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Management and Conservation Article

Weather-Related Indices of Autumn–Winter Dabbling Duck Abundance in Middle North America

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ABSTRACT Research on effects of key weather stimuli influencing waterfowl migration during autumn and winter is limited. We investigated relationships between changes in relative abundances of mallard (*Anas platyrhynchos*) and other dabbling ducks (*Anas* spp.) and weather variables at midlatitude locations in North America. We used waterfowl survey data from Missouri Conservation Areas and temperature and snow cover data from the Historical Climatology Network to evaluate competing models to explain changes in relative abundance of ducks in Missouri, USA, during autumn–winter, 1995–2005. We found that a cumulative weather severity index model (CumulativeWSI; calculated as mean daily temp − degrees C + no. of consecutive days with mean temp $\leq 0^\circ$ C + snow depth + no. of consecutive days with snow cover) had the greatest weight of evidence in explaining changes in relative abundance of ducks. We concluded the CumulativeWSI reflected current and cumulative effects of ambient temperatures on energy expenditure by ducks, and snow cover and wetland icing, on food availability for ducks. The CumulativeWSI may be useful in determining potential changes in autumn–winter distributions of North American waterfowl given different climate change projections and associated changes in habitat conservation needs. Future investigations should address interactions between CumulativeWSI and landscape habitat quality, regional waterfowl populations, hunter harvest, and other anthropogenic influences to increase understanding of waterfowl migration during autumn–winter.

KEY WORDS *Anas platyrhynchos*, climate, duck, mallard, migration, snow, temperature, waterfowl, weather severity.

From 1955 through 2005, annual mean air temperature increased in North America, with greatest increases in winter (Walther et al. 2002, Hengeveld et al. 2005). Additionally, simulations have indicated a similar intensifying pattern in coming decades (Ruosteenoja et al. 2003, Field et al. 2007). Changes in climate and extreme weather events may have ecological consequences, including phenological shifts in species' life cycles and possibly asynchronies (Glynn 1990, Anderson and Sorenson 2001, Thomas et al. 2001, Crick 2004, Inkely et al. 2004). Phenological shifts by waterfowl and other birds include changes in timing of breeding and migration, as well as population distributions (Walther et al. 2002, Parmesan and Yohe 2003, Sedinger et al. 2006). Researchers have investigated influences of climate change and weather events on spring migration and breeding waterfowl (Sedinger et al. 2006, DeVink 2007, Bauer et al. 2008). Although an understanding of factors influencing movement and distribution of migratory birds is important for conservation planning (Johnson et al. 2005, Browne and Dell 2007, Newton 2008), little information exists concerning influences of weather events on abundance of waterfowl during the nonbreeding season, a period encompassing nearly 9 months of the annual cycle for some species (Baldassarre and Bolen 2006).

Temperature and snow cover seem to influence timing and extent of the southerly migration by northern hemispheric waterfowl (Bellrose 1980, Nichols et al. 1983, Švažas et al. 2001). Theoretically, when temperature declines below a threshold, remaining at northern latitudes becomes more energetically costly than migrating southward to a warmer environment (i.e., energy conservation theory; Alerstam 1990, Newton 2007). Further, effects of declining temperature on waterfowl energy budgets may be exacerbated by snow and ice cover that constrains or precludes foraging (i.e., energy acquisition theory; Albright et al. 1983, Jorde et al. 1983, Lovvorn 1994). Overall, the combined influence of declining temperature and increasing snow and ice cover may be a proximate cue associated with waterfowl migration during autumn and winter. Energy costs associated with increasing severity of weather at waterfowl staging areas may be ameliorated by increases in food quantity and quality resulting from active management (Fredrickson and Taylor 1982; Jorde et al. 1983, 1984; Robb et al. 2001). However, food accessibility can decline to near zero during periods of extended cold and snow or ice cover at northern latitudes (Jorde et al. 1983, Jorde et al. 1984; Browne and Dell 2007), often resulting in mass southern migrations by waterfowl (Bellrose and Sieh 1960, Beason 1978, Robb et al. 2001).

