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Spring migration phenology of birds in the Northern Prairie region is correlated with local climate change

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ABSTRACT. In apparent response to recent periods of global warming, some migratory birds now arrive earlier at stopover sites and breeding grounds. However, the effects of this warming on arrival times vary among locations and species. Migration timing is generally correlated with temperature, with earlier arrival during warm years than during cold years, so local variation in climate change might produce different effects on migration phenology in different geographic regions. We examined trends in first spring arrival dates (FADs) for 44 species of common migrant birds in South Dakota (1971–2006) and Minnesota (1964–2005) using observations compiled by South Dakota and Minnesota Ornithologists' Unions. We found significant trends in FAD over time for 20 species (18 arriving earlier and two later) in South Dakota and 16 species (all earlier) in Minnesota. Of these species, 10 showed similar significant trends for both states. All 10 of these species exhibited significantly earlier arrival, and all were early spring migrants, with median FADs before 10 April in both states. Eighteen of the 44 species showed significant negative correlations of FADs with either winter (December–February) or spring (arrival month plus previous month) temperatures in one or both states. Interestingly, spring temperatures in both South Dakota and Minnesota did not warm significantly from 1971–2006, but winter temperatures in both states warmed significantly over the same time period. This suggests that the warmer winters disproportionately affected early spring migrants, especially those associated with aquatic habitats (seven of the 10 species showing significantly earlier spring arrival in both states). The stronger response to climate change by early spring migrants in our study is consistent with the results of several other studies, and suggests that migrants, especially early migrants, are capable of responding to local temperature conditions experienced on wintering grounds or along the migration route.

RESUMEN. **Fenología durante la migración primaveral de aves en las praderas del norte esta correlacionada con cambios climáticos locales**

En una respuesta aparente a recientes periodos de calentamiento global, algunas aves migratorias actualmente están arribando más temprano en los lugares de paradas y zonas de reproducción. Sin embargo, el efecto de este calentamiento sobre los tiempos de llegada varia entre localidades y especies. El inicio de la migración esta generalmente correlacionado con la temperatura, con llegadas tempranas durante años cálidos que en los años fríos, entonces variación local en cambios climáticos puede producir diferentes efectos en la fenología de migración en diferentes regiones geográficas. Examinamos tendencias en la fecha de la primera llegada primaveral (FPLL) para 44 especies de migrantes comunes en South Dakota (1971–2006) y Minnesota (1964–2005) usando observaciones acumuladas por la unión de ornitólogos de South Dakota y Minnesota. Encontramos tendencias significativas en FPLL a través del tiempo para 20 especies (28 llegaron temprano y dos tarde) en South Dakota y 16 especies (todas temprano) en Minesota. De estas especies, 10 mostraron tendencias significativas similares en ambos estados. Todas de las 10 especies exhibieron una llegada significativamente temprana, y todos fueron migrantes primaverales tempranos, con una media de FPLL antes del 10 de abril en ambos estados. Dieciocho de estas 44 especies mostraron una correlación negativa significativa en FPLL de manera similar en las temperaturas de invierno (Diciembre-Febrero) o primavera (mes de arribo más el mes anterior) en uno o ambos estados. Interesantemente, temperaturas de primavera en ambos South Dakota y Minnesota no se calentaron significativamente entre 1971–2006, pero temperaturas invernales en ambos estados se calentaron significativamente durante el mismo periodo de tiempo. Esto sugiere que los inviernos calientes afectan de manera desproporcional la llegada temprana de migrantes durante la primavera, especialmente los asociados con hábitat acuáticos (siete de las 10 especies mostraron una llegada significativamente mas temprana en la primavera en ambos estados). La fuerte respuesta a cambio climático por aves migrantes durante la primavera en nuestro estudio es consistente con los resultados de varios estudios y sugiere que migrantes, especialmente migrantes tempranos, son capaces de responder a condiciones locales de temperaturas experimentadas en las zonas de invierno o a lo largo de la ruta de migración.

Key words: Climate change, migration arrival, migration timing, Minnesota, South Dakota

Climatic warming influences the phenology of many seasonal processes, including timing of migration and breeding in birds, as well as plant and insect cycles that could impact

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bird foraging (Bradley et al. 1999, Peñuelas et al. 2002, Cotton 2003, Marra et al. 2005). Differing responses to climate change can result in mismatches between timing of avian cycles and timing of plant and insect cycles that impact migration and breeding in birds (Thomas et al. 2001, Strode 2003, Crick 2004, Marra et al. 2005, Both et al. 2006). In general, avian migration and arrival on breeding grounds occur earlier during recent periods of global warming (Lehikoinen et al. 2004, Mills 2005, Crick and Sparks 2006, Miller-Rushing et al. 2008a). However, considerable variation in trends in migratory phenology occurs among species and at different locations along migration routes (Butler 2003, Sparks et al. 2007), and some studies have revealed little change in the migration phenology of migrants at some locations (Wilson et al. 2000, Strode 2003). Moreover, short-distance migrants that migrate earlier in the spring tend to be disproportionately affected by climate change compared to long-distance migrants (Butler 2003, Tryjanowski et al. 2005, MacMynowski and Root 2007; but see Jonzén et al. 2006).

The most commonly studied metric of migration phenology is the first arrival date for a species in the spring because these are often the only data on migration timing available. First arrival dates (FADs) represent the early tail of the normal (Gaussian) curve for migration timing and may, as a result, be more variable than other measures of migration timing and, therefore, may not be representative of changes in migration timing for the entire migration period (Møller and Merilä 2004). However, FADs are usually correlated with other measures of migration timing (e.g., medians and quartiles), although they may not be precise predictors of such measures (Sparks et al. 2005, Tøttrup et al. 2006), and Sparks et al. (2001) argued that FADs can be used, cautiously (e.g., Miller-Rushing et al. 2008b), to reveal the impacts of climate change on migration phenology.

Recent studies of FADs generally show trends toward earlier arrival dates consistent with recent periods of global warming, but the strength of these trends varies among species (Sparks et al. 2007). In addition, FADs are also correlated with proximate temperatures during (or preceding) the migratory period, but again there is much variability among species (Butler 2003, Sparks et al. 2007). In addition, variation exists among locations in trends in FADs, so changes occurring at some locations along a migration route may not be evident along the entire route (Strode 2003, Sparks et al. 2007).

