

Changes in Avian Spring Arrival Dates of 115 Species in the Central Appalachians over 127 Years

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Abstract

Global climate change affects many facets of avian ecology, such as shifts in breeding phenology and migration patterns. Migrating bird species respond to changes in climate by shifting their temporal patterns of spring migration. However, variation in species' responses exists based on various life history traits, which exposes some species to an increased risk of phenological mismatch. This study examined the spring arrival dates of 115 migrating species over 127 years (1889-2015) using archival sources in West Virginia, USA, making this research unique in the length of study, the high number of species studied, and the historical crowd-sourced observations analyzed. Of the 115 taxa, 45 showed significant negative slopes of spring arrival dates (arriving earlier in the spring) plotted against the year. In contrast, only nine species showed positive slopes (arriving later in the spring), albeit non-significant. The average advance of spring arrival date for all species was 1.7 days per decade, and an advance of 2.6 days per decade in species that showed significance. Arrival dates were associated with increasing spring temperatures—for each 1°C increase, the arrival date advanced by 0.81 days/decade. Several life history traits were linked to species that advanced their first arrival dates, including a shorter distance migrated to reach wintering grounds, increasing populations, and foraging habitat. Most avian species are advancing their spring arrival dates in response to climate change. However, the implications of earlier spring arrival are unclear. We draw attention to shifts in arrival dates and wintering ranges, leading to a possible increase in overwintering in the mid-latitudes of North America.

Keywords

Avian Migration, Climate Change, Historical Migration, Long-Term Dataset, Migration Phenology, Spring Arrival

1. Introduction

Phenological trends in plants and animals have been linked to changes in climate, including increased temperature (Butler, 2003; Mills, 2005; Vegvari et al., 2010; Kullberg et al., 2015; McDermott & Degroote, 2016), varying precipitation patterns (Studds & Marra, 2011), and more instances of climate extremes (La Sorte et al., 2016). These changes lead to an increased risk of phenological mismatches (McKinney et al., 2012), decreased reproductive success (Kerby & Post, 2013), and ultimately reduced biodiversity (Willis et al., 2008). Phenological mismatches, or decoupled phenologies, occur during species interactions, such as predator-prey or pollinator relationships, when the changes in the timing of one species' life history trait (e.g., the timing of insect emergence) (Anderson, 1997; Anderson et al., 2013) decrease the success of another dependent species (e.g., insect-foragers) (Crick, 2004; Both et al., 2006). These changes in climatic variables are linked to many facets of avian ecology, including shifts in breeding phenology (Both & Visser, 2001; Ahola et al., 2004; Visser et al., 2006; McDermott & Degroote, 2016), patterns of migration (Butler, 2003; Cotton, 2003; Visser & Both, 2005; Ellwood et al., 2010), and general distribution (Kullberg et al., 2015; La Sorte et al., 2016).

Migrating bird populations have been highlighted as a conservation concern (Langham et al., 2015) based on their complex life history strategies covering vast geographic areas, multiple habitat and land cover types, and various climatic pressures throughout the year. Given the myriad biotic and abiotic interaction opportunities presented to avian species each year, it follows that shifts in avian phenology can be attributed to several environmental variables (Both & Visser, 2001) and changes in vegetative phenology (Marra et al., 2005). Understanding which specific life history traits contribute to these shifts is essential for conserving these species.

Shifts in spring migration have been studied using first arrival dates (FADs) (Butler, 2003; Mills, 2005) or average arrival (Ellwood et al., 2010). Comparing the appearance of one species over time can reveal patterns of spring migration. Archival records have been used to collect the first arrival dates of migrants for temporal analyses in the past (Bradley et al., 1999; Butler, 2003; Ellwood et al., 2010; McKinney et al., 2012; Travers et al., 2015). Evidence exists that spring arrival is advancing due to several variables, including climatic factors such as increasing spring temperatures (Swanson & Palmer, 2009), increased spring precipitation (Arab et al., 2016), the North Atlantic Oscillation (Marra et al., 2005), increased temperatures in wintering grounds (Cotton, 2003), and changes in the

length of the growing season (Travers et al., 2015). Avian migrants that have advanced their spring arrival correlate with increased abundance trends, demonstrating survival benefits for highly adaptable species (Newson et al., 2016). There have been efforts to examine the factors relating to avian ecology and populations that would affect the timing of spring arrival, including changes in population sizes (Møller et al., 2008), foraging habitat (Butler, 2003), distance migrated (Kullberg et al., 2015; Gill et al., 2014), and sampling effort (Miller-Rushing et al., 2008).

The population status of migratory birds has interested birders and researchers for decades. Based on analyses of 426 species from The North American Breeding Bird Survey (1966-2011), 57% of bird species are experiencing population declines (Sauer et al., 2013). Of the 133 Neotropical migrants included in the study, 60% demonstrated negative trend estimates (Sauer et al., 2013), and these population declines were first noted several decades ago (Robbins et al., 1989). These population reductions have sometimes been largely attributed to deforestation and fragmentation in the tropics (Robbins et al., 1989; Shaw et al., 2013), which reduces habitat for Neotropical migrants. Species that show declining populations over the study timeline could be deceptively arriving later due to decreased migration cohort sizes, leading to an underestimated change in FAD in these species (Miller-Rushing et al., 2008). A similar phenomenon occurs in species with increasing populations—a bird's spring arrival date is likely to be detected earlier with increased population sizes (Tryjanowski & Sparks, 2001). Therefore, population status is an essential factor in explaining historical migration patterns.