Given current knowledge of the contribution of environmental stimuli to waterfowl migration, assessment of effects of changes in distributions of waterfowl resulting from climatic variability is difficult (Walther et al. 2002). Northward shifts in distributions of wintering waterfowl may increase foraging intensity and habitat needs at northern latitudes while reducing habitat needs at southerly locations (Newton 1998, Crick 2004, Inkley et al. 2004). Northward shifts in distribution of wintering waterfowl may increase habitat demands at midlatitudes of North America, where only 10–15% of historic wetlands remain, which is the lowest proportion in North America (Dahl 1990, 2006). Although long-term climate data indicate a trend toward increased temperatures and reduced snow cover across

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Table 1. Name, latitude, and longitude of Missouri Conservation Areas (MCA) and Historical Climate Network (HCN) weather stations (and station no.) and the distance between them in a study of the relationship between rate of change in relative abundance of mallard and other dabbling ducks and cumulative weather severity in Missouri, USA, during autumn–winter, 1995–2005.

MCA name	MCA location	HCN weather station name (station no.)	HCN station location	Distance from MCA to HCN station (km)
Bob Brown	39°57′42″N, 95°14′31″W	Horton (143810)	39°40′12″N, 95°31′12″W	40.46
Fountain Grove	39°41′53″N, 93°17′13″W	Brunswick (231087)	39°25′12″N, 93°07′12″W	33.14
Grand Pass	39°14′32″N, 93°18′14″W	Brunswick (231087)	39°25′12″N, 93°07′12″W	21.11
B. K. Leach	39°11′55″N, 90°45′59″W	White Hall 1E (119241)	39°26′24″N, 90°23′24″W	42.05
Eagle Bluff	38°47′09″N, 92°21′50″W	Jefferson City Water Plant (234271)	38°35′24″N, 92°11′24″W	35.98
Four Rivers	37°59′21″N, 94°20′21″W	Appleton City (230204)	38°12′36″N, 94°02′24″W	35.82
Shell-Osage	38°01′43″N, 94°06′40″W	Appleton City (230204)	38°12′36″N, 94°02′24″W	20.66

North America (Houghton et al. 2001, Johnson et al. 2005, Field et al. 2007), influences of temperature and snow cover on waterfowl distribution and migration phenology are not clearly understood. Although some research indicated waterfowl are wintering at increasingly northern latitudes in recent years (Švažas et al. 2001, Petrie and Schummer 2002, Abraham et al. 2005, Link et al. 2006), other research has concluded either no change or only short-term changes in distribution in response to annual variation (Otis 2004, Greene and Krementz 2008).

Understanding how weather influences waterfowl movement during fall–winter is important for managers and conservation planners (Mallory et al. 2003) because of potential effects on waterfowl harvest (Greene and Krementz 2008), habitat use (Nichols et al. 1983), and survival during the nonbreeding season (Johnson et al. 1992, Blums et al. 2002). Our objective was to evaluate whether different indices of weather severity could be used to explain changes in relative abundance of mallards (*Anas platyrhynchos*) and other dabbling ducks (*Anas* spp.). We used midlatitude locations in North America because of their historic use by mallards and other dabbling ducks during autumn migration (Bellrose 1980, Havera 1999). We chose mallards and other dabbling ducks because of differential adaptations in body size, physiology, and migration chronology; data availability; and an interest in waterfowl–weather relationships (i.e., climate change) by conservationists (Bellrose 1980, North American All Bird Conservation Initiative 2000, North American Waterfowl Management Plan [NAWMP] 2004, Browne and Dell 2007).

STUDY AREA

We obtained waterfowl survey data collected at Waterfowl Conservation Areas (CAs) managed by the Missouri Department of Conservation (MDC) and weather data from nearby United States Historical Climatology Network (HCN) weather stations (Quinlan et al. 1987, Williams et al. 2006), 1995–2005 (Table 1). We selected Missouri, USA, because of the availability of these data compared with other midlatitude areas of North America and the importance of this region to migrating and wintering waterfowl (Bellrose 1980). We paired CAs with the closest HCN weather station for analyses (Table 1). We used CAs that 1) had a HCN station within 48 km because of similarity in environmental conditions and maximum home range size of dabbling ducks during the nonbreeding season (Jorde et al. 1983, Cox and Afton 1996); 2) were subject to similar habitat management regimes and were typified by shallow, seasonal wetlands; and 3) contained complete count data for 1995–2005.