With two exceptions (Strode 2003, Murphy-Klassen et al. 2005), changes in migration phenology of birds in the northern prairie region of North America have received little attention. Murphy-Klassen et al. (2005) studied 96 species of birds at Delta Marsh, Manitoba, and found that 26% of these species showed significant trends in FADs toward earlier spring arrival, with short-distance migrants showing stronger responses than long-distance migrants. In Fargo, North Dakota, Strode (2003) studied 12 species of wood warblers and only one (Yellow-rumped Warblers, *Dendroica coronata*) showed a tendency toward earlier arrival over a 40-yr period. Both of these studies focused on single sites in the northern prairie region, and trends in arrival dates can vary dramatically among different sites within geographic regions (Butler 2003, Sparks et al. 2007). To date, no one has examined the possible effects of climate changes on the timing of migration arrival over broader geographic scales in the northern prairie region.

Our objective was to examine temporal trends in spring FADs for 44 common species of migrants in South Dakota and Minnesota. We collected FADs data from published and online records of the South Dakota and Minnesota Ornithologists' Unions for the periods from 1971–2006 and 1964–2005, respectively. We also examined local trends in climate change for the period from 1971–2006 for both winter (December–February) and spring (March–May) in South Dakota and Minnesota. Finally, we examined correlations between FADs and local temperatures to determine whether migratory phenology for these 44 species was correlated with variation in local temperatures.

METHODS

We collected FAD records for South Dakota for the period from 1971–2006, where records were available, from the online bird records database of the South Dakota Ornithologists' Union (http://homepages.dsu.edu/palmerj/sdousbor/) and from published reports in *South Dakota Bird Notes*. South Dakota FAD records were not complete for all years in the 1970s and 1980s for the species we analyzed, but sufficient records were present to determine temporal trends in FADs. We collected FAD records for Minnesota for the period from 1964–2005, where such data were available, from published data in *The Loon*, the official publication of the Minnesota Ornithologists' Union. Minnesota FAD records for the 44 species in our study were nearly complete over this time period. We calculated FAD as the number of days since 28 February, to account for leap years, and used this number in subsequent analyses. For data on observer effort over the period of this study, we counted the number of cited observers contributing to spring season bird reports published in *South Dakota Bird Notes* and *The Loon*.

We obtained weather records for average daily temperature for South Dakota and Minnesota from the NOAA Climate Division database (http: // climate.sdstate. edu/ClimateDivisions/ Seasonal.cfm). The climate division database divided South Dakota and Minnesota into nine separate geographic regions, and we analyzed temperature data for each region separately to provide an overall picture of climate change in South Dakota and Minnesota during the period from 1971–2006.

Bird species. We chose 44 species of migrants for analysis in our study, and all were common, easily identified species, reducing the potential bias from misidentifications. In addition, none of the 44 species regularly winter in either state (Janssen 1987, Tallman et al. 2002), so FAD observations represent true migration rather than individuals that might have overwintered. The 44 species also included both early arriving, short-distance migrants and later-arriving, long-distance migrants. The latest median FAD for any species in our study was 15 May (Table 1), so we used 7 April, the date halfway between this date and the beginning of the migratory period, to arbitrarily split species into early and late migrant categories. Two species, Purple Martin (*Progne subis*) and Swainson's Hawk (*Buteo swainsoni*), had median FADs earlier than 7 April in one state, but slightly later in the other state (up to 10 April), so we modified the arbitrary cut-off in median FADs between early and late migrant categories to 10 April.

Statistical analyses. We performed least-squares regressions of FADs against year for each of the 44 species to determine temporal trends in FADs for each species. To determine if differences in observer effort over the study period may have influenced FAD data, we used least-squares regression to analyze the relationship between number of observers and

Table 1. Temperature trends (Δ°C/decade) for spring (March–May) and winter (December–February) for the period 1971–2006 from NOAA Climate Division data for South Dakota (SD) and Minnesota (MN). Note that little warming is occurring during spring, but that winters are significantly warmer in all climate divisions of both states.

State/Region	Spring Δ°C/10 yr	Spring *P*-value	Winter Δ°C/10 yr	Winter *P*-value
SD/Southwest	+0.017	0.936	+0.911	0.020
SD/Southeast	+0.069	0.777	+1.039	0.014
SD/South-central	+0.054	0.806	+0.978	0.016
SD/Northwest	+0.072	0.762	+1.128	0.013
SD/Northeast	+0.024	0.929	+1.050	0.024
SD/North-central	+0.131	0.612	+1.078	0.026
SD/East-central	−0.001	0.997	+1.050	0.018
SD/Central	+0.039	0.866	+1.017	0.024
SD/Black Hills	+0.273	0.201	+0.622	0.037
MN/West-central	+0.145	0.607	+1.100	0.011
MN/Southwest	+0.065	0.807	+0.994	0.014
MN/Southeast	+0.263	0.304	+1.194	0.002
MN/South-central	+0.082	0.765	+1.006	0.011
MN/Northwest	+0.209	0.494	+1.306	0.003
MN/Northeast	−0.013	0.958	+0.939	0.010
MN/North-central	+0.113	0.691	+1.161	0.004
MN/East-central	+0.368	0.153	+1.311	<0.001
MN/Central	+0.196	0.484	+1.117	0.005

year for the study periods in both states. In addition, to evaluate whether observer effort affected the FAD versus year relationship, we performed multiple regressions with FAD as the dependent variable and year and number of cited observers as independent variables. We also performed least-squares regressions of FADs against the season-wide mean of average daily temperatures (from Climate Division Data) for the preceding winter (December–February) and spring (arrival month plus the preceding month, following the method of MacMynowski and Root 2007) periods for each species. For species with median FADs during the first week of the month, average temperatures during the month of arrival may not be a good indicator of the effect of temperature on FAD, so, for these species, we performed separate linear regressions of FADs on average daily temperature for the arrival month plus the preceding month and for the 2 mo preceding arrival. We then used the regression with the lowest *P*-value in subsequent analyses.