The distance traveled between the wintering grounds and breeding grounds differs among avian species. Migrations vary from 35,000 km for the Arctic Tern (*Sterna paradisaea*) that flies between the Arctic and Antarctic to less than 1000 km for some populations of the Dark-eyed Junco (*Junco hyemalis*) that migrate only to higher elevations for breeding. The cues associated with the start of migration differ depending on the distance migrated each year. Short-distance migrants that winter close to the breeding grounds are more inclined to follow changes in day length (Marra et al., 2005) and seasonal climatic shifts (Miller-Rushing et al., 2008). In contrast, species near the equator would not be affected by photoperiod or weather at the breeding grounds (Jonzén et al., 2006). Long-distance migrants rely on circannual rhythms to cue their migration (Both & Visser, 2001; Gwinner, 1996). These different migration strategies could impact species' flexibility to respond to environmental changes. Advancement of spring arrival is greater in short-distance migrants than long-distance migrants (Butler, 2003; Mills, 2005; Vegvari et al., 2010; Sauer et al., 2013; Bitterlin & Buskirk, 2014), with few exceptions (Jonzén et al., 2006). Categorizing species by the distance migrated each year could bring insight into the factors affecting avian migration.

Another factor that could contribute to changing population sizes and affect migration patterns is foraging habitat. Habitat destruction is a leading cause of

declining avian populations (Gilroy et al., 2016), so species occupying particular habitats may have experienced increased pressure from habitat loss, which could affect their ability to respond to environmental cues. Some studies indicate that habitat affects changes in migration time (Butler, 2003), while others show no significant effect on timing (Vegvari et al., 2010; Miller-Rushing et al., 2008), which supports the need for more research into this topic. Foraging habitats could also offer insight into species interactions affecting spring arrival. For example, species that rely on insects as their main foraging item could suffer an increased risk of phenological mismatch if the insect populations respond differently to changes in local climate (Robinnet & Roques, 2010) or are more responsive to changes in climate because they depend on the emergence of their prey (Anderson, 1997; Anderson et al., 2013). Avian migrants with a more generalized diet advance their FADs more than species with specialized diets (Vegvari et al., 2010). If changes in FADs differ among species with different foraging niches, then increased conservation efforts could be identified for specific habitats.

This study analyzed FADs of 115 bird species over 127 years (1889-2015) to determine any shifts over time. Data were gathered as part of the West Virginia Climate History Project, a crowd-sourced effort to uncover long-term phenology data for the state of West Virginia, USA, by the West Virginia University Natural History Museum (Petruski et al., 2019, 2020). Historical FADs were considered to be the observations before 1970 when global surface temperatures began to increase (IPCC, 2014) steadily. Species were also analyzed by distance migrated, habitat, and population status to understand better the complicated ecological factors of avian life history and how they relate to spring arrival. We predicted an overall advancement of spring arrival dates across species, with variation depending on life history variables. Observations across species from higher elevations were predicted to be later in the spring compared to lower elevations, and years with warmer spring temperatures were expected to have earlier first-arrival observations. Short-distance migrants were expected to advance their first arrival dates more than long-distance migrants, species with increasing populations to have advanced more than species with decreasing populations, and species associated with threatened habitats or insectivorous diets to advance their spring arrival less than species occupying more stable habitats or diets other than insects or other invertebrates.

2. Materials and Methods

2.1. Study Area

West Virginia is a heavily forested, mountainous state in the Appalachian region of the United States. Temperature, elevation, and precipitation differ considerably throughout the state. The average statewide yearly temperature is 6°C - 17°C, where the lower southern regions are warmer than the mountainous regions. The average elevation is 457 m, with the highest point (Spruce Knob) at 1482 m

and the lowest (Harper's Ferry) at 149 m above sea level. Annual precipitation ranges between 81 and 132 cm statewide. West Virginia is 79% forested, and the forests are 94% deciduous hardwoods. Oak-hickory (*Quercus* spp.-*Carya* spp.) forest type covers 74% of West Virginia forestlands, followed by northern hardwood forest type (18%) (Morin et al., 2017). West Virginia has eastern hemlock (*Tsuga canadensis*) and red spruce (*Picea rubens*) forests in high elevations. The rich avian diversity of West Virginia offers itself well to studying phenology (Forcey & Anderson, 2002a; Veselka et al., 2010; Anderson & Chadbourne, 2015; Clipp et al., 2017; Bailey & Rucker, 2021; Becker et al., 2022).

2.2. Historical Observations

Observations of first arrival dates were gathered from multiple sources: Earl Brooks and his colleagues (1890-1916), members of the Brooks Bird Club (1929-2008), George Breiding (1955-2006), and members of the online birding community eBird (2003-2015) in the state of West Virginia (Table 1). The FADs for spring migrants were taken from the personal records of Earl Brooks and George Breiding, from the publication of the Brooks Bird Club, The Redstart, and eBird's "First of the Year" spreadsheet. Daily temperatures were obtained through the United States Historical Climatology Network from 13 climate stations in West Virginia between 1879-2015 (Williams et al., 2007) (Figure 1).

The spring arrival date was assumed to be closely associated with each species' first-of-the-year sighting. Earl Brooks was a student at West Virginia University, class of 1897, who collected ornithological data, including first arrival dates, between 1889 and 1916. These observations eventually were compiled into 40 Common Birds of West Virginia, a book considered a pioneering classic in the field of ornithology, along with several publications between 1900 and 1916. The handwritten lists Brooks and his coworkers collected are archived at the West Virginia Regional History Center in Morgantown, West Virginia. The observations were in Clay, Marion, Lewis, Kanawha, Mineral, Upshur, and Wood counties (Figure 1).

The Brooks Bird Club is a nature club that has operated in West Virginia since 1932. Starting in 1933, the Brooks Bird Club released a newsletter to the club's members called The Redstart. This newsletter, which is still in operation today,

Table 1. Sources used to find historical first arrival dates of migrating bird species in West Virginia, USA from 1890-2015.