METHODS

Waterfowl Abundance and Weather Data

We obtained unpublished survey data on waterfowl abundance from the MDC, 1995–2005. The MDC annually conducts coordinated aerial transect and ground surveys of waterfowl, using CAs, at intervals from October to January. Waterfowl were normally concentrated on refuges during surveys (Raedeke et al. 2003). The MDC attempted to conduct waterfowl surveys once every 2 weeks, although the period between surveys varied based on weather conditions and staff availability, and shorter survey intervals were used during key migration periods. Mean interval between consecutive surveys from 1995 to 2005 for mallards and other dabbling ducks combined was 11.4 days (SE 0.26). Although MDC staff recorded species-specific counts, precision of estimates for species other than mallards are variable because of species variation in bird size, behavior, habitat use, and distribution (Lougheed 1999). Thus, in addition to counts of mallards, we also used the total count of dabbling ducks other than mallards, which primarily included gadwall (*Anas strepera*), American green-winged teal (*Anas crecca carolinensis*), blue-winged teal (*Anas discors*), northern pintail (*Anas acuta*), northern shoveler (*Anas clypeata*), and American wigeon (*Anas americana*). We assumed that the MDC survey and our analytical techniques adequately tracked temporal changes in ducks, allowing us to calculate the rate of change in relative abundance of mallards and other dabbling ducks.

We obtained corresponding temperature and snow data for CAs from the United States HCN (Quinlan et al. 1987, Williams et al. 2006). When weather data were missing, we estimated temperature and snow depth between consecutive dates for which data existed. For temperature and snow depth, 2.8% and 9.8% of data were missing, and period length of missing data averaged 3.7 (SE 0.9) days and 5.2 (SE 0.4) days, respectively. When temperature data were missing, we interpolated by scaling data between 2 dates for which data existed. We used snowfall and temperature data to estimate snow depth when data were missing.

Table 2. Candidate models evaluated as predictors of rate of change in relative abundance of mallard and other dabbling ducks at Missouri Conservation Areas, USA, 1995–2005.

Models	Description	Calculation examples
TEMP[a]	−(daily temp mean)[b]	Example 1: −5° C = 5; Example 2: 5° C = −5
TEMPDAYS[a]	Consecutive days with mean temp ≤ 0° C	Example 1: day 1, 2° C; day 2, −2° C; day 3, −5° C = 2 Example 2: day 1, 2° C; day 2, 1° C; day 3, −5° C = 1
SNOW[a]	(Snow depth in cm) × 0.394	Example 1: 3 cm = 1; Example 2: 26 cm = 10
SNOWDAYS[a]	Consecutive days ≥ 2.54 cm of snow	Example 1: day 1, 0 cm; day 2, 3 cm; day 3, 26 cm = 2 Example 2: day 1, 0 cm; day 2, 0 cm; day 3, 26 cm = 1
CumulativeWSI[c]	TEMP + TEMPDAYS + SNOW + SNOWDAYS	Example: temp (day 1, 2° C; day 2, −1° C; day 3, −5° C) snow (day 1, 0 cm; day 2, 3 cm; day 3, 26 cm) CumulativeWSI (day 1 = −2; day 2 = 4; day 3 = 19)
TEMPMean	Mean temp between 2 surveys	Example 1: day 1, 2° C; day 2, 0° C; day 3, −2° C = 0 Example 2: day 1, 10° C; day 2, 0° C; day 3, −7° C = 1
WSIMean[d]	TEMPMean + TEMPDAYS + SNOW + SNOWDAYS	
PC1	PCA[e] for TEMP, TEMPDAYS, SNOW, and SNOWDAYS	
SURVEYDATE	Julian date unless > 365 days, then Julian date + 365	
MINUTES	Mean civil twilight day length between surveys	
SURVEYINTERVAL	No. of days between 2 consecutive surveys	

[a] Selected as the max. value between 2 surveys starting at time $t - 1$ and ending 1 day before time t.
[b] Temp < 0° C was given a positive algebraic sign (i.e., more severe), and temp > 0° C was given a negative sign.
[c] Weather severity index (WSI) calculated daily and then selected as the max. value between 2 surveys starting at time $t - 1$ and ending 1 day before time t.
[d] WSI calculated as the mean temp between 2 surveys plus values for TEMPDAYS, SNOW, and SNOWDAYS.
[e] PCA, principal components analysis.