We also used least-squares regression to analyze temporal trends in winter and spring temperature over the 1971–2006 time periods for both states. For these analyses, we regressed average daily temperature for winter (December–February) and spring (March–May) periods against year for each of the nine climate divisions in the two states. For all analyses, statistical significance was accepted as $P < 0.05$. We followed Miller-Rushing et al. (2008b) in not adjusting α-levels for multiple, table-wide comparisons because such corrections reduce statistical power and can be overly conservative (Nakagawa 2004).

RESULTS

Winter and spring temperature trends. Average daily temperatures during the spring (March–May) showed positive correlations with year for eight of the nine climate divisions in both states (Table 1). However, the mean ($\pm$SD) rate of increase in spring average daily temperature for the region was only $0.12 \pm 0.11^{\circ}$C/decade, and the maximum rates of temperature increase were 0.27°C/decade in South Dakota and 0.37°C/decade in Minnesota. None of the climate divisions in either South Dakota or Minnesota showed significant variation in spring average daily temperature among years, so spring temperatures in this region do not show strong warming trends (Table 1). In contrast, average daily temperature for the winter period (December–February) increased significantly in all climate divisions in both states (Table 1). The mean rate of winter average daily temperature increase was $1.06 \pm 0.12^{\circ}$C/decade, with rates of temperature increase ranging from 0.62°C/decade for the Black Hills of South Dakota to 1.31°C/decade for east-central Minnesota. Thus, winter temperatures in the region show significant warming trends over the period of our study.

Temporal trends in FADs. Significant negative correlations between FAD and year, suggestive of earlier migration timing, were apparent for 24 of 44 species (54.5%) in one or both states (18 species in South Dakota and 16 species in Minnesota). Ten species exhibited similar significant negative correlations in both states (Table 2), so we conservatively considered these 10 species to show definitive trends toward earlier arrival. All 10 of these species had median FADs before 10 April. In addition, least squares regression of slopes of FAD versus year regressions against median FAD (using median FADs for each state) for individual species yielded significant positive relationships for both South Dakota (slope = 0.0068 [median FAD] – 0.5819; $R^2 = 0.26$, $P < 0.001$) and Minnesota (slope = 0.0088 [median FAD] – 0.5122; $R^2 = 0.49$, $P < 0.001$; Fig. 1). Finally, 16 of 19 species (84.2%) with median FADs on or before 10 April showed significantly earlier arrival in at least one state, but only eight of 25 species (32.0%) with median FADs after 10 April exhibited significantly earlier arrival. These data suggest stronger responses to climate change in early-arriving migrants in the Northern Prairie region. We found significant positive correlations of FAD with year for only two species, Purple Martins and Dickcissels (*Spiza americana*), both in South Dakota (although the positive trend for Dickcissels in Minnesota was nearly significant, $P = 0.06$; Table 2).

We found an increase in the number of reporting observers over time in Minnesota (number of observers = 4.05 [yr] – 7924; $N = 38$, $R^2 = 0.63$, $P < 0.001$), but no such relationship was apparent for South Dakota (number of observers = 0.298 [yr] – 555.6; $N = 32$, $R^2 = 0.08$, $P = 0.13$; Fig. 2). However, the number of

Table 2. Results for simple (FAD vs. year) and multiple (FAD vs. year and number of observers) regressions for South Dakota (1971–2006) and Minnesota (1964–2005) for the 44 species of birds in our study. Significant correlations are marked in pale gray. The median presents the median FADs for each species from each state. The population trend column represents significant increases (+), decreases (−), or stability (S) in population sizes as determined for the central North American region from Breeding Bird Survey data (Sauer et al. 2008).

Species/State	State	N^1	Multiple year slope	SE	P	Multiple obs. no. slope	SE	P	N^2	Simple year slope	SE	P	Median	Population trend
Blue-winged Teal	SD	24	−0.498	0.221	0.035	−0.191	0.219	0.39	24	−0.559	0.208	0.014	16 Mar	S
Anas discors	MN	35	−0.336	0.190	0.09	−0.006	0.036	0.86	38	−0.300	0.102	0.006	7 Mar	
Northern Shoveler	SD	22	−0.578	0.162	0.002	−0.273	0.158	0.10	22	−0.664	0.161	<0.001	11 Mar	+
Anas clypeata	MN	32	−0.674	0.154	<0.001	0.056	0.032	0.09	36	−0.496	0.097	<0.001	6 Mar	
Common Loon	SD	24	−0.644	0.195	0.003	−0.428	0.189	0.034	24	−0.761	0.205	0.001	29 Mar	+
Gavia immer	MN	36	−0.408	0.156	0.013	0.047	0.031	0.14	40	−0.142	0.097	0.15	27 Mar	
Western Grebe	SD	26	−0.172	0.142	0.24	−0.132	0.137	0.35	26	−0.217	0.134	0.12	10 Apr	+
Aechmophorus occidentalis	MN	36	−0.428	0.151	0.008	−0.006	0.030	0.85	39	−0.433	0.087	<0.001	9 Apr	
American White Pelican	SD	23	−0.358	0.182	0.06	−0.069	0.171	0.69	23	−0.381	0.169	0.035	27 Mar	S
Pelecanus erythrorhynchos	MN	35	−0.998	0.217	<0.001	0.090	0.045	0.053	38	−0.681	0.130	<0.001	23 Mar	
Double-crested Cormorant	SD	25	−0.344	0.129	0.014	−0.075	0.124	0.55	25	−0.374	0.118	0.004	27 Mar	+
Phalacrocorax auritus	MN	35	−0.892	0.197	<0.001	0.057	0.039	0.16	38	−0.726	0.119	<0.001	17 Mar	
Great Blue Heron	SD	25	−0.305	0.142	0.043	−0.263	0.140	0.07	25	−0.381	0.143	0.014	21 Mar	S
Ardea herodias	MN	33	−0.552	0.125	<0.001	0.071	0.026	0.010	36	−0.253	0.083	0.005	12 Mar	
Turkey Vulture	SD	25	−0.656	0.259	0.019	0.156	0.253	0.54	25	−0.603	0.240	0.020	31 Mar	S
Cathartes aura	MN	33	−0.816	0.175	<0.001	0.042	0.037	0.26	36	−0.628	0.115	<0.001	7 Mar	
Swainson's Hawk	SD	26	−0.302	0.148	0.053	−0.159	0.152	0.31	26	−0.328	0.146	0.034	1 Apr	S
Buteo swainsoni	MN	35	−0.879	0.169	<0.001	0.152	0.034	<0.001	37	−0.299	0.127	0.025	9 Apr	
Sandhill Crane	SD	24	−0.562	0.154	0.001	−0.140	0.155	0.38	24	−0.613	0.143	<0.001	25 Mar	S
Grus canadensis	MN	37	−0.765	0.132	<0.001	0.004	0.026	0.87	41	−0.780	0.076	<0.001	12 Mar	
Killdeer	SD	24	−0.060	0.108	0.59	−0.291	0.120	0.024	24	−0.086	0.119	0.48	10 Mar	−
Charadrius vociferus	MN	33	0.028	0.141	0.84	0.013	0.026	0.62	35	0.096	0.076	0.21	8 Mar	
American Avocet	SD	25	−0.109	0.147	0.47	−0.245	0.148	0.11	25	−0.201	0.141	0.17	11 Apr	S
Recurvirostra americana	MN	36	−0.392	0.164	0.023	0.015	0.032	0.63	40	−0.411	0.103	<0.001	19 Apr	
Upland Sandpiper	SD	22	0.250	0.216	0.26	−0.485	0.217	0.038	22	0.056	0.217	0.80	23 Apr	+
Bartramia longicauda	MN	36	0.003	0.150	0.98	0.018	0.030	0.56	40	0.024	0.087	0.78	27 Apr	