Collector	Location of record	Type of record	Timeframe	No. of observations
Earl Brooks	West Virginia Regional History Center	Handwritten ornithological notes of breeding and migration	1890-1916	674
Brooks Bird Club	West Virginia Regional History Center	Printed spring bird arrival dates from the <i>Redstart</i>	1929-2008	4023
George Breiding	Personal Collection	Handwritten and typed lists of arrival dates	1955-2006	729
eBird	https://ebird.org/home	Spreadsheet of first-of-the-year sightings	2003-2015	1101
Total			1890-2015	6527

Species were categorized by population status (increasing, decreasing, or steady), distance migrated (short- or long-distance), and foraging habitat (aerial, grassland, scrub, forest, or wetland) (Tables 2-4). The population status of each species was determined using data from the Breeding Bird Survey (1966-2011) (Sauer et al., 2013). A short-distance migrant was primarily wintering in the southern United States, Mexico, into the Caribbean. A long-distance migrant primarily wintered south of the Caribbean. Each species was assigned one of five habitat categories (forest, wetland, aerial, scrub, grassland) based on its primary feeding habitat (Forcey & Anderson, 2002a, 2002b; Butler, 2003; Kahler & Anderson, 2006; Veselka et al., 2010; Anderson & Chadbourne, 2015; Clipp et al., 2017; Bailey & Rucker, 2021; Becker et al., 2022).

Table 2. Species that demonstrated significant trends towards earlier first arrival dates (FADs) in West Virginia, USA. Habitat is denoted by f (forest), w (wetland), a (aerial), s (scrub), and g (grassland). Population status is denoted by + (increasing), - (decreasing), and = (steady). Distance is categorized by short-distance migrants (primarily wintering north of the Caribbean) or long-distance migrants (primarily wintering south of the Caribbean). Historical FAD is the average arrival date before 1970, and current FAD is the average arrival date of 1970 or after. Species are listed by change in days from highest to lowest.

Species	Common Name	n	Slope	Status	Distance	Habitat	Historical FAD	Current FAD	Change in Days
<i>Setophaga pinus</i>	Pine Warbler	32	-0.553	+	Short	f	16-Apr	11-Mar	36
<i>Tachycineta bicolor</i>	Tree Swallow	49	-0.66	-	Short	a	15-Apr	11-Mar	35
<i>Vireo solitarius</i>	Blue-headed Vireo	61	-0.38	+	Short	f	25-Apr	31-Mar	25
<i>Ardea herodias</i>	Great Blue Heron	17	-0.764	=	Short	w	29-Mar	4-Mar	25
<i>Dendroica coronata</i>	Yellow-rumped Warbler	68	-0.271	=	Short	f	20-Apr	28-Mar	23
<i>Charadrius vociferus</i>	Killdeer	21	-0.354	-	Short	g	16-Mar	23-Feb	22
<i>Anas discors</i>	Blue-winged Teal	38	-0.288	=	Short	w	9-Apr	19-Mar	21
<i>Setophaga virens</i>	Black-throated Green Warbler	92	-0.216	=	Long	f	25-Apr	4-Apr	21
<i>Rallus limicola</i>	Virginia Rail	17	-0.665	=	Short	w	4-May	14-Apr	20
<i>Passerculus sandwichensis</i>	Savannah Sparrow	54	-0.538	-	Short	g	15-Apr	26-Mar	20
<i>Petrochelidon pyrrhonota</i>	Cliff Swallow	37	-0.23	-	Long	a	3-May	13-Apr	20
<i>Pandion haliaetus</i>	Osprey	31	-0.637	+	Long	w	18-Apr	30-Mar	19
<i>Setophaga dominica</i>	Yellow-throated Warbler	54	-0.494	+	Short	f	24-Apr	6-Apr	18
<i>Stelgidopteryx serripennis</i>	Northern Rough-winged Swallow	62	-0.362	=	Short	a	16-Apr	29-Mar	18
<i>Geothlypis trichas</i>	Common Yellowthroat	61	-0.203	-	Long	s	29-Apr	12-Apr	17
<i>Pheucticus ludovicianus</i>	Rose-breasted Grosbeak	60	-0.279	-	Long	f	5-May	18-Apr	17
<i>Tyrannus tyrannus</i>	Eastern Kingbird	72	-0.283	-	Long	f	1-May	16-Apr	15
<i>Actitis macularius</i>	Spotted Sandpiper	55	-0.149	-	Short	w	24-Apr	11-Apr	13
<i>Tringa solitaria</i>	Solitary Sandpiper	39	-0.229	=	Long	w	1-May	18-Apr	13
<i>Setophaga americana</i>	Northern Parula Warbler	81	-0.173	+	Long	f	28-Apr	16-Apr	12
<i>Chroicocephalus philadelphia</i>	Bonaparte's Gull	28	-0.327	+	Short	w	11-Apr	31-Mar	11
<i>Seiurus aurocapilla</i>	Ovenbird	84	-0.121	=	Short	f	30-Apr	19-Apr	11

