35°N were selected to provide long-term state-wide weather data for North Dakota, South Dakota, Nebraska, Kansas, Minnesota, Iowa, Missouri, Wisconsin, Illinois, Michigan, Indiana, Kentucky, Ohio, New York, Pennsylvania, West Virginia, Maryland, Virginia, Vermont, Delaware, New Jersey, New Hampshire, Massachusetts, Connecticut, Rhode Island and Maine (Quinlan *et al.* 1987; Williams *et al.* 2006; Fig. 1). The median latitude HCN station was selected within each state and inspected for missing temperature and snow data. If > 10% of daily temperature or snow data were missing, we alternately selected stations immediately north and south until a weather station that contained < 10% missing data was identified. For states ≥ 28,500 km^2 in area (*i.e.* larger than Maryland), two additional weather stations were also included (one in the north and the other in the south of the state), starting with the 25% and 75% quartile latitude HCN weather stations and using the aforementioned criterion for missing data. We also selected a station in Michigan's upper peninsula which met this criterion. Only two HCN weather stations in Nebraska were found that met our quality criteria.

Daily mean temperature and snow data were obtained for November–January 1950–2008 from selected HCN weather stations to calculate a daily WSI for each station (*n* = 330,832 values), as follows: WSI = Temp + Temp days + Snow depth + Snow days (following Schummer *et al.* 2010), where Temp = mean daily temperature (°C; with temperatures < 0°C given a positive algebraic sign to indicate more severe weather, and those > 0°C a negative sign, as described above); Temp days = consecutive days with mean temperature ≤ 0°C; Snow depth = (snow depth, in cm) × 0.394; and Snow days = consecutive days ≥ 2.54 cm of snow. Values for snow depth and snow days convert to 1 inch of snow, a measurement used in weather forecasting and reporting in the United States. For days when temperature and snow depth data were missing, we interpolated missing values as being the mean of data recorded on days next before and after these date(s) (see Schummer *et al.* 2010); however, months with ≥ 7 consecutive days of missing WSI values were omitted from the analyses. Annual monthly mean WSI values were calculated from the daily WSI values for each HCN station, for November–January 1950–2008 (*n* = 10,788; PROC MEANS in SAS Institute 2009). For each month, we also calculated a long-term (1950–2008) monthly mean (± 95% C. I.s) from annual monthly mean WSI values for each HCN station. Monthly PNA, AO and NAO (November–January) and three-month mean ENSO indices (September–November, SON; October–December, OND; and November–January, NDJ) were obtained from the National Oceanic and Atmospheric Administration/Climate Prediction Center at College Park, Maryland, USA (NOAA 2010).

Spatial analyses

Interpolation analyses were conducted using the natural neighbour method in ArcView Spatial Analyst, with a cell output size of 0.07 degrees (*c.* 7.7 km; ESRI 2009), to depict the long-term average WSI spatially, and to calculate ± 95% C.I. for monthly mean WSI values (for November–January,1950–2008) from the 62 HCN weather stations (Fig. 1). Schummer *et al.* (2010) reported that daily WSI values of ≥ 7.2 coincided with an increased likelihood of Mallard leaving mid-latitude locations in North America. We assumed that Mallard reacted similarly to weather severity throughout the range of our present study as in our earlier study area (at *c.* 33˚–49˚N), and a conservative threshold WSI value of 8 therefore was used to demarcate by month and year the geographic extent of the WSI threshold value. Three polylines were digitised as layers representing the long-term average (LTA) WSI and the upper and lower 95% C.I.s for each month of the study (Fig. 1). We conducted the same interpolation analyses to produce a monthly WSI threshold demarcation line for November–January 1950–2008 inclusive (n = 232 maps). The areas above and below the 95% C.I.s were digitised as polygon layers to determine the area (km^2) assumed to be available or unavailable to Mallard, based on the LTA and 95% C.I.s (Fig. 1). The "extract by mask" function in ArcView Spatial Analyst (ESRI 2009) was then used to develop polygon areas (*i.e.* km^2) above and below the 95% C.I. within the U.S. Fish and Wildlife Service waterfowl banding regions 13–16 in eastern North America (hereafter, banding regions; Fig. 1). Banding regions were modified by extending the northern border to capture areas of southern Canada where data interpolation of WSI occurred. Within the banding regions, we subtracted polygon areas (*i.e.* km^2) below the lower 95% C.I. from polygon areas above the upper 95% C.I. to determine changes to net potential habitat for Mallard ($\pm$ km^2; hereafter the weather severity index anomaly, WSIA) for each region. Thus, the WSIA is the area assumed available or unavailable for use by Mallard compared to the LTA by banding region on a monthly basis (November–January) for each year (1950–2008). Data were summarised by banding regions because they represent different Mallard populations and migratory flyways (*i.e.* the Mississippi and Atlantic Flyways).