To estimate snow depth (ESTIMATE), we used the following processes: if snow depth data were missing, we used snowfall data from the same day in a 1:1 ratio to estimate snow depth, unless snow depth was >0 on the day preceding the day with missing snow depth data. In the latter case, we added snowfall of the current day to snow depth of the preceding day to estimate snow depth. However, if mean daily temperature was >0° C on the day with missing snow data, we estimated snow depth as zero. We tested for potential bias in snow depth estimates by randomly selecting 200 known snow depth data points (ACTUAL), used a paired t-test to compare ACTUAL to ESTIMATE values, and found no difference and correlation between ACTUAL and ESTIMATE values (t_{199} = 0.01, $P > 0.90$; $r_{198} = 0.97$, $P < 0.001$). Because photoperiod may influence avian migration (Gwinner 1996), we also determined average day length (MINUTES) between consecutive waterfowl surveys using timetables for the beginning and end of civil twilight at Columbia, Missouri (38°56′16.23″N, 92°20′03.32″W) provided by the Astronomical Applications Department of the U.S. Naval Observatory (2009).

Model Development

We developed an a priori candidate set of weather severity index (WSI) models and other variables (e.g., photoperiod, Julian date) possibly influencing waterfowl migration (Table 2; Bellrose 1980, Nichols et al. 1983, Ridgill and Fox 1990, Gwinner 1996, Švažas et al. 2001). We developed indices because of the advantage of synthesizing weather conditions into a single variable (Gordo et al. 2005, Gordo 2007, Saino et al. 2007). We developed candidate WSI models on the basis of the logic that 1) ambient temperature and number of consecutive freezing or relatively cold days influence energy expenditure in homeotherms (Blem 2000), 2) snow depth and number of consecutive days of snow cover influence nutrient acquisition by waterfowl, and 3) the combination of current and cumulative effects of temperature and snow cover and wetland ice influence energy expenditure and nutrient acquisition in waterfowl. To ensure that increasing WSI values indicated increasing weather severity, we gave temperatures <0° C a positive algebraic sign and temperatures >0° C a negative sign. We did not include rainfall metrics (e.g., Nichols et al. 1983) because we had no reliable way to determine the spatial and temporal relationships between precipitation and wetland availability on the landscape. Moreover, Pearse (2007) reported that winter temperature and landscape snow coverage in mid–North America were more important in explaining variation in waterfowl abundance in the Mississippi Alluvial Valley, USA, than variables measuring winter precipitation, barometric pressure, and river levels in this region. Finally, we also used principal components analysis (PCA) to produce an index (the first principal component [PC1]) of weather variables that explained the maximum variance among original variables. We used simple correlation analysis to compare PC1 to our a priori developed indices of weather severity.

Statistical Analyses

We applied PCA (Release 9.1.3, 2002, Service Pack 4; SAS Institute, Cary, NC) to the correlation matrix of TEMP, TEMPDAYS, SNOW, and SNOWDAYS because the variables generally were correlated ($P < 0.05$). We report eigenvectors for individual variables in PC1 because they represent the combined correlation effects of all variables in PCA analyses (Rencher 1992). We also calculated Pearson correlation coefficients for relationships between candidate WSI, PC1, MINUTES, and SURVEYDATE. We included MINUTES and SURVEYDATE as separate candidate models to distinguish between potential weather (related to

Table 3. Akaike's Information Criteria for relationships between rate of change in relative abundances of mallard (n = 482) and other dabbling ducks (n = 397) and candidate weather severity indices near Missouri Conservation Areas, USA, 1995–2005.[a]