Continued

<i>Buteo platypterus</i>	Broad-winged Hawk	57	-0.186	+	Long	f	18-Apr	8-Apr	10
<i>Contopus virens</i>	Eastern Wood Pewee	67	-0.2	-	Long	f	7-May	27-Apr	10
<i>Hirundo rustica</i>	Barn Swallow	90	-0.209	-	Long	a	17-Apr	6-Apr	10
<i>Mniotilta varia</i>	Black and White Warbler	95	-0.133	-	Long	f	21-Apr	11-Apr	10
<i>Vireo flavifrons</i>	Yellow-throated Vireo	89	-0.148	+	Short	f	27-Apr	17-Apr	10
<i>Butorides virescens</i>	Green Heron	62	-0.169	-	Short	w	24-Apr	14-Apr	10
<i>Podilymbus auritus</i>	Horned Grebe	21	-0.532	=	Short	w	1-Apr	22-Mar	10
<i>Icterus galbula</i>	Baltimore Oriole	87	-0.086	-	Long	f	28-Apr	18-Apr	9
<i>Piranga olivacea</i>	Scarlet Tanager	83	-0.184	-	Long	f	27-Apr	18-Apr	9
<i>Setophaga citrina</i>	Hooded Warbler	84	-0.145	+	Short	f	28-Apr	19-Apr	9
<i>Toxostoma Rufum</i>	Brown Thrasher	83	-0.187	-	Short	s	9-Apr	31-Mar	9
<i>Archilochus colubris</i>	Ruby-throated Hummingbird	69	-0.255	+	Long	f	3-May	25-Apr	8
<i>Helmitheros vermivorus</i>	Worm-eating Warbler	74	-0.095	=	Short	f	29-Apr	21-Apr	8
<i>Leiostylypis ruficapilla</i>	Nashville Warbler	74	-0.088	=	Long	f	2-May	24-Apr	8
<i>Vermivora cyanoptera</i>	Blue-winged Warbler	77	-0.177	=	Long	s	29-Apr	21-Apr	8
<i>Cardellina Canadensis</i>	Canada Warbler	57	-0.088	-	Long	f	12-May	5-May	7
<i>Setophaga cerulea</i>	Cerulean Warbler	77	-0.117	-	Long	f	29-Apr	22-Apr	7
<i>Setophaga pensylvanica</i>	Chestnut-sided Warbler	80	-0.103	-	Long	s	3-May	26-Apr	7
<i>Setophaga Ruticilla</i>	American Redstart	91	-0.122	=	Long	f	29-Apr	22-Apr	7
<i>Poliophtila caerulea</i>	Blue-gray Gnatcatcher	93	-0.202	+	Short	f	16-Apr	10-Apr	6
<i>Vireo gilvus</i>	Warbling Vireo	87	-0.078	-	Long	f	27-Apr	21-Apr	6
<i>Passerina cyanea</i>	Indigo Bunting	71	-0.124	-	Long	g	1-May	26-Apr	5
<i>Chaetura pelagica</i>	Chimney Swift	83	-0.083	-	Long	a	16-Apr	12-Apr	4

Table 3. Species that demonstrated non-significant, later trends in first arrival dates (FADs) in West Virginia, USA. Habitat is denoted by f (forest), w (wetland), a (aerial), s (scrub), and g (grassland). Population status is denoted by + (increasing), - (decreasing), and = (steady). Distance is categorized by short-distance migrants (primarily wintering north of the Caribbean) or long-distance migrants (primarily wintering south of the Caribbean). Historical FAD is the average arrival date before 1970, and current FAD is the average arrival date of 1970 or after. Species are listed by change in days from highest to lowest.

Species	Common Name	n	Slope	Status	Distance	Habitat	Historical FAD	Current FAD	Change in Days
<i>Lanius ludovicianus</i>	Loggerhead Shrike	14	0.045	-	Short	s	4-Apr	21-Mar	14
<i>Empidonax flaviventris</i>	Yellow-bellied Flycatcher	15	0.001	=	Short	f	15-May	12-May	3
<i>Piranga rubra</i>	Summer Tanager	38	0.018	=	Long	f	25-Apr	26-Apr	-1
<i>Ammodramus henslowii</i>	Henslow's Sparrow	27	0.035	-	Short	g	2-May	5-May	-3
<i>Botaurus lentiginosus</i>	American Bittern	38	0.094	=	Short	w	21-Apr	27-Apr	-6
<i>Euphagus carolinus</i>	Rusty Blackbird	18	0.1	-	Short	w	16-Mar	25-Mar	-9
<i>Limnothlypis swainsonii</i>	Swainson's Warbler	35	0.145	=	Short	f	26-Apr	6-May	-10
<i>Oxyura jamaicensis</i>	Ruddy Duck	11	0.177	=	Short	w	25-Mar	13-Apr	-19
<i>Molothrus ater</i>	Brown-headed Cowbird	46	0.027	-	Short	g	27-Mar	15-Apr	-19

Table 4. Species that demonstrated non-significant but earlier trends in first arrival dates (FADs) in West Virginia, USA. Habitat is denoted by f (forest), w (wetland), a (aerial), s (scrub), and g (grassland). Population status is denoted by + (increasing), – (decreasing), and = (steady). Distance is categorized by short-distance migrants (primarily wintering north of the Caribbean) or long-distance migrants (primarily wintering south of the Caribbean). Historical FAD is the average arrival date before 1970, and current FAD is the average arrival date of 1970 or after. Species that are bold would be significant if no Bonferroni corrections were used. Species are listed by change in days from highest to lowest.