Decadal analysis of winter severity index anomalies (WSIA)

We summed WSIA from banding regions 13 and 14 (hereafter, Mississippi Flyway) for each month and year, likewise summed data for regions 15 and 16 (Atlantic Flyway) to follow regional scales at which Mallard migrate, and thus conservation planning decisions are made for Nearctic waterfowl (Baldassarre & Bolen 2006), and because data from individual banding regions were not normally distributed. We also calculated mean WSIA within the Mississippi Flyway (MSF), the Atlantic Flyway (AF) and the combined MSF and AF means for the three-month period (November–January; NDJ). Data passed normality and equal variance tests (P > 0.05). A one-way Analysis of Variance (ANOVA) therefore was used to test the null hypothesis that there is no difference between the six decadal periods (1950s–2000s inclusive) in the WSIA values recorded (α = 0.05; Sokal & Rohlf 1981; Systat Software Inc. 2008). We predicted that WSIA during the 2000s would be greater in comparison with other decades because of observations of interrupted or delayed (*i.e.* "short-stopping") migration by Mallard to southern latitudes in eastern North America in the last decade (Greene & Krementz 2008; Brook *et al.* 2009; Nevin *et al.* 2010).

Effects of atmospheric teleconnections

We used an information-theoretic approach (Burnham & Anderson 2002) to investigate climatic factors potentially influencing variation in WSIA. Five candidate teleconnection-based models, associated with weather patterns in eastern North America, were developed *a priori* for this analysis as listed below.

El Niño Southern Oscillation (ENSO)

Climate variability resulting from ENSO can produce wide-ranging ecological consequences (Stenseth *et al.* 2003). ENSO is most often characterised as El Niño, La Niña or Neutral. El Niño occurs when the equatorial Pacific Ocean sea surface temperatures (SSTs) are unusually warm, whereas La Niña occurs when the same region is dominated by unusually cold SSTs, and Neutral occurs when SSTs are near normal. The Oceanic Niño Index (ONI) is the principal tool for monitoring and assessing ENSO. To be considered a full El Niño or La Niña episode, the ONI must exceed ± 0.5 (°C) for ≥ 5 consecutive overlapping 3-month seasons (Tozuka *et al.* 2005; NOAA 2010). During winter months, a positive ONI (El Niño, ≥ +0.5) is associated with increased precipitation and colder than normal temperatures in the southeast United States, but warmer than normal temperatures and reduced ice coverage in the Great Lakes region and eastern Canada (Ropelewski & Halpert 1987; Halpert & Ropelewski 1992; Assel *et al.* 2000). A negative ONI (La Niña, ≤ –0.5) commonly results in warmer and drier conditions over the southeast United States, but colder than normal air penetrating into the northern Great Plains of Canada and the United States (Ropelewski & Halpert 1987; Halpert & Ropelewski 1992). During ONI neutral phases (–0.5 to 0.5), equatorial Pacific Ocean SSTs appear to have much less influence on global climates and forecasting long-term regional weather patterns becomes difficult (Bridgman & Oliver 2006).