Taxon	Models[b]	AIC	ΔAIC	w_i	R^2
Mallard[c]	CumulativeWSI^2	1,930.2	0.00	1.00	0.40
	PC1^2	1,948.8	18.60	0.00	0.37
Other dabbling ducks	PC1^2	1,692.1	0.00	0.50	0.42
	CumulativeWSI^2	1,692.4	0.30	0.43	0.42
	TEMPDAYS	1,697.1	5.00	0.04	0.39
	CumulativeWSI	1,697.6	5.50	0.03	0.39

[a] Abbreviations: AIC, Akaike's Information Criterion; ΔAIC, change in Akaike's Information Criterion; w_i, Akaike wt; CumulativeWSI, weather severity index calculated daily and then selected as the max. value between 2 surveys starting at time $t - 1$ and ending 1 day before time t; PC1, first principal component from index produced by principal components analysis; TEMPDAYS, selected as the max. value between 2 surveys starting at time $t - 1$ and ending 1 day before time t.

[b] Squared models (e.g., CumulativeWSI^2, PC1^2) represent quadratic functions, all others are linear.

[c] For mallards, we present PC1^2 to depict how it performed relative to CumulativeWSI^2, even though w_i = 0 for PC1^2.

SURVEYDATE) and photoperiod (MINUTES) influences on rate of change in relative abundance of waterfowl (Gwinner 1996). We used an information theoretic approach for model selection (Burnham and Anderson 2002) and calculated an Akaike's Information Criterion (AIC) for each model. We used ΔAIC and AIC weights (w_i) to assess the relative support for various weather severity indices WSI, PC1, MINUTES, SURVEYDATE, and SURVEYINTERVAL (Table 2) and, for descriptive purposes, reported all models with $w_i \geq 0.01$. To standardize waterfowl survey data, we calculated rate of change (r) in relative abundance of mallards (MALLARD) and other dabbling ducks (DABBLER) as

$$r = \ln(\textit{duck abundance}_t) - \ln(\textit{duck abundance}_{t-1}),$$

thus, measuring increases and decreases in relative abundance of ducks between 2 surveys at CAs. We tested candidate WSI, PC1, MINUTES, and SURVEYDATE variables for linear and quadratic relationships. We evaluated separate models using SURVEYINTERVAL as a random effect to explore whether duration between consecutive surveys influenced variation in rate of change in relative abundance of ducks.

RESULTS

For mallards, PC1 described positive correlations among 4 weather variables; eigenvector for PC1 was 0.90 (TEMP), 0.41 (TEMPDAYS), 0.10 (SNOWDAYS), and 0.09 (SNOW). The PC1 accounted for 88.0% of the variation in the variables. For other dabbling ducks, PC1 also described positive correlations in these 4 variables: Eigenvector PC1 was 0.92 (TEMP), 0.32 (TEMPDAYS), 0.09 (SNOWDAYS), and 0.08 (SNOW), and PC1 accounted for 90.4% of the variation in the variables. The PC1 was positively correlated with the cumulative weather severity index model (CumulativeWSI; calculated as mean daily temp − degrees C + no. of consecutive days with mean temp $\leq 0°$ C + snow depth + no. of consecutive days with snow cover) in mallard and other dabbler analyses (MALLARD, r = 0.98, $P <$ 0.001, n = 482; DABBLER, r = 0.98, $P < 0.001$, n = 397). We also found negative relations between candidate WSI and MINUTES (MALLARD, $-0.74 \leq r \leq -0.28$, $P < 0.001$; DABBLER, $-0.72 \leq r \leq -0.29$, $P < 0.001$) and positive relations between candidate WSI and SURVEYDATE (MALLARD, $0.79 \leq r \leq 0.32$, $P < 0.001$; DABBLER, $0.77 \leq r \leq 0.29$, $P < 0.001$). Because of the latter results, we did not include MINUTES or SURVEYDATE in models containing candidate WSI or PC1. Instead, we tested for a relationship between rate of change in relative abundance of mallards and other dabbling ducks with MINUTES and SURVEYDATE separately to evaluate the possible influence of day length and seasonality on rates of change in relative abundances of ducks during autumn and winter. Although rates of change in relative abundance of mallard and other dabbling ducks varied with MINUTES ($r_{mallard}$, β = 8.31, R^2 = 0.13, $P < 0.001$; $r_{dabbler}$, β = 12.08, R^2 = 0.23, $P <$ 0.001) and SURVEYDATE ($r_{mallard}$, β = −11.24, R^2 = 0.20, $P < 0.001$; $r_{dabbler}$, β = −13.36, R^2 = 0.30, $P <$ 0.001), we did not include MINUTES or SURVEYDATE in the final AIC candidate models because w_i was zero (Table 3). Including SURVEYINTERVAL did not improve AIC values for any candidate model of mallards, and we removed it from subsequent analyses of weather-related data. For other dabbling ducks, inclusion of SURVEYINTERVAL improved models; thus, we retained it for potential improved model performance. Including latitude of CAs as a random effect to account for potential spatial autocorrelation did not improve AIC values or change selection of top models; hence, we removed latitude from subsequent analyses.