Species	Common Name	n	Slope	Status	Distance	Habitat	Historical FAD	Current FAD	Change in Days
<i>Catharus guttatus</i>	Hermit Thrush	42	–0.2176	=	Short	f	17-Apr	20-Mar	28
<i>Gallinago delicata</i>	Wilson’s Snipe	19	–0.3399	=	Short	w	5-Apr	10-Mar	26
<i>Anas acuta</i>	Northern Pintail	12	–0.1426	–	Short	w	16-Mar	27-Feb	18
<i>Tringa Melanoleuca</i>	Greater Yellowlegs	29	–0.2798	+	Long	w	18-Apr	2-Apr	16
<i>Passerella iliaca</i>	Fox Sparrow	23	–0.4797	=	Short	f	3-Apr	21-Mar	13
<i>Nycticorax nycticorax</i>	Black-crowned Night Heron	20	–0.2558	=	Short	w	25-Apr	13-Apr	12
<i>Riparia riparia</i>	Bank Swallow	56	–0.0989	–	Long	a	30-Apr	19-Apr	12
<i>Tringa flavipes</i>	Lesser Yellowlegs	30	–0.2214	–	Long	w	23-Apr	12-Apr	11
<i>Melospiza georgiana</i>	Swamp Sparrow	26	–0.2629	=	Short	w	7-Apr	27-Mar	11
<i>Cathartes aura</i>	Turkey Vulture	22	–0.4018	+	Short	g	22-Mar	12-Mar	10
<i>Porzana carolina</i>	Sora	24	–0.1905	=	Long	w	3-May	23-Apr	10
<i>Chordeiles minor</i>	Common Nighthawk	59	–0.1793	–	Long	a	7-May	27-Apr	10
<i>Quiscalus quiscula</i>	Common Loon	30	–0.1816	=	Short	w	21-Apr	12-Apr	9
<i>Parkesia motacilla</i>	Louisiana Waterthrush	102	–0.1108	+	Long	f	8-Apr	30-Mar	9
<i>Melospiza lincolni</i>	Lincoln’s Sparrow	23	–0.513	–	Short	s	8-May	29-Apr	9
<i>Anas americana</i>	American Wigeon	20	–0.2624	–	Short	w	29-Mar	21-Mar	8
<i>Icterus spurius</i>	Orchard Oriole	72	–0.1237	–	Long	f	1-May	23-Apr	8
<i>Anas clypeata</i>	Northern Shoveler	28	–0.1871	+	Short	w	26-Mar	19-Mar	7
<i>Fulica americana</i>	American Coot	21	–0.2159	=	Short	w	8-Apr	1-Apr	7
<i>Setophaga striata</i>	Blackpoll Warbler	64	–0.1007	=	Long	f	12-May	5-May	7
<i>Protonotaria citrea</i>	Prothonotary Warbler	33	–0.2867	–	Long	f	4-May	27-Apr	7
<i>Vireo olivaceus</i>	Red-eyed Vireo	98	–0.0747	+	Long	f	28-Apr	21-Apr	7
<i>Setophaga palmarum</i>	Palm Warbler	36	–0.109	=	Short	f	29-Apr	22-Apr	7
<i>Setophaga castanea</i>	Bay-breasted Warbler	54	–0.0717	=	Long	f	12-May	5-May	7
<i>Dendroica caerulescens</i>	Black-throated Blue Warbler	68	–0.0837	+	Long	f	4-May	28-Apr	6
<i>Dolichonyx oryzivorus</i>	Bobolink	35	–0.138	–	Long	g	5-May	29-Apr	6
<i>Setophaga magnolia</i>	Magnolia Warbler	67	–0.0769	=	Long	f	7-May	1-May	6
<i>Spizella passerina</i>	Chipping Sparrow	60	–0.2345	–	Short	s	30-Mar	24-Mar	6
<i>Sayornis phoebe</i>	Eastern Phoebe	78	–0.2744	=	Short	s	22-Mar	17-Mar	5
<i>Empidonax minimus</i>	Least Flycatcher	62	–0.0939	–	Short	f	7-May	2-May	5
<i>Cardellina pusilla</i>	Wilson’s Warbler	49	–0.0907	=	Short	f	13-May	8-May	5
<i>Geothlypis philadelphia</i>	Mourning Warbler	28	–0.0901	–	Long	f	12-May	7-May	5

Continued

<i>Catharus fuscescens</i>	Veery	48	-0.048	-	Long	f	6-May	1-May	5
<i>Leiothlypis peregrina</i>	Tennessee Warbler	77	-0.0853	=	Long	f	6-May	2-May	4
<i>Setophaga petechia</i>	Yellow Warbler	102	-0.0777	-	Long	f	20-Apr	16-Apr	4
<i>Vireo griseus</i>	White-eyed Vireo	55	-0.1277	+	Short	s	23-Apr	19-Apr	4
<i>Progne subis</i>	Purple Martin	91	-0.1018	-	Long	a	6-Apr	2-Apr	4
<i>Empidonax virescens</i>	Acadian Flycatcher	58	-0.1097	-	Long	f	5-May	1-May	4
<i>Setophaga fusca</i>	Blackburnian Warbler	80	-0.0463	=	Long	f	2-May	29-Apr	4
<i>Parkesia noveboracensis</i>	Northern Waterthrush	28	-0.0654	=	Long	f	6-May	2-May	4
<i>Spinus tristis</i>	American Goldfinch	9	-0.3416	=	Short	s	12-Apr	7-Apr	4
<i>Geothlypis formosa</i>	Kentucky Warbler	82	-0.0693	-	Long	f	29-Apr	26-Apr	3
<i>Troglodytes aedon</i>	House Wren	80	-0.1039	=	Short	s	17-Apr	14-Apr	3
<i>Catharus ustulatus</i>	Swainson's Thrush	59	-0.0282	-	Long	f	3-May	30-Apr	3
<i>Scolopax minor</i>	American Woodcock	47	-0.1033	=	Short	f	19-Mar	16-Mar	2
<i>Caprimulgus vociferus</i>	Whippoorwill	66	-0.1193	-	Short	f	18-Apr	16-Apr	2
<i>Hylocichla mustelina</i>	Wood Thrush	106	-0.0588	-	Long	f	21-Apr	19-Apr	2
<i>Pooecetes gramineus</i>	Vesper Sparrow	56	-0.0845	-	Short	g	1-Apr	30-Mar	2
<i>Larus argentatus</i>	Herring Gull	13	-0.0392	-	Short	w	24-Mar	23-Mar	1
<i>Coccyzus americanus</i>	Yellow-billed Cuckoo	54	-0.0859	-	Long	f	6-May	5-May	1
<i>Sturnella magna</i>	Eastern Meadowlark	23	-0.0177	-	Short	g	9-Mar	8-Mar	1
<i>Icteria virens</i>	Yellow-breasted Chat	85	-0.0316	-	Short	s	1-May	30-Apr	1
<i>Myiarchus crinitus</i>	Crested Flycatcher	68	-0.0991	=	Short	f	26-Apr	25-Apr	1
<i>Spizella pusilla</i>	Field Sparrow	57	-0.0953	-	Short	g	24-Mar	23-Mar	1
<i>Coccyzus erythrophthalmus</i>	Black-billed Cuckoo	49	-0.0944	-	Long	f	7-May	7-May	0
<i>Setophaga discolor</i>	Prairie Warbler	45	-0.0486	-	Short	s	23-Apr	23-Apr	0
<i>Vermivora chrysoptera</i>	Golden-winged Warbler	69	-0.0179	-	Long	s	3-May	3-May	0
<i>Agelaius phoeniceus</i>	Red-winged Blackbird	36	-0.2551	-	Short	w	18-Mar	18-Mar	0
<i>Dumetella carolinensis</i>	Gray Catbird	91	-0.0292	-	Short	s	24-Apr	24-Apr	0
<i>Ammodramus savannarum</i>	Grasshopper Sparrow	54	-0.0126	-	Short	g	25-Apr	27-Apr	-2
<i>Setophaga tigrina</i>	Cape May Warbler	63	-0.0376	-	Long	f	5-May	8-May	-3