North Atlantic Oscillation (NAO)

The NAO is often associated with interdecadal and interannual shifts in ecological processes in marine and terrestrial systems of Europe and North America (Hurrell *et al.* 2003). A positive NAO index increases the likelihood of mild, wet winters in the eastern United States while increased cold accompanies a negative NAO index over the same area (Hurrell 1995). Because the NAO is also correlated with the Arctic Oscillation (AO), there is considerable debate as to whether the NAO is merely a regional expression of the AO, which is a hemispheric mode of climatic variability (Ambaum *et al.* 2001; Hurrell *et al.* 2003). Moreover, scientists are uncertain if the NAO or the AO has the greatest influence on winter climates and related ecological processes in North America (Aanes *et al.* 2002; Stenseth *et al.* 2003).

Arctic Oscillation (AO)

Effects of the AO on North American climate are most pronounced from December through March (Serreze & Barry 2005). A positive AO index reduces the number of cold air intrusions east of the Rocky Mountains, causing much of the eastern United States to experience warmer winters than normal. A negative AO index produces the opposite effect over the same area (Serreze & Barry 2005; Bridgman & Oliver 2006).

Pacific North American Oscillation (PNA)

Like the AO, the PNA tends to be most pronounced during the winter months. The positive phase of the PNA is associated with above average temperatures in western Canada and the Pacific coast of the United States, but below average temperatures across the south-central and southeast United States. The PNA has also been associated with moisture variability in the same region (Coleman & Rogers 1995; Rogers & Coleman 2003). Anomalies in regional temperatures, ice cover and snow cover have been related to the PNA phase (Assel 1992; Serreze *et al.* 1998). Also, positive PNA index values are more frequent during El Niño episodes (Wang & Fu 2000).

Plausible interactions and combined influences

Several studies have investigated modulation of the ONI by other atmospheric teleconnections (Gershunov & Barnett 1998, Bridgman & Oliver 2006) and the combined influences of atmospheric teleconnections on winter temperature, precipitation and snowfall (Serreze *et al.* 1998). For example, during El Niño or La Niña episodes, inclusion of other atmospheric teleconnections as covariates improves explained variation in precipitation and temperature throughout much of North America (Higgins *et al.* 2000). However, several atmospheric teleconnections are often correlated and their combination in models could create statistical bias. We calculated Pearson's correlation coefficients for relationships between continuous variables (NAO, AO, PNA) and did not include combinations of model predictors that were correlated ($r \geq 0.70$; Dormann *et al.* 2013). We also used ANOVA to test the null hypothesis of no difference in NAO, AO and PNA among the ONI categories of El Niño, La Niña and Neutral ($P < 0.05$). Data passed normality and equal variance tests ($P > 0.05$, Sokal & Rohlf 1981). If an ANOVA approached significance ($P < 0.10$), we did not include that atmospheric teleconnection in models containing ONI categories. Positive associations were detected between the AO and NAO ($0.64 \leq r_{58} \leq 0.76$, $P < 0.001$) and the ONI and PNA ($0.37 \leq r_{58} \leq 0.40$, $P < 0.01$). The PNA also varied with ONICAT ($3.49 \leq F_{2,55} \leq 8.16$, $P < 0.05$) but not with the AO and NAO ($0.64 \leq F_{2,55} \leq 0.09$, $P > 0.05$). Because of the latter results, we did not include the AO and PNA within models containing the NAO and ONICAT, respectively. Thus, we evaluated 18 candidate models for explaining variation in WSIA: 1) AO, 2) NAO, 3) PNA, 4) ONI (categorical, ONICAT), 5) ONI (continuous, ONI), 6) ONICAT AO, 7) ONICAT NAO, 8) ONICAT × AO, 9) ONICAT × NAO, 10) ONI AO, 11) ONI NAO, 12) ONI × AO, 13) ONI × NAO, 14) PNA AO, 15) PNA NAO, 16) PNA × AO, 17) PNA × NAO, and 18) the NULL. In addition to appropriate multivariate models, we modelled interactions of continuous variables and ONI category to determine if including the relationship among slopes improved the model fit.