Rate of change in relative abundance of mallards and other dabbling ducks varied with increasing weather severity during fall and winter and best fit a quadratic function (Figs. 1, 2). We found substantial weight of evidence (w_i) for a single quadratic model (CumulativeWSI^2) describing rate of change in relative abundance of mallards (Table 3; Fig. 1). The quadratic function of the PC1^2 explained slightly less variability (i.e., R^2) in rate of change in relative abundance of mallards compared with CumulativeWSI^2, but w_i was zero for PC1^2 (Table 3). Similarly, weight of evidence for CumulativeWSI^2 and PC1^2 was greatest in explaining variation in rate of change in relative abundance of other dabbling ducks (Table 3; Fig. 2). Both quadratic models, composed of the weather data (i.e., Cumula-

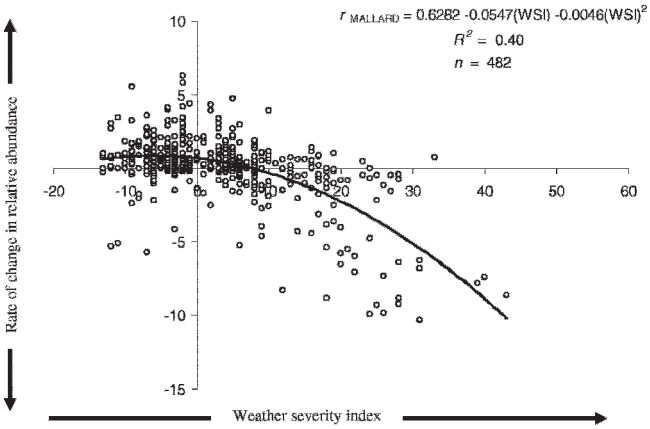

Figure 1. Relationship between rate of change in relative abundance of mallard and a cumulative weather severity index derived from Historical Climatology Network weather stations 20.66–42.05 km from Missouri Conservation Areas, USA, 1995–2005.

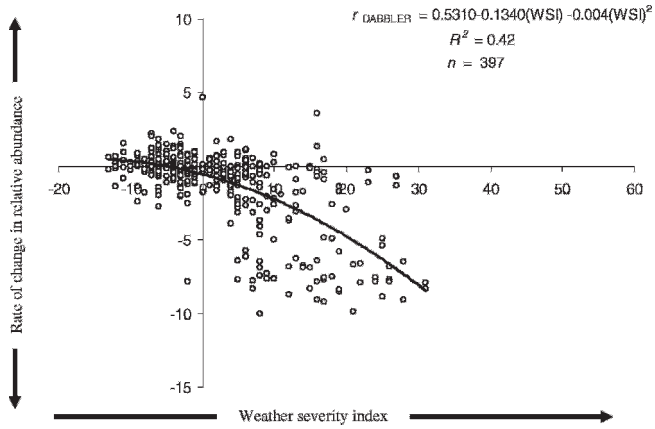

Figure 2. Relationship between rate of change in relative abundance of other dabbling ducks and a cumulative weather severity index derived from Historical Climatology Network weather stations 20.66–42.05 km from Missouri Conservation Areas, USA, 1995–2005.

tiveWSI^2), explained $\geq$40% of the variation in change in relative abundance of mallards and other dabbling ducks in Missouri during autumn–winter of 1995–2005.