Continued.

Table 2. Continued.

Species/State	State	N^1	Multiple year slope	SE	P	Multiple obs. no. slope	SE	P	N^2	Simple year slope	SE	P	Median	Population trend
Wilson's Phalarope	SD	21	−0.566	0.191	0.008	0.224	0.212	0.30	21	−0.463	0.165	0.011	19 Apr	S
Phalaropus tricolor	MN	34	−0.034	0.093	0.72	−0.008	0.018	0.64	38	−0.038	0.052	0.46	22 Apr	
Franklin's Gull	SD	26	−0.278	0.185	0.15	−0.279	0.182	0.14	26	−0.357	0.183	0.06	23 Mar	S
Leucophaeus pipixcan	MN	37	−0.372	0.219	0.10	0.088	0.043	0.050	41	−0.009	0.126	0.94	27 Mar	
Black Tern	SD	24	−0.350	0.128	0.012	0.288	0.132	0.041	24	−0.264	0.132	0.06	6 May	S
Chlidonias niger	MN	35	−0.027	0.185	0.89	0.041	0.036	0.27	39	0.116	0.104	0.28	1 May	
Common Nighthawk	SD	19	0.013	0.243	0.96	−0.139	0.279	0.63	19	−0.060	0.190	0.76	15 May	S
Chordeiles minor	MN	36	0.184	0.256	0.48	0.028	0.050	0.58	40	0.269	0.140	0.06	1 May	
Chimney Swift	SD	27	−0.085	0.091	0.36	−0.166	0.091	0.08	27	−0.143	0.089	0.12	27 Apr	−
Chaetura pelagica	MN	37	−0.175	0.125	0.17	0.044	0.024	0.08	41	0.002	0.074	0.98	21 Apr	
Ruby-throated Hummingbird	SD	22	−0.517	0.113	< 0.001	0.075	0.120	0.54	22	−0.478	0.094	< 0.001	13 May	S
Archilochus colubris	MN	36	−0.023	0.093	0.81	−0.012	0.018	0.53	40	−0.086	0.053	0.11	1 May	
Least Flycatcher	SD	23	−0.050	0.086	0.57	−0.010	0.088	0.91	23	−0.054	0.077	0.50	4 May	S
Empidonax minimus	MN	37	−0.174	0.146	0.24	0.085	0.029	0.006	41	0.156	0.092	0.10	4 May	
Western Kingbird	SD	25	−0.044	0.125	0.73	−0.026	0.125	0.84	25	−0.053	0.114	0.64	30 Apr	+
Tyrannus verticalis	MN	36	0.036	0.108	0.74	0.011	0.021	0.61	40	0.071	0.060	0.24	9 May	
Eastern Kingbird	SD	23	−0.091	0.106	0.40	−0.142	0.108	0.20	23	−0.137	0.102	0.19	3 May	−
Tyrannus tyrannus	MN	36	−0.190	0.209	0.37	0.051	0.041	0.22	40	0.035	0.119	0.77	24 Apr	
Warbling Vireo	SD	25	−0.150	0.103	0.16	−0.147	0.101	0.16	25	−0.221	0.093	0.025	7 May	S
Vireo gilvus	MN	35	−0.180	0.089	0.052	0.044	0.017	0.017	39	0.023	0.057	0.69	3 May	
Red-eyed Vireo	SD	17	−0.218	0.166	0.21	0.149	0.212	0.50	17	−0.161	0.142	0.27	12 May	+
Vireo olivaceous	MN	36	−0.067	0.109	0.54	0.024	0.021	0.27	40	0.033	0.060	0.60	7 May	
Purple Martin	SD	26	0.282	0.125	0.034	−0.043	0.119	0.72	26	0.272	0.120	0.032	10 Apr	S
Progne subis	MN	36	−0.060	0.169	0.72	0.022	0.033	0.51	40	0.050	0.092	0.59	4 Apr	
Tree Swallow	SD	27	−0.416	0.093	< 0.001	−0.015	0.089	0.87	27	−0.419	0.089	< 0.001	7 Apr	+
Tachycineta bicolor	MN	38	−0.451	0.140	0.003	0.025	0.028	0.37	42	−0.303	0.081	< 0.001	20 Mar	
Barn Swallow	SD	26	−0.050	0.081	0.55	−0.144	0.082	0.09	26	−0.087	0.081	0.29	15 Apr	S
Hirundo rustica	MN	36	−0.318	0.159	0.054	0.033	0.031	0.30	40	−0.181	0.088	0.046	10 Apr	
House Wren	SD	24	−0.115	0.093	0.23	−0.222	0.099	0.036	24	−0.201	0.092	0.040	22 Apr	+
Troglodytes aedon	MN	34	−0.062	0.181	0.73	0.035	0.036	0.34	38	0.119	0.104	0.26	17 Apr	

Continued.