An Akaike's Information Criterion (AIC*c*) was calculated for each model (PROC MIXED; SAS Institute 2009). Competing models were ranked according to Δ AIC*c* values and selection was based on the lowest Δ AIC*c* value (Burnham & Anderson 2002; Littell *et al.* 2007). We considered models competitive when Δ AIC*c* values were ≤ 2 units of the best model (*i.e.* with Δ AIC*c* =

0; Burnham & Anderson 2002). Year was included as a random variable and variance components (VC) were used from a suite of tested covariance structures (*i.e.* CS, UN, TOEP, AR(1), ARH(1), VC), because VC produced the best fit models (lowest AIC*c* values: Littell *et al.* 2007). We calculated Akaike weights (w_i) to assess relative support for each atmospheric teleconnection-based model in explaining variation in WSIA. When top and competing models contained an interaction effect, results were interpreted from the slopes and intercepts of the relationship between the dependent and interacting explanatory variables (Gutzwiller & Riffell 2007; SAS Institute 2009).

Effects of the snow advance index (SAI)

To evaluate whether the SAI was better than random at predicting WSIA during November–January, AIC*c* values for the SAI model were compared with those for the null models (PROC MIXED; SAS Institute 2009 to determine whether SAI was better than random chance of it predicting WSIA. SAI is a strong predictor for AO (Cohen & Jones 2011) and NAO and AO are correlated (Hurrell *et al.* 2003) so we only included SAI and the null in our analysis. Analyses were conducted on 1972–2008 data because the SAI values were available only for 1972 onwards. Whether removing ONI-neutral years improved the utility of the model for predicting WSIA was also investigated.

Results

Decadal analysis of WSIA

The WSIA rank recorded for NDJ each year did not differ significantly across the decades ($F_{5,52}$ = 1.31, P = 0.26, n.s.; Table 1). The 2000s had the highest mean WSIA but also greatest range in values (Table 1; Appendix 1). Inspection of data indicated that winter 2000/01 was a statistical outlier (with WSIA > 200 units in comparison with the next

Table 1. Descriptive statistics for Weather Severity Index Anomalies (WSIA , ± thousands of km^2), by decade, for November–January in eastern North America.

Decade	*n*	Mean (± s.e.) WSIA (× 1,000 km^2)	Median WSIA (× 1,000 km^2)	25% Quartile WSIA (× 1,000 km^2)	75% Quartile WSIA (× 1,000 km^2)
1950s	9	69.0 (50.5)	72.5	–77.4	210.0
1960s	10	–4.9 (25.1)	–15.8	–57.6	52.9
1970s	10	–33.5 (32.9)	–16.2	–123.5	74.0
1980s	10	68.7 (57.9)	60.2	–51.9	252.5
1990s	10	14.3 (43.9)	8.5	–113.3	110.3
2000s	9	129.2 (85.4)	129.4	49.6	272.1

coldest winters, whereas WSIA values for the two warmest winters differed by *c.* 10 units) and ranked as the most negative WSIA in the 58 years of the study (Appendix 1). On removing 2000/01 data, the mean WSIAs differed significantly among decades (ANOVA: $F_{5,51}$ = 2.99, P = 0.02). *Post-hoc* Tukey pair-wise comparisons with 2000/01 data removed detected that WSIA was greater in the 2000s ($\bar{x}$ = 197.7 ± 57.9) than the 1970s (P = 0.01) and 1960s (P = 0.04) but no other decadal differences were detected for WSIA ($P \geq 0.30$, n.s.; Table 1).