Threshold levels of CumulativeWSI differed between mallards (CumulativeWSI = 7.2) and other dabbling ducks (CumulativeWSI = −4.6). A CumulativeWSI of zero corresponded to the first day temperature reached 0° C without snowfall, whereas a CumulativeWSI >0 represented temperatures <0° C and sometimes included combined influences of cold temperatures and snow cover. When temperatures approached 0° C, CumulativeWSI predicted mallards would increase in abundance, whereas abundance of other dabbling ducks decreased. Increasing severe weather generally was needed to decrease mallard abundance on CAs. Rapid declines in mallard abundance (e.g., $r_{mallard} < -5$) were generally associated with increasing duration of cold temperatures and snow cover (e.g., CumulativeWSI > 7.2).

DISCUSSION

Our models explained substantial variation in rates of change in relative abundances of mallards and other dabbling ducks using either CumulativeWSI or PC1. Contrary to derivation of PC1, CumulativeWSI was easily calculated from raw data. Given significant correlation between PC1 and CumulativeWSI, both indices should consistently predict changes in waterfowl abundance from autumn–winter movements or migration. We encourage colleagues with access to long-term waterfowl and other avian abundance data to evaluate our and other models. Stopover duration at CAs for some ducks may be shorter than the interval between surveys in our study, and CumulativeWSI may not reliably predict movements of these birds (Bellrose and Crompton 1970). However, our models could be evaluated using movement data from individual birds monitored by telemetry (e.g., Miller et al. 2005).

Relationships between rate of change in relative abundance of ducks and weather metrics were best explained by a quadratic function. A quadratic function may indicate that duck numbers were stable or slightly increasing on CAs with CumulativeWSI until some threshold, when rate of change in relative abundance became negative along the quadratic trend line (x-intercept; Figs. 1, 2). At points beyond thresholds, rate of change in relative abundance of ducks at CAs became increasingly negative (Figs. 1, 2). A quadratic function may also result from simultaneous ingress and egress of waterfowl at CAs at lower CumulativeWSI and mass egress of waterfowl from CAs during harsh weather events. Our results suggest weather-related migration cues differ between mallards and other smaller-bodied dabblers, with migration of the latter starting before freeze events in Missouri and likely elsewhere (Bellrose 1980). In contrast, mallards often experienced freezing temperatures, snowfall, and likely wetland icing before departing temporarily or migrating southward.

Given increases in energy demands, animals can take action to conserve energy, increase energy intake, or metabolize endogenous reserves to meet daily needs (Blem 2000). Pearse (2007) reported that colder temperatures at latitudes of approximately 38°N (at Kansas City and St. Louis, MO) and, to a lesser degree, snow cover in this region, were associated positively with duck abundance in Mississippi, USA. Ambient temperature and number of consecutive days $\leq$0° C have direct energetic consequences for waterfowl (Calder 1974, Baldassarre and Bolen 2006), and these cumulative effects also influence water temperature and ice formation. Increasing ice coverage can decrease availability of wetland foods, reducing nutrient acquisition by wetland-obligate waterfowl (e.g., gadwall, northern shoveler). However, field-feeding waterfowl (e.g., mallard) can acquire nutrients following wetland icing, at least until snow and ice cover preclude foraging. We found that PC1 eigenvectors were more heavily weighted toward relationships associated with energy conservation (i.e., TEMP, TEMPDAYS) than energy acquisition (i.e., SNOWDAYS, SNOW), with the latter slightly more influential for mallards than other dabbling ducks. Differential foraging

strategies among waterfowl may also partly explain differences in threshold WSI between mallards and other dabblers.