2.3. Statistical Analyses

Species with at least four years of historical arrival dates (before 1970) and at least five years after 1970 were included in the analyses, which included 6527 observations covering 52 of West Virginia's 55 counties. Most (31.5%) of the observations occurred in 1929-1949, 25% in 1990-2015, 21.9% in 1950-1969, 10.7% in 1970-1989, and 10.2% in 1889-1928. We performed three general calculations using these data: the change in FAD for each species, the average change over time across all species, and the difference between average historical and current FADs for each species. Historic FADs were considered observations

before 1970, and current FADs were calculated from 1970 to 2015. All analyses were performed in program R Version 3.2.1 (R Core Team, 2013) with package: Car (Fox & Weisberg, 2011) at alpha level 0.05, unless specified.

First, the Julian dates of the FAD for each species were regressed against year using a generalized linear model to assess changes in spring arrival for each species over time. Overall normality was confirmed using the Shapiro-Wilk test ($W = 0.99$, $P = 0.82$), and equal variances were documented using Levene's test ($F = 2.61$, $P = 0.34$). Bonferroni corrections were made to the alpha value based on the number of species in each Order (Table 5) to counteract the increased chance of incorrectly rejecting a null hypothesis that comes with multiple comparisons. Second, the slopes for all species were averaged to determine the average change in spring arrival. Lastly, average historical and current FADs for each species were calculated. Both the historical (Shapiro-Wilk test, $W = 0.92$, $P < 0.01$) and present (Shapiro-Wilk test, $W = 0.95$, $P < 0.01$) dates were non-normal with non-equal variances (Kolmogorov-Smirnov test, $D = 0.23$, $P < 0.01$) despite transformations. Therefore, the Wilcoxon signed-rank test assessed the difference between historical and current arrival dates. The Wilcoxon signed-rank test is a nonparametric version of the matched-pairs t-test that is robust to non-normality and unequal variances as long as the data distributions of the samples are similar (Kerby, 2014), which makes it suitable for these data.

A 3-way Analysis of Variance test (ANOVA) was used to determine differences among changes in spring arrival based on population status (increasing, decreasing, or steady), distance migrated (short- or long-distance), and foraging habitat (aerial, grassland, scrub, forest, or wetland) (Tables 2-4). A Shapiro-Wilks test was used to confirm a normal distribution ($W = 0.98$, $P = 0.15$), and a Kolmogorov-Smirnov test was used to verify equal variances ($D = 0.12$, $P = 0.052$).

Table 5. Bonferroni corrections were made to the alpha values (0.05) based on the number of species within an Order.

Order	Number of Species	Alpha Value	Significant Species
Gaviiformes	1	0.0500	0
Podicipediformes	1	0.0500	1
Pelecaniformes	4	0.0125	2
Cathartiformes	1	0.0500	0
Anseriformes	5	0.0125	1
Accipitriformes	2	0.0250	2
Gruiformes	3	0.0167	1
Charadriiformes	9	0.0056	4
Cuculiformes	2	0.0250	0
Caprimulgiformes	2	0.0250	0
Apodiformes	2	0.0250	2
Passeriformes	83	0.0006	32

Each year's average March-April temperature (C) was calculated using data from the United States Historical Climatology Network (Williams et al., 2007) for West Virginia stations and regressed against the average FAD for each year using a generalized linear model. Normality was confirmed using a Shapiro-Wilk test ($W = 0.99$, $P = 0.44$), and equal variances were documented using a Kolmogorov-Smirnov test ($D = 0.25$, $P = 0.08$). Average county elevation (m) was included for observations with county information, and elevation was regressed against arrival date using a generalized linear model. County-level data included 72.6% of the total observations ($n = 4743$). Normality was confirmed using a Shapiro-Wilk test ($W = 0.99$, $P = 0.73$). However, a Kolmogorov-Smirnov test revealed non-equal variances ($D = 0.35$, $P < 0.01$). Various transformations, including log and square root, did not improve results.

3. Results

Of the 115 taxa, 45 species showed significant negative slopes of spring arrival dates (arriving earlier in the spring) plotted against the year (Table 3). In contrast, only nine species showed positive albeit non-significant slopes (arriving later in the spring) (Table 4). The other 61 species showed negative, non-significant slopes (Table 5). The mean slope of arrival date against year is -0.17 , equivalent to an average change (\pm SD) in migration of 1.7 ± 1.6 days earlier every decade (Figure 2). Current arrival dates were significantly earlier than historical arrival dates ($W = 8479$, $P < 0.01$), and the average difference between historical and current arrival dates was 8.2 days across species. Passeriformes ($N = 5117$) was the most represented order, including 83 species.

Overall, there was a significant difference in change of arrival among species based on life history traits ($F_{22,92} = 1.998$, $P = 0.012$), based explicitly on population status ($F_{2,92} = 4.725$, $P = 0.011$) and distance migrated ($F_{1,92} = 4.036$, $P = 0.047$). Tukey's posthoc test results showed that species with increasing populations ($\bar{x} = -2.65$ days/decade, $SE = 0.167$) advance their spring migration significantly more than species with declining populations ($\bar{x} = -1.40$ days/decade, $SE = 0.018$). Short-distance migrants ($\bar{x} = -2.06$ days/decade, $SE = 0.026$) are advancing more than long-distance migrants ($\bar{x} = -1.40$ days/decade, $SE = 0.014$). Therefore, it is not surprising that short-distance migrants with increasing populations ($\bar{x} = -2.97$ days/decade, $SE = 0.156$) advance their FADs significantly more than long-distance migrants with declining populations ($\bar{x} = -1.29$ days/decade, $SE = 0.074$). There was also a significant interaction between distance migrated and foraging habitat ($F_{4,92} = 2.504$, $P = 0.046$). Long-distance migrants that forage in forests ($\bar{x} = -1.16$ days/decade, $SE = 0.074$) are not advancing their FADs as much as aerial foragers that migrated short distances ($\bar{x} = -5.11$ days/decade, $SE = 0.210$).