Table 2. Continued.

Species/State	State	N^1	Multiple year slope	SE	*P*	Multiple obs. no. slope	SE	*P*	N^2	Simple year slope	SE	*P*	Median	Population trend
Ruby-crowned Kinglet	SD	23	−0.061	0.190	0.75	−0.114	0.194	0.57	23	−0.107	0.170	0.54	4 Apr	S
Regulus calendula	MN	36	−0.389	0.196	0.056	0.012	0.039	0.75	40	−0.333	0.108	0.004	26 Mar	
Gray Catbird	SD	24	−0.089	0.290	0.76	−0.365	0.295	0.23	24	−0.268	0.254	0.30	4 May	S
Dumetella carolinensis	MN	36	−0.624	0.290	0.039	0.117	0.057	0.047	40	−0.142	0.166	0.40	28 Apr	
Brown Thrasher	SD	20	−0.491	0.349	0.18	0.135	0.397	0.74	20	−0.429	0.290	0.16	18 Apr	−
Toxostoma rufum	MN	36	0.055	0.285	0.85	0.004	0.056	0.94	40	0.056	0.157	0.72	11 Apr	
Orange-crowned Warbler	SD	26	−0.203	0.098	0.050	0.181	0.097	0.08	26	−0.138	0.096	0.16	21 Apr	S
Vermivora celata	MN	35	−0.008	0.104	0.94	−0.011	0.021	0.60	39	−0.047	0.058	0.43	21 Apr	
Yellow Warbler	SD	22	−0.071	0.112	0.53	0.043	0.119	0.72	22	−0.054	0.099	0.59	1 May	S
Dendroica petechia	MN	34	−0.030	0.134	0.83	−0.021	0.025	0.41	38	−0.075	0.077	0.33	25 Apr	
Yellow-rumped Warbler	SD	22	−1.183	0.360	0.004	0.673	0.466	0.17	22	−0.775	0.230	0.003	6 Apr	S
Dendroica coronata	MN	36	−0.283	0.211	0.19	−0.006	0.041	0.89	40	−0.320	0.115	0.008	28 Mar	
American Redstart	SD	20	−0.094	0.154	0.55	−0.129	0.175	0.55	20	−0.149	0.132	0.27	11 May	S
Setophaga ruticilla	MN	35	−0.107	0.077	0.17	0.016	0.015	0.30	39	−0.020	0.046	0.68	4 May	
Common Yellowthroat	SD	21	−0.422	0.131	0.005	0.087	0.146	0.56	21	−0.376	0.104	0.002	2 May	−
Geothlypis trichas	MN	36	0.099	0.116	0.40	−0.005	0.023	0.84	40	0.085	0.069	0.23	3 May	
Chipping Sparrow	SD	22	−0.630	0.287	0.041	−0.012	0.328	0.97	22	−0.632	0.272	0.031	6 Apr	+
Spizella passerina	MN	36	−0.114	0.197	0.57	−0.020	0.039	0.61	40	−0.189	0.107	0.09	26 Mar	
Lincoln's Sparrow	SD	20	−0.168	0.230	0.48	−0.015	0.243	0.95	20	−0.175	0.192	0.38	18 Apr	−
Melospiza lincolnii	MN	35	−0.164	0.220	0.46	0.002	0.043	0.96	39	−0.158	0.123	0.21	13 Apr	
Rose-breasted Grosbeak	SD	20	−0.065	0.069	0.36	−0.294	0.073	<0.001	20	−0.168	0.087	0.07	5 May	S
Pheucticus ludovicianus	MN	36	0.324	0.182	0.08	−0.042	0.035	0.25	40	0.126	0.103	0.23	28 Apr	
Indigo Bunting	SD	20	0.224	0.204	0.29	0.043	0.242	0.86	20	0.237	0.187	0.22	9 May	S
Passerina cyanea	MN	35	−0.014	0.098	0.89	−0.034	0.019	0.09	39	−0.150	0.060	0.018	2 May	
Dickcissel	SD	21	0.330	0.142	0.032	0.096	0.154	0.54	21	0.339	0.139	0.025	10 May	S
Spiza americana	MN	35	0.258	0.220	0.25	−0.015	0.043	0.73	39	0.251	0.129	0.06	11 May	
Bobolink	SD	24	−0.075	0.255	0.77	−0.194	0.255	0.46	24	−0.136	0.240	0.58	6 May	S
Dolichonyx oryzivorus	MN	36	0.045	0.111	0.69	−0.009	0.022	0.67	40	0.049	0.071	0.50	1 May	
Yellow-headed Blackbird	SD	18	−0.093	0.364	0.80	−0.273	0.389	0.49	18	−0.247	0.286	0.40	2 Apr	S
Xanthocephalus xanthocephalus	MN	36	−0.603	0.180	0.002	0.087	0.035	0.018	40	−0.246	0.114	0.037	30 Mar	
Baltimore Oriole	SD	18	−0.076	0.216	0.73	−0.350	0.264	0.21	18	−0.308	0.129	0.030	3 May	S
Icterus galbula	MN	35	0.128	0.190	0.51	−0.050	0.037	0.19	39	−0.042	0.112	0.71	28 Apr	

[1] Sample size for multiple regressions of FAD against year and observer number. We were not able to extract observer number data for all years from *The Loon*.
[2] Sample size for simple linear regressions of FAD against year.