Effects of atmospheric teleconnections

Models containing interactions of AO or NAO with ONICAT were the only models that were ≤ 2 Δ AIC*c* units from the best model for all locations and time periods (Table 2). The AO and NAO explained a greater portion of variation (R^2) in WSIA during El Niño and La Niña episodes than during Neutral conditions for all locations and periods. Models derived using 3-month means generally were better fit models (*i.e.* by w_i and R^2) than those using monthly data. In the Mississippi Flyway, AO had a greater influence on WSIA during NDJ, whereas the NAO was more influential in the Atlantic Flyway (Table 2). Greatest weight of evidence explaining variation in WSIA for Mississippi and Atlantic Flyways combined was associated with the interaction of AO with ONICAT (Table 2). However, AIC*c* values for the interaction of NAO and ONICAT were < 2 units from the top model (ONICAT × AO) and received substantial weight of evidence (Table 2). For eastern North America, a substantial portion of the variation in WSIA was explained by the AO during El Niño and La Niña episodes but not during Neutral conditions (Table 2, Fig. 2).

Effects of SAI

The SAI (AIC*c* = 477.3) was a better predictor of WSIA than the null model (AIC*c* = 481.9), but utility of the model for predicting WSIA was relatively poor (Fig. 3). Including the ONI category (El Nino, La Nina or Neutral) did not improve the predictive ability of our model (AIC*c* = 480.7). Despite poor model fit, the SAI did predict correctly whether WSIA would be positive (mild winter compared to normal) or negative (severe winter compared to normal) in 27 (75%) of 36 years (Fig 3).

Discussion

So far as we are aware, this study is the first to assess the influence of long-term trends in annual weather severity (*i.e.* ± WSIA) on the autumn–winter distribution of Mallard in the Nearctic (Schummer *et al.* 2010). We detected a trend toward less severe weather (+ve WSIA) during recent decades (1990s and 2000s) but also detected that severe events (–ve WSIA) occurred during this period (*e.g.* winter 2000/2001). The results identified that WSIA was positively related to the Arctic and North Atlantic Oscillation Indices during El Niño and La Niña episodes but not during ONI Neutral conditions. Similar to other studies, Arctic and North Atlantic Oscillation Indices were found to be strongly correlated (Ambaum *et al.* 2001; Hurrell *et al.* 2003). Our models indicate that weather severity, which is known to influence autumn–winter

Table 2. Akaike's Information Criteria (AIC*c*) for linear relationships between Weather Severity Index Anomalies (WSIA, ± thousands km²) and atmospheric teleconnection models in the Mississippi and Atlantic Flyways, in November–January 1950–2008. Eighteen candidate models for explaining variation in WSIA were considered for each time period (including combinations of AO, NAO, PNA, continuous ONI (ONI), categorical ONI (ONICAT) and year; Methods section provides further details); the top two models in each case are presented here.

Location[a]	Period[b]	Models[c]	Δ AIC*c*	AIC*c*	w_i	R^2 by Category[d]
Mississippi Flyway	November (N)	ONICAT × NAO	1404.5	0.00	0.92	EL (0.02), LA (0.23), NA (0.06)
		ONICAT × AO	1409.3	4.80	0.08	EL (0.00), LA (0.30), NA (0.00)
	December (D)	ONICAT × AO	1449.3	0.00	0.51	EL (0.16), LA (0.51), NA (0.12)
		ONICAT × NAO	1449.4	0.01	0.49	EL (0.31), LA (0.21), NA (0.08)
	January (J)	ONICAT × AO	1415.4	0.00	0.76	EL (0.25), LA (0.46), NA (0.03)
		ONICAT × NAO	1417.7	2.30	0.24	EL (0.01), LA (0.17), NA (0.10)
	NDJ	ONICAT × AO	1374.9	0.00	0.67	EL (0.14), LA (0.55), NA (<0.00)
		ONICAT × NAO	1376.3	1.40	0.33	EL (0.18), LA (0.32), NA (<0.00)
Atlantic Flyway	December (D)	ONICAT × AO	1378.3	0.00	0.51	EL (0.41), LA (0.60), NA (0.04)
		ONICAT × NAO	1378.4	0.01	0.49	EL (0.47), LA (0.49), NA (0.01)
	January (J)	ONICAT × AO	1316.4	0.00	0.93	EL (0.34), LA (0.43), NA (0.06)
		ONICAT × NAO	1321.6	5.20	0.07	EL (0.20), LA (0.25), NA (0.01)
	NDJ	ONICAT × NAO	1292.3	0.00	0.66	EL (0.66), LA (0.48), NA (0.00)
		ONICAT × AO	1293.6	1.30	0.34	EL (0.60), LA (0.55), NA (0.04)
Mississippi and Atlantic Flyways	NDJ	ONICAT × AO	1401.0	0.00	0.66	EL (0.32), LA (0.64), NA (0.01)
		ONICAT × NAO	1402.3	1.30	0.34	EL (0.28), LA (0.27), NA (0.01)