Between 1970 and 2014, average spring temperatures (March-April) in West Virginia increased ten times as much as they did between 1879 and 1970 (Figure 3). For every 1°C increase in average spring temperature in West Virginia between 1892 and 2014, the first average arrival date advanced by 0.81 days ($F_{1,6114}$

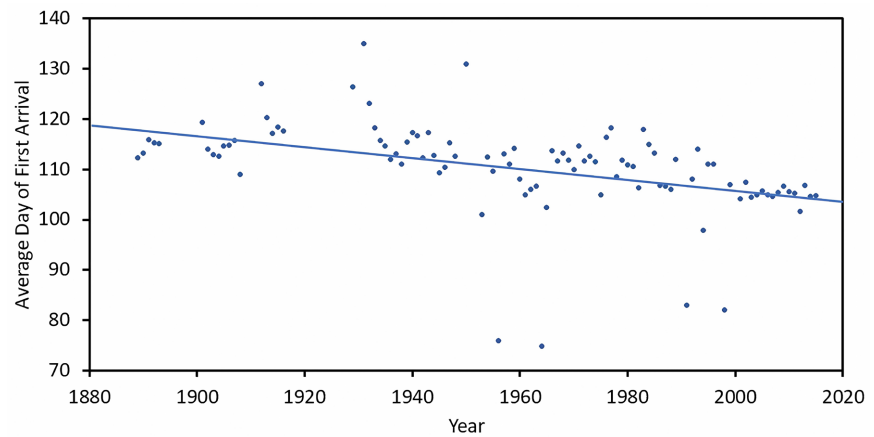


Figure 2. The average yearly first arrival date across 115 species in West Virginia, USA (1889-2015).

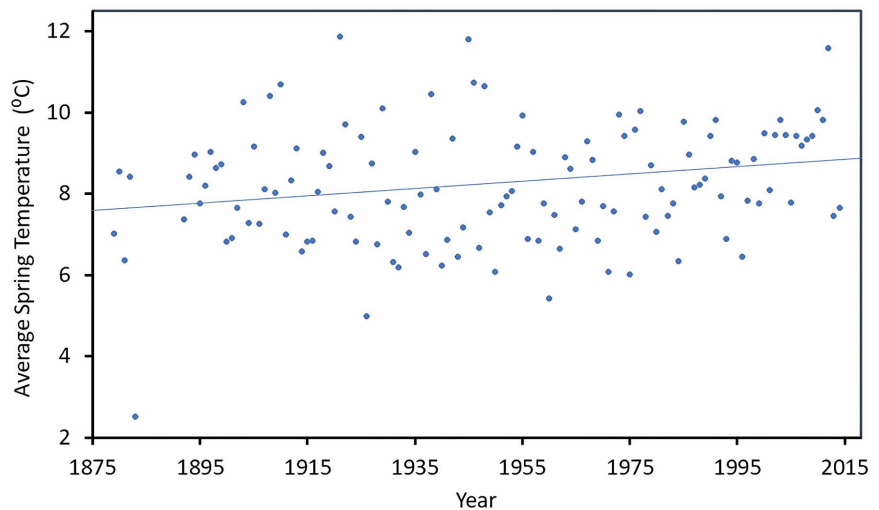


Figure 3. Mean March-April temperatures in West Virginia, USA (1879-2014). Data recorded by the United States Historical Climate Network.

= 28.7, $P < 0.001$, $N = 6115$). The average spring temperature in West Virginia over the last century ranged from 5.4°C (1960) to 11.6°C (2012) (**Figure 3**). Average county elevation affected FAD ($F_{1,4743} = 3.88$, $P = 0.049$, $N = 4743$). For each 1000 m increase in elevation, FAD advanced by 4.0 days. However, this result is minor, given the range of observations ($\bar{x} = 381$ m, $SE = 127.7$).

4. Discussion

The shift to earlier spring migration has substantial implications for the future of these 45 species. With the threats of climate change and habitat destruction (Root et al., 2003; Jetz et al., 2007), it is a concern that anthropogenic factors are changing global habitats too quickly for species to acclimate or evolve (Parmesan & Yohe, 2003; Crick, 2004). This research, however, demonstrates the plasticity of responses of some avian species and highlights several factors that could lead to increased risk to other species due to climate change. The average migrating

bird species arrive in West Virginia 1.7 days earlier each decade. Of the 115 species, 45 showed a significant trend towards earlier spring arrival, and zero showed a significant trend towards arriving later. West Virginia migrants from 12 orders indicated earlier spring arrival, demonstrating a definite pattern in spring migration.

Avian migrants ideally arrive at their breeding grounds early enough to compete for superior territory but not so early that foraging resources are unavailable. Individuals arriving too early experience harsh fitness consequences. However, arriving after competitors could also decrease reproductive success. Given that spring plant phenology, such as leaf-out, is advancing (Marra et al., 2005; Ellwood et al., 2010; Kelly et al., 2016) and the growing season has extended (Butler, 2003), the window of suitable spring arrival should also advance. Therefore, historically, individuals that may have arrived too early may be rewarded in recent years. Several life history traits were associated with species that advanced their spring arrival, but we also acknowledge the importance of species-specific responses to changes in climate (McDermott & Degroote, 2016).