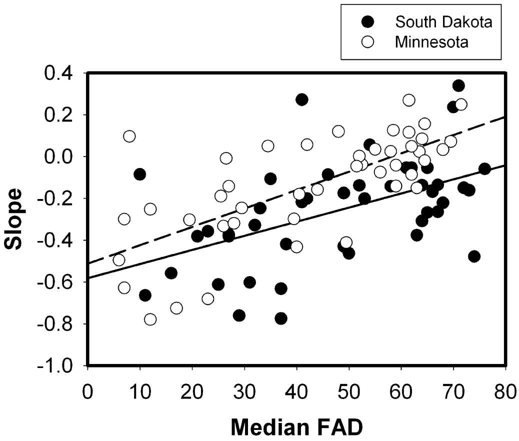

Fig. 1. Relationship between the slope of the regressions between FAD and year versus median FAD for individual species in South Dakota and Minnesota. Median FAD is presented as the number of days since 28 February. Both states showed significant positive relationships, indicating that earlier arriving species showed stronger tendencies to arrive earlier in the spring.

observers had a significant effect on FAD in multiple regressions for only seven species in Minnesota and six species in South Dakota (Table 2). The effect of observer number on FAD was not consistent in multiple regressions; all seven significant correlations were positive for Minnesota, but five of six significant correlations in South Dakota were negative (Table 2).

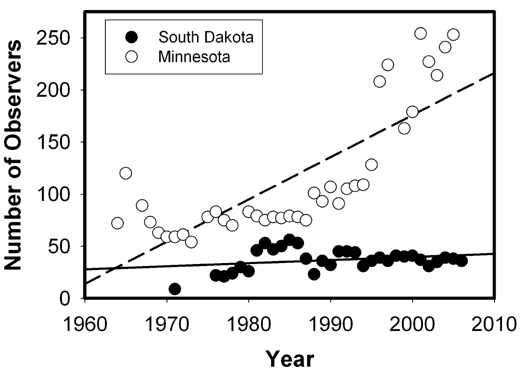

Fig. 2. Number of cited observers as a function of year for South Dakota (data from *South Dakota Bird Notes*) and Minnesota (data from *The Loon*). The number of observers reporting increased significantly with year in Minnesota, but not in South Dakota.

FAD correlations with winter and spring temperatures. Eighteen of 44 species (41%) exhibited significant negative correlations between FAD and average daily temperature for winter or spring periods for one or both states (Table 3). The FADs of only two species, Least Flycatchers (*Empidonax minimus*) and Rose-breasted Grosbeaks (*Pheucticus ludovicianus*), exhibited significant positive trends with average daily temperature, and both in Minnesota (Least Flycatchers with winter temperature and Rose-breasted Grosbeaks with spring temperature). Interestingly, both these species exhibited opposite trends in South Dakota, with significant negative correlations of FADs with average daily temperature; Least Flycatchers for both winter and spring, and Rose-breasted Grosbeaks for spring (Table 3).

We found significant negative correlations between FAD and average daily temperature for 47.4% of the species with median FAD on or before 10 April (19 species), and for 36.0% of the species with median FAD after 10 April (25 species). In addition, for all comparisons (winter and spring for both states) of temperature against FAD, 26.3% of early migrants exhibited significant negative correlations, whereas only 11.0% of late migrants exhibited significant negative correlations. These data suggest a general tendency toward earlier FADs with warmer temperatures for migrant birds in this region. However, the greater percentage of negative correlations for early migrants suggests that the relationship is stronger for short-distance early migrants than for long-distance later migrants.

DISCUSSION

Climate trends over the study period were similar in South Dakota and Minnesota, with little change in average spring temperatures, but with significantly warmer winters in both states. Climate trends in South Dakota and Minnesota are consistent with regional trends over the period of our study, with relatively large increases in winter (December–February) temperature (approximately 1°C/decade) throughout central North America (NOAA, National Climatic Data Center; http://www.ncdc.noaa.gov/gcag/index.jsp). Spring (March–May) temperatures in the north-central United States and southern Canada have generally been stable, as were spring temperatures for South Dakota

Table 3. Slopes and *P*-values for linear regressions of FADs against mean daily temperature for winter (W; December–February) and spring (Sp; arrival month plus previous month, see text) in South Dakota (SD) and Minnesota (MN) for the 44 species in our study. Pale gray shading indicates a significant negative relationship, whereas underlining indicates a significant positive relationship. See Table 1 for scientific names.