[a] Mississippi Flyway = USFWS banding regions 13 and 14; Atlantic Flyway = USFWS banding regions 15 and 16 (see Fig. 1).
[b] November is not included in the Atlantic Flyway because most observations were outside of the study area (see Fig. 1).
[c] ONICAT = Oceanic Niño Index category (*e.g.* El Niño, La Niña and Neutral), AO = Arctic Oscillation Index, NAO = North Atlantic Oscillation Index. Only models with weight of evidence (w_i) are included.
[d] derived R^2 by category: EL = El Niño, LA = La Niña and NA = Neutral.

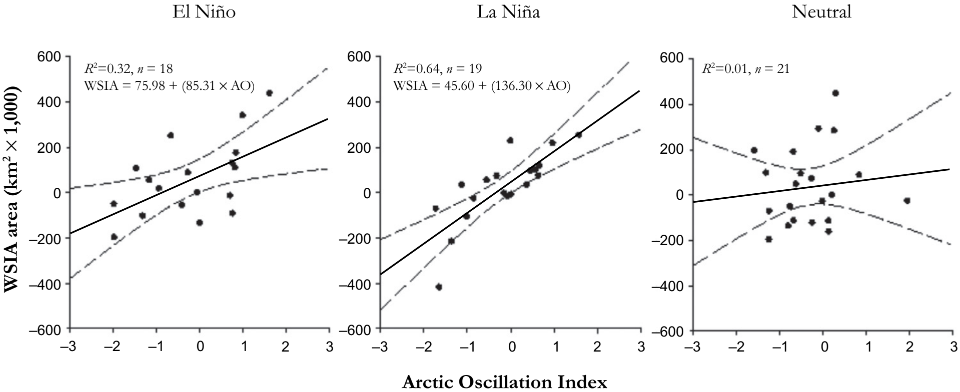

Figure 2. Relationships between the Arctic Oscillation Index (AO) and Weather Severity Index Anomalies (WSIA, ± thousands of km^2) in eastern North America by Oceanic Niño Index category (El Niño, La Niña and Neutral) for November–January, 1950–2008.

Mallard migration (Bellrose 1980; Schummer *et al.* 2010), is reduced during El Niño and La Niña episodes when the Arctic and North Atlantic Oscillation Indices are in a positive phase. Thus, we think Mallard migration may be interrupted or delayed (*i.e.* "short-stopping") during these conditions. Investigation of the usefulness of the SAI, as a long-term seasonal predictor of weather influencing Mallard migration, provided mixed results. The SAI predicted accurately the coming winter (NDJ) as being either less or more severe than normal 75% of the time, but its capacity to predict WSIA was limited. We suggest continued investigation of the SAI with additional weather indices. Long-term forecasting of weather known to influence Mallard and other waterfowl migrations would be helpful for managers charged with providing waterfowl habitat at key times of migration throughout the non-breeding season and for managing timing of hunting seasons (Schummer *et al.* 2010).