Short-distance migrants are advancing their FAD more than long-distance migrants, which supports our predictions and the idea that short-distance migrants are more affected by local weather conditions and can better respond to changing local climates by advancing their arrival. This advantage allows short-distance migrants to decide on the timing of migration based on local weather conditions that more closely match the requirements at the breeding grounds. The increased plasticity of short-distance migrants has been well-documented (Butler, 2003; Miller-Rushing et al., 2008; Ellwood et al., 2010; Sauer et al., 2013). When comparing migration between long-distance and short-distance migrants, it is crucial to consider the cues associated with spring migration. Long-distance migrants depend on endogenous circannual rhythms to cue the beginning of their spring journey (Hagan et al., 1991), and short-distance migrants are more prone to use environmental cues (Miller-Rushing et al., 2008). The stopover length can also vary with local habitat quality and food abundance (Marra et al., 2005), contributing to the arrival date's plasticity. Long-distance migrants do have the ability to adjust their timing of arrival by altering their rate of migration to maximize resource availability based on ambient temperatures (Marra et al., 2005). However, since long-distance migrants are not advancing their spring migration at the same rate as short-distance migrants, long-distance migrants may be of increased conservation concern.

In line with our predictions, species with declining populations are not advancing their spring arrival dates as much as species with increasing populations. This result may be due to thriving populations having greater plasticity in their responses or underestimated arrival dates in declining populations. FADs are especially susceptible to bias due to the prevalence of decreasing populations (Miller-Rushing et al., 2008). However, the bias leads to mistakenly observing later arrival dates due to fewer individuals in a population available for detec-

tion. Therefore, any bias in the data due to population declines can be attributed to a conservative interpretation of the results.

Habitat alone was not a significant factor when analyzing FADs. These results are consistent with others' data (Miller-Rushing et al., 2008) but not all (Butler, 2003), who found that grassland species were not advancing their arrival as much as others. An interaction between foraging habitat and distance migrated highlighted a disproportionate advancement of FADs between long-distance migrants that forage in forested habitats and short-distance migrants that are aerial foragers. Aerial foragers could advance their spring arrival more than other foragers due to their dependence on insects, given that insects are highly responsive to local changes in climate (Robinet & Roques, 2010). However, species occupying forested habitats are also likely to be insectivores. Perhaps the prey insects of aerial foragers emerge sooner than insects in forested areas, which would drive the aerial foragers to arrive earlier. It may be due to observer bias, given that aerial species could be seen more efficiently and, therefore, earlier. Since there was not an overall difference in FADs between aerial foragers and other species occupying different habitat types, the significant difference is only noticeable in short-distance migrants that also have the benefit of increased plasticity to environmental change. The long-distance migrants that forage in forested habitats are advancing their FADs less than the average long-distance migrant.

The arrival dates were significantly related to decadal spring temperatures, supporting similar studies' conclusions (Ellwood et al., 2010; Swanson & Palmer, 2009). Advancing spring temperatures have been linked to advancing plant phenologies (Wang et al., 2015; Monahan et al., 2016; Petruski et al., 2019), making the resource availability window for habitat and forage earlier in the spring. This scenario would reward earlier-arriving individuals and successfully explains the trend of earlier arrival for most avian migrants (especially short-distance migrants with increasing populations). Elevation had a surprising effect on FAD: as elevation increased, the FAD became earlier, which did not support our prediction. However, given the range of observed observations ($\bar{x} = 381$ m, $SE = 127.7$), this result could be the consequence of several issues, including the low number of observations at high elevations. Most observations with specific locations (and therefore, elevations) were in the years before 1970, which would bias the data towards later FADs, or a combination of both. The state of West Virginia is highly variable geographically, so we argue that more exact location information is needed. Using the average county elevation for observations does not capture enough of the variability in each county to make definite conclusions about the effect of elevation on spring arrival.

Several biases from the data sources have been considered in the results. It has been shown that increased observers result in seemingly earlier arrival dates (Courter et al., 2013; Arab et al., 2016). However, an argument for the integrity of the sources in this study can be made. All observers were experienced natu-

ralists who visited a variety of habitats to observe migrating species. Earl Brooks' notes were gathered by himself and several of his colleagues; the Brooks Bird Club, and eBird notes were compilations of observations from multiple observers; and most of George Breiding's lists were first-of-the-year sightings for where he worked in Oglebay Park, Wheeling, WV, which the staff and visitors to the park compiled. The observer skill, time taken each week for birding, and distance covered during observations are still relatively unknown. However, similar datasets have been analyzed together with reputable results (Ellwood et al., 2010; Travers et al., 2015).

Given that most avian migrants are advancing their spring arrival and, in some cases postponing autumn migration (Miles et al., 2017), a surge in the prevalence of individuals overwintering in the breeding grounds is increasingly possible (Kullberg et al., 2015; Newson et al., 2016), especially in short-distance migrants and species with increasing populations. This study included species such as the Eastern Bluebird (*Sialia sialis*), Brown Creeper (*Certhia americana*), Eastern Towhee (*Pipilo erythrophthalmus*), Common Grackle (*Quiscalus quiscula*), White-throated Sparrow (*Zonotrichia albicollis*), and White-crowned Sparrow (*Zonotrichia leucophrys*) that were not analyzed because only historical records of first arrival were found. These six species can now be found in West Virginia year-round, possibly due to increased temperatures, urbanization, or household feeder presence (Miller-Rushing et al., 2008). Further research on the potential of shifting wintering ranges would be necessary for the future management of avian migrants.

5. Conclusions

More than 39% of the birds we evaluated arrive in West Virginia earlier in the spring than historical arrival dates. These species are adapting to climate change and likely taking advantage of the early onset of appropriate conditions. Species most at an increased risk of phenological decoupling and reduced success due to unchanging spring arrival include long-distance migrants and species with decreasing populations, especially those species that fall into both categories, such as the Cerulean Warbler (*Setophaga cerulea*) and Rose-breasted Grosbeak (*Pheucticus ludovicianus*). Species with these two characteristics were more likely not to have advanced their spring arrival. Responsiveness to changes in climate could predict a species' ability to survive in a global climate change scenario.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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