Apparent differences in migration patterns between mallards and other dabbling ducks may also be partially explained by mechanisms related to photoperiod. Rates of change in relative abundance of mallards and other dabblers were related to photoperiod, but the relationship was stronger in other dabbling ducks than mallards. Day length decreases during autumn until late December in the northern hemisphere, and reaction of dabbling ducks, other than mallards, to changes in photoperiod may partially explain migration of other dabbling ducks before the winter solstice. Mallards often do not migrate any farther south than necessary to obtain food (Bellrose 1980, Jorde et al. 1983, 1984), and this behavior may explain the difference in photoperiodic effect between mallards and other dabbling ducks. Photoperiod (MINUTES) was not included in top models for mallards and other dabbling ducks, perhaps suggesting weather-related mechanisms (i.e., WSI) may influence autumn–winter migration more than nonweather-related mechanisms (i.e., photoperiod). Our findings are consistent with the concept that photoperiod influences waterfowl migration, but plasticity exists in migration rhythms of birds regarding fine-scale environmental conditions, such as weather severity (Gordo 2007, Netwon 2008).

Our study focused on weather factors (i.e., temp, snow cover) linked to waterfowl movements and migration during autumn–winter. Food availability, habitat, disturbance, precipitation, and other factors also influence migration of waterfowl (Bellrose 1980, Reinecke et al. 2006, Pearse 2007). We interpret points above the trend line (positive residuals; Figs. 1, 2) as points in space and time when food availability, limited disturbance, flooding, and other exogenous factors may offset negative effects of weather severity. Points below the trend line (negative residuals) may represent earlier movement or migration resulting from habitat resource limitations, disturbances, dry conditions, or some combination of these factors. Also, lipid reserves of ducks can greatly influence migration strategies (Miller et al. 2005). Lipid reserve levels of ducks affect risk of starvation and influence length of time ducks can sustain physiological functions without foraging (Alerstam and Hedenström 1998). Unexplained variation in the rate of change in relative abundance of ducks in our study may also be associated with nutrient reserves related or unrelated to weather. We submit that further investigations into weather and other factors are needed to increasingly understand waterfowl migration. Refining our understanding of factors influencing autumn–winter waterfowl migration will enhance our ability to predict influences of climate change on the distribution of waterfowl in North America.

We encourage a conceptual, adaptive approach to increasing our understanding of how changes in climate and related metrics (i.e., food and habitat availability) may influence waterfowl distribution during autumn and winter in North America (Walters 1986). Such an approach may include 1) testing our WSI at different waterfowl staging areas on mallards, other species, and at the individual bird level (e.g., satellite-monitored ducks); 2) developing projections of the timing and extent of change in distributions of waterfowl into the future under various climate change models (e.g., Ruosteenoja et al. 2003); 3) testing projections developed above via currently available, long-term North American monitoring efforts (e.g., midwinter waterfowl surveys, United States Fish and Wildlife Service National Wildlife Refuge waterfowl surveys; duck-band recovery data); 4) updating steps 2 and 3 because new and improved models are likely to alter current climate change projections (Seavy et al. 2008); and 5) refining the WSI and the projections of changes in distributions of waterfowl and other migratory birds on the basis of well-defined inputs from steps 1–4. Finally, we discussed how species may react differently to severe weather and pose that further research is needed to determine species-specific migration cues. Changing climate may also pose new threats to waterfowl that migrate, regardless of weather, possibly causing asynchrony in the timing of migration and the availability of food resource (i.e., the mismatch hypothesis; Thomas et al. 2001, Walther et al. 2002).

MANAGEMENT IMPLICATIONS

Our WSI and subsequent evaluations should improve biologists' and managers' abilities to predict fall and winter movements and migration of waterfowl and other birds. Additionally, the index could be adapted to model relationships between spring migration by waterfowl and weather metrics, thereby possibly revealing weather influences on avian migration and distribution during the annual cycle. The WSI and other models may help bird conservationists assess how recent and long-term weather dynamics may influence spatial and temporal distributions of waterfowl and other birds and provide guidance for planning and implementing landscape-scale habitat conservation (NAWMP 2004, Johnson et al. 2005). At a local scale, use of the WSI to predict when large influxes of migrant waterfowl may be expected would help managers manipulate water levels and provide food resources at key periods for arriving birds. Finally, use of the WSI, in conjunction with analyses of long-term weather and harvest data (Williams et al. 2006), may provide insight for biologists responsible for managing waterfowl hunting seasons in relation to migration chronology.

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