The results of the study provides a potential explanation for recent observations of delayed autumn–winter migration in Nearctic Mallard and other migratory birds (National Flyway Council and Wildlife Management Institute 2006; Nevin *et al.* 2010) and may be helpful in modelling future autumn–winter distributions of Mallard (and possibly other migratory birds) in eastern North America and more widely (see Notaro *et al.* 2014). Colleagues are encouraged to test for the influence of WSIA on the movements and annual distribution of Mallard and other waterfowl, its influence on waterfowl hunter demographics and behaviour, and whether WSIA affects survival rates and trends in population size. To facilitate these analyses we suggest development of weather indices for other waterfowl and web-based tools for distribution of these data to scientists and managers. Overall, the results suggest that recent observations of delayed waterfowl migration (National Flyway Council and Wildlife Management Institute 2006; Brook *et al.* 2009) may be related to reduced weather

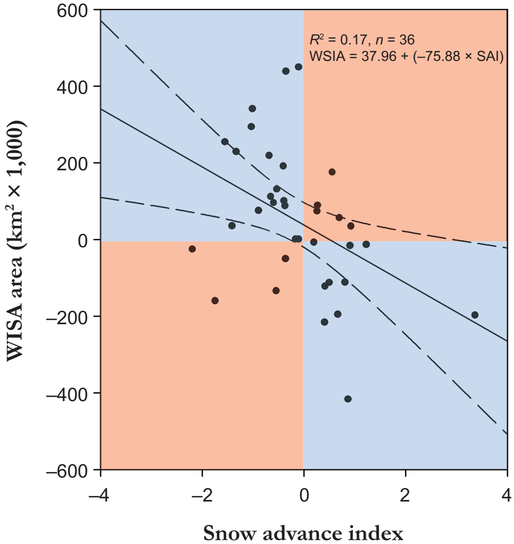

Figure 3. Relationship between the Snow Advance Index (SAI) and Weather Severity Index Anomalies (WSIA, ± thousands of km²) in eastern North America for November–January 1972–2008. Data within blue areas were correctly designated as WSIA greater or lesser than normal by SAI (27 of 36 years, 75%), whereas red areas were incorrectly designated.

severity at northern and mid-latitudes in eastern North America.

The results can also be used for determining the relative contributions of weather severity and habitat availability to the winter distribution and migration phenology of waterfowl and other migratory wildlife. WSIA was quantified here for Mallard in eastern North America, but the availability and quality of wetland habitat, human-related disturbance, waterfowl population sizes, and other factors potentially influencing habitat use, migration and population dynamics should also be taken in account (Bellrose 1980; Kaminski & Gluesing 1987; Newton 2008). Such an evaluation would add clarity to the debate regarding the mechanism(s) that influence the current winter distributions of Nearctic waterfowl (Greene & Krementz 2008). In addition, such information could potentially aid conservationists in predicting future winter distributions of Nearctic waterfowl and habitat protection, management and restoration needs under various climate change models (*e.g.* Ruosteenoja *et al.* 2003; La Sorte & Jetz 2010). Further, WSIA could be included in models used to determine benefits of wetland restoration because habitat use by birds (*i.e.* a metric of restoration success) can be highly dynamic and may be related to the severity of winter weather in addition to habitat quality and other metrics (Newton 1998).

A sustained positive Arctic Oscillation Index could result in increased frequency of mild winters (+ve WSIA), during which decreased ice cover, snowfall and increased temperatures may allow Mallard to remain at more northern latitudes during autumn–winter (Schummer *et al.* 2010). Overall, reduced weather severity may result in delayed migration or reduced numbers of Mallard and possibly other birds migrating to southern latitudes in North America. Nearctic waterfowl (millions of birds), use a diversity of aquatic and terrestrial foraging niches, and can feed at rates capable of causing strong trophic influences (Newton 1998; Abraham *et al.* 2005; Baldassaree & Bolen 2006). Sustained northern shifts in autumn–winter distributions of these abundant species could increase foraging pressure at northern latitudes while reducing such effects at southerly locations and cause changes in trophic relationships (*i.e.* trophic cascades) throughout eastern North America (Crick 2004; Inkley *et al.* 2004). An increase in foraging intensity at more northern latitudes during autumn and winter may also deplete the food available for waterfowl during spring migration in some locations (Straub *et al.* 2012; Greer *et al.* 2007; Long Point Waterfowl, unpubl. data). Predicting future distributions of waterfowl using forecasts of WSIA may help conservationists develop adaptive plans to meet the habitat needs of waterfowl and other migratory birds in a changing climate (Lehikoinen *et al.* 2006; Seavy *et al.* 2008; La Sorte & Jetz 2010, Notaro *et al.* 2014).