Species	*N*	SD W temp	*P*	SD Sp temp	*P*	*N*	MN W temp	*P*	MN Sp temp	*P*
Blue-winged Teal	24	−1.355	0.001	−1.042	0.01	32	−0.331	0.28	−0.607	0.034
Northern Shoveler	22	−0.969	0.007	−1.277	0.004	29	−0.615	0.042	−0.925	0.003
Common Loon	24	−1.231	0.004	−1.236	0.02	33	−0.437	0.13	−0.913	0.012
Western Grebe	26	−0.226	0.39	−0.277	0.63	32	−0.129	0.67	−0.281	0.47
American White Pelican	23	−0.488	0.23	−0.174	0.72	31	−0.587	0.25	−0.926	0.059
Double-crested Cormorant	25	−0.085	0.78	−0.338	0.35	31	−0.683	0.15	−0.815	0.09
Great Blue Heron	25	−0.162	0.60	−0.235	0.53	29	−0.200	0.38	−0.218	0.33
Turkey Vulture	25	−0.632	0.26	−0.514	0.55	29	−1.017	0.007	−0.571	0.25
Swainson's Hawk	26	−0.112	0.71	−0.025	0.96	31	−0.323	0.35	−0.654	0.14
Sandhill Crane	24	−0.305	0.42	−0.630	0.18	34	−1.049	0.003	−1.081	0.002
Killdeer	24	−0.323	0.12	−0.551	0.021	31	−0.189	0.33	−0.393	0.032
American Avocet	25	0.061	0.85	−0.239	0.63	34	−0.274	0.28	−0.104	0.76
Upland Sandpiper	22	0.058	0.90	−0.945	0.18	33	−0.242	0.34	−0.341	0.31
Wilson's Phalarope	21	−0.775	0.033	0.188	0.78	32	0.099	0.48	0.207	0.23
Franklin's Gull	26	−0.709	0.064	−0.952	0.055	34	−0.657	0.066	−0.669	0.06
Black Tern	24	−0.193	0.47	0.327	0.49	32	0.117	0.71	0.233	0.57
Common Nighthawk	19	−0.265	0.50	0.112	0.87	33	0.040	0.92	−1.122	0.051
Chimney Swift	27	−0.138	0.46	−0.807	0.006	34	−0.054	0.79	−0.146	0.60
Ruby-throated Hummingbird	22	−0.084	0.77	0.581	0.27	33	−0.177	0.29	0.214	0.31
Least Flycatcher	23	−0.406	0.01	−0.511	0.031	34	0.622	0.03	0.408	0.29
Western Kingbird	25	−0.011	0.96	−0.482	0.19	33	−0.096	0.53	−0.255	0.27
Eastern Kingbird	23	−0.264	0.21	−0.462	0.19	33	0.635	0.068	−0.647	0.22
Warbling Vireo	25	−0.355	0.049	−0.793	0.014	32	−0.191	0.26	−0.717	0.002
Red-eyed Vireo	17	0.140	0.63	0.495	0.33	33	0.026	0.90	−0.826	0.002
Purple Martin	26	0.008	0.98	−0.865	0.033	33	−0.064	0.82	−0.944	0.007
Tree Swallow	27	−0.257	0.24	−0.344	0.21	35	−0.598	0.01	−0.561	0.017
Barn Swallow	26	0.179	0.24	−0.223	0.42	33	−0.064	0.81	−0.090	0.80
House Wren	24	−0.193	0.32	−0.259	0.45	31	−0.200	0.50	−0.089	0.82
Ruby-crowned Kinglet	23	0.132	0.71	0.222	0.72	33	−0.252	0.47	−0.548	0.22
Gray Catbird	24	0.306	0.54	0.170	0.86	33	−0.286	0.58	−0.358	0.65
Brown Thrasher	20	−1.013	0.10	0.318	0.76	33	−0.387	0.42	−0.129	0.84
Orange-crowned Warbler	26	−0.416	0.024	−0.337	0.31	32	0.087	0.62	0.190	0.41
Yellow Warbler	22	−0.358	0.064	−0.748	0.029	32	−0.191	0.39	−0.086	0.77
Yellow-rumped Warbler	22	−0.692	0.22	−0.197	0.76	33	−0.265	0.49	−0.823	0.09
American Redstart	20	−0.543	0.03	−0.191	0.68	32	0.073	0.61	−0.117	0.58
Common Yellowthroat	21	−0.642	0.005	−0.215	0.65	33	−0.159	0.31	−0.203	0.39
Chipping Sparrow	22	−0.554	0.32	−0.142	0.88	33	−0.028	0.93	−0.436	0.31
Lincoln's Sparrow	20	−0.083	0.84	−0.561	0.42	32	−0.258	0.48	0.223	0.65
Rose-breasted Grosbeak	20	−0.290	0.11	−0.584	0.047	33	0.101	0.74	0.818	0.037
Indigo Bunting	20	0.065	0.85	−0.153	0.82	32	−0.149	0.45	−0.008	0.98
Dickcissel	21	0.286	0.36	0.392	0.45	32	0.215	0.47	0.402	0.49
Bobolink	24	−0.522	0.29	−0.793	0.37	33	0.279	0.19	0.309	0.27
Yellow-headed Blackbird	18	0.292	0.65	0.430	0.68	33	0.189	0.56	−0.473	0.28
Baltimore Oriole	18	−0.321	0.32	0.163	0.79	32	0.136	0.69	0.510	0.25

and Minnesota in our study, whereas the south-central United States has experienced a slight warming trend over the period of our study (NOAA, National Climatic Data Center; http://www.ncdc.noaa.gov/gcag/index.jsp).

Of the 44 species in our study, 24 (54.5%) exhibited significant trends toward earlier arrival over the study period in one or both states, and 10 (22.7%) showed consistent trends toward earlier arrival in both states. Early migrants (median FADs on or before 10 April), primarily short-distance migrants (Swainson's Hawks and Franklin's Gulls [*Leucophaeus pipixcan*] were notable exceptions), were more likely to show trends toward earlier FADs than later-migrating, long-distance migrants. The stronger response of early migrants relative to later, long-distance migrants in our study is consistent with the results of other studies (Zalakevicus and Zalakeviciute 2001, Butler 2003, MacMynowski and Root 2007; but see Jonzén et al. 2006). The stronger trend toward earlier arrival in short-distance migrants has been interpreted as a response to proximate local climate trends, whereas long-distance migrants far-removed geographically from local climate on breeding grounds and along the migratory route must rely more on predictable or larger-scale environmental cues (e.g., photoperiod and the North Atlantic Oscillation) for migration timing and are, therefore, less responsive to local climate variation (Butler 2003, MacMynowski and Root 2007).

In the northern prairie region, warmer winters should result in less ice on bodies of water, resulting in earlier ice-out and availability of open-water habitats. Warmer winters could also stimulate earlier bud-break and leaf flush in plants (Peñuelas et al. 2002, Marra et al. 2005). If birds are responding to local climate factors, and winter climate is warming while spring climate remains stable, then early migrants, especially those associated with water, would be expected to be disproportionately affected by warmer winters. Our results are consistent with that scenario because seven of the 10 species with significantly earlier spring arrival in both states are associated with aquatic habitats.