We used a simplistic WSI developed for Mallard and other dabbling ducks (Schummer *et al.* 2010) to examine their potential past and future distributions. Results from our study corroborate those for European Mallard which showed reduced winter migration distance with long-term warming (Sauter *et al.* 2010). We encourage including a broader suite of influences such as potential species interactions, physiology and energy-dependent "bottle-necks" at different stages of migration, concurrent habitat changes, and other biotic interactions, to increase biological realism in future analyses (Seavy *et al.* 2008; La Sorte & Jetz 2010). Further examination of Mallard distribution using satellite telemetry and volunteer observation programmes (*e.g.* Christmas Bird Count, Mallard Migration Network) in relation to the WSI and WSIA would provide further validation of temporal and spatial distributions of these birds. Other Nearctic waterfowl and migratory species may react differently to annual variation in winter severity and changing climate (Crick 2004; Sauter *et al.* 2010), for instance because habitat generalists (*e.g.* Mallard) often respond to climate change more readily than habitat specialists (La Sorte & Jetz 2010). Thus, we also encourage continued research aimed at understanding the effects and threats of a changing climate for a variety of migratory species (Thomas *et al.* 2001; Walther *et al.* 2002).

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Appendix 1. Rank of Weather Severity Index Anomalies (WSIA, ± thousands of km^2) for eastern North America (Atlantic and Mississippi Flyway combined) in November–January 1950–2008.

Winter	WSIA (× 1,000 km^2)	Rank*	Winter	WSIA (× 1,000 km^2)	Rank*
1950/51	–26.8	21	1979/80	292.0	55
1951/52	–93.5	13	1980/81	93.8	39
1952/53	197.0	49	1981/82	–51.9	18
1953/54	283.4	54	1982/83	339.2	56
1954/55	72.5	35	1983/84	–161.5	5
1955/56	–106.9	11	1984/85	33.1	29
1956/57	117.9	45	1985/86	–197.1	4
1957/58	249.0	52	1986/87	–0.4	27
1958/59	–72.0	15	1987/88	87.3	38
1959/60	96.8	41	1988/89	252.5	53
1960/61	–137.5	6	1989/90	–114.4	9
1961/62	–27.8	19	1990/91	86.1	37
1962/63	–72.5	14	1991/92	110.3	44
1963/64	–57.6	16	1992/93	–27.1	20
1964/65	52.9	32	1993/94	–0.8	26
1965/66	106.5	43	1994/95	173.8	47
1966/67	47.0	31	1995/96	–217.4	2
1967/68	–3.7	25	1996/97	–113.3	10
1968/69	–53.0	17	1997/98	–17.8	28
1969/70	–103.3	12	1998/99	227.6	51
1970/71	–17.5	22	1999/00	217.1	50
1971/72	94.8	40	2000/01	–418.5	1
1972/73	–14.8	23	2001/02	447.7	58
1973/74	–9.0	24	2002/03	54.8	33
1974/75	99.2	42	2003/04	71.7	34
1975/76	74.0	36	2004/05	129.4	46
1976/77	–198.9	3	2005/06	189.8	48
1977/78	–135.6	7	2006/07	437.1	57
1978/79	–123.5	8	2007/08	33.9	30

* Rank 1 = most severe winter; 58 = least severe.