General trends toward earlier arrival and initiation of breeding by birds with recent periods of global warming have been documented in both Europe and North America (Crick 2004, Lehikoinen et al. 2004, Crick and Sparks 2006). However, much variability exists in early arrival trends among species and locations. Studies of migratory arrival timing that include at least 20 species with broad phylogenetic representation indicate that 18–48% of species show trends toward earlier arrival (Butler 2003, Murphy-Klassen et al. 2005, MacMynowski and Root 2007, Miller-Rushing et al. 2008a), and many species do not exhibit consistent earlier arrival among sites and studies. For example, Butler (2003) studied FADs of 103 species of migrants in New York and Massachusetts, and found that 43.7% of species arrived earlier in New York and 47.6% arrived earlier in Massachusetts, but only 27.2% arrived earlier at both sites. These data are qualitatively similar to ours, with 40.9% of species arriving earlier in South Dakota, 36.4% arriving earlier in Minnesota, but only 22.7% arriving earlier arrival in both states. Our results are also similar to those for another northern prairie location (Delta Marsh, Manitoba, Canada), where 26% of 96 species showed significant trends toward earlier arrival (Murphy-Klassen et al. 2005). Interestingly, of the 10 species showing consistent trends toward earlier arrival in both South Dakota and Minnesota in our study, eight were also included in the study by Murphy-Klassen et al. (2005; Turkey Vultures [*Cathartes aura*] and Swainson's Hawks were not included) and six of these species also showed significant or nearly significant trends toward earlier arrival in Manitoba (Tree Swallows [*Tachycineta bicolor*] and Yellow-rumped Warblers were exceptions). In contrast, Wilson et al. (2000) compared the periods from 1899–1911 and 1994–1997 and found little evidence for earlier arrival of migrants in Maine. Thus, even though general trends toward earlier arrival are apparent, much variability remains in the strength and pervasiveness of this trend.

The use of different measures of migratory arrival is one factor that could contribute to this variability (Sparks et al. 2001, 2005, Tøttrup et al. 2006). FADs are often the only information available about migratory phenology. FADs represent the far left tail of the total distribution of arrival times of a migratory population, but FADs are generally correlated with other measures of migration timing that incorporate the entire distribution of migration (e.g., mean, median, and quartiles), although they are not necessarily accurate predictors of other measures of migration timing (Sparks et al.

2001, 2005, Tøttrup et al. 2006). FADs are also more variable, more susceptible to outliers and errors associated with differential sampling efforts or changes in population size, and are typically more sensitive to climate change than other measures of migration timing, so they provide little information about trends in the total arrival distribution of a species (Møller and Merilä 2004, MacMynowski and Root 2007). However, FADs usually represent individual early-arriving males that are the territory-establishing sex for most bird species, and early-arriving individuals often show increased fitness (e.g., Moore et al. 2005). In addition, Sparks et al. (2001) argued that trends in one tail of the overall distribution will result in a change in the distribution even if the median remains unchanged, so they suggest that cautious use of FADs should reveal information about the response of migrants to climate change and that using FADs, when they are the only data available for a region, is preferable to not studying the impact of climate on migration phenology.

Potential bias in analyses of FADs may also stem from differences in observer effort or abilities. For example, if an increase in the number of observers increases the likelihood of detecting early-arriving individuals, then trends toward earlier arrival over time could be due to increased observer effort, rather than real trends toward earlier arrival (Butler 2003). Butler (2003) examined this potential bias, but found no significant difference in number of observers over time and concluded that bias due to differences in observer numbers was unlikely. We found an increase over time in the number of observers in Minnesota, but not in South Dakota. In addition, few multiple regressions identified number of observers as a significant effector of FAD and directions of the effect were not consistently in the predicted direction. The minor and inconsistent influence of observer number on FAD and the similar trends in early arrival between the two states, despite the different temporal trends in observer numbers, suggest that trends in arrival dates in our study are not explained by differences in observer effort, and likely represent true responses to climate change.

Observer skill level could also potentially impact FADs if more skilled observers are better able to detect birds. Bird identification skills among amateur observers have likely increased over the period of our study with an increase in bird-identification resources. However, we chose common, easily identified species for analyses and most species in our study exhibiting changes in arrival dates are large, conspicuous species, so changes in observer skill level probably explain little of the observed trends in arrival dates.

Changes in population size can also influence trends in arrival timing, particularly for FADs, with increasing populations more likely to result in earlier arrival and decreasing populations likely to show the opposite trend (Tryjanowski and Sparks 2001, Miller-Rushing et al. 2008a). Of the 28 species with stable population sizes in our study, 57% exhibited earlier arrival in at least one state, whereas, of the 10 species with increasing populations, 70% showed earlier arrival in at least one state, so species with stable populations were as likely as species with increasing populations to show earlier FADs. In addition, the only species showing consistent later arrival in both states was the Dickcissel and, although grassland habitats occupied by this species have decreased in availability since European settlement of the northern prairie, recent data suggest stable population sizes for this species in central North America (Sauer et al. 2008). Thus, population size alone does not appear to explain the trends in arrival dates in our study.

Of the 44 species in our study, 41% exhibited significant correlations between arrival date and local winter or spring temperatures. This percentage falls within the range for such correlations reported in other studies (range = 13–60%) where arrival dates were examined as a function of local climate (Sokolov et al. 1998, Marra et al. 2005, Murphy-Klassen et al. 2005, Wilson 2007, MacMynowski and Root 2007, Miller-Rushing et al. 2008a). Higher percentages of early-arriving than late-arriving species exhibited significant negative correlations between winter or spring temperatures and FAD in our study. These data suggest that a negative correlation between arrival dates of migrants and local temperature is a common phenomenon among migratory birds, but that the trend is stronger for early, short-distance migrants than for later, long-distance migrants. As noted previously, such results are consistent with the idea that migration timing for short-distance migrants is more responsive to local climate change than that for long-distance migrants.

Only Least Flycatchers and Rose-breasted Grosbeaks in Minnesota showed significant positive correlations with average daily temperature and both these species showed opposite trends in South Dakota. We have no explanation for the different trends in the two states for these two species, so it seems likely that the positive relationships for these species in Minnesota are statistical artifacts. The few positive relationships with temperature among the species in our study provide additional support for a general negative correlation between temperature and migratory arrival.

In summary, spring FADs for migrant birds in the northern prairie region generally trend toward earlier arrival during the period from 1971–2006. However, this trend is not apparent for all migratory species and early arriving species, particularly those associated with aquatic habitats, are responding most strongly to climate changes in this region. This is likely due to warmer winters that result in less ice formation and earlier availability and seasonal progression of open-water habitats. Thus, our results are consistent with those of other studies suggesting that the migratory timing of early arriving short-distance migrants is most affected by local climate change (Butler 2003, Murphy-Klassen et al. 2005, MacMynowski and Root 2007).

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