

Climate-related drivers of migratory bird health in the south-central USA

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ABSTRACT

Migratory birds are species of concern that play important ecological roles while also supporting recreational opportunities for the hunting and birdwatching public. Direct and indirect effects of climate variability, extremes, and change on migratory bird health manifest at the individual, population, species, and community levels. This review focuses on the effects of climate on migratory birds that spend part of their life cycles in the south-central USA. Although gaps in knowledge remain, prior studies provide a solid foundation to understand how climate affects migratory birds to inform management priorities and actions.

Key words: migratory birds, wildlife health, climate change, south-central USA, Central Americas Flyway.

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I. INTRODUCTION

(1) Background

An accumulation of anthropogenically produced and long-lived heat-trapping gases (i.e. anthropogenic greenhouse gases), resulting primarily from the burning of fossil fuels, has caused and will continue to cause Earth's atmosphere to warm (IPCC, 2021). This global-scale warming has generated an array of local-to-global impacts, including more days of extreme heat, greater moisture-carrying capacity of the atmosphere, changes in the strength and location of atmospheric jet streams and wind currents, and lengthening of the growing season (Marvel *et al.*, 2023). These physical changes disturb ecosystems, habitats, and the life they support (McElwee *et al.*, 2023), thus creating additional challenges and opportunities for wildlife and natural resource managers.

Migratory birds – birds that fly substantial distances between breeding and wintering grounds – are species of management concern that play important ecological roles and also support human activities such as hunting and bird-watching. Although their mobility may imply these birds are less affected by climate change than less-mobile species, vulnerability assessments that consider their entire annual cycle and multi-faceted life-history needs have revealed that this assumption is not necessarily true (Culp *et al.*, 2017).

In a changing climate, effects on migratory bird health may manifest at the individual, population, species, and community levels. These effects may be direct or indirect. Climate can directly affect vital statistics (e.g. breeding success, survival) and abundance *via* physiological stress from temperature changes or extreme storms. Individual birds have different sensitivities to different atmospheric variables (e.g. temperature, wind), and certain times during their life cycle (e.g. egg laying) or life stage (e.g. fledgling) are more sensitive than others (Jenouvrier, 2013). Age, sex, experience, body size, and other traits also interact with climate to complicate our understanding. Indirect effects can be more challenging to describe with clear causal connections, yet research suggests that they may be more detrimental than direct effects (Culp *et al.*, 2017). Indirect effects may include challenges associated with habitat changes, altered nutritional quality and availability, interactions within novel assemblages, or increased exposure or susceptibility to pathogens.

At the population and larger levels, climate change has been associated with changes in species abundance and distribution (e.g. Chuine, 2010), trophic mismatches (e.g. Jones & Cresswell, 2010), number of broods (e.g. Bulluck *et al.*, 2013), and different or more abundant disease vectors or invasive species (e.g. Van Hemert, Pearce & Handel, 2014). Migrant bird populations depend on conditions in their breeding and wintering grounds as well as on factors during spring and autumn migration (Sherry & Holmes, 1995). Because of the wide geographic range covered during their lifetimes, migratory birds may be more affected than other fauna by the faster rate of warming temperatures at high and mid-latitudes than

at low latitudes (i.e. Arctic amplification; Previdi, Smith & Polvani, 2021), especially during winter. Populations of the same species that breed, winter, or migrate across different locations can be subject to different climate conditions, resulting in different outcomes. To obtain or maintain robust and healthy populations of these migratory birds, it is important to understand how climate variability and change may affect any portion of their life cycle.

(2) Context for this review

This review is one component of a broader project conducted by the U.S. Geological Survey (USGS) and the University of Oklahoma through the South Central Climate Adaptation Science Center (CASC). Funded by the USGS, the South Central CASC is a 'partnership-driven program that teams scientists with natural and cultural resource managers and local communities to help fish, wildlife, water, land, and people adapt to a changing climate' (USGS, 2024) and serves managers in Louisiana, New Mexico, Oklahoma, and Texas. The broader project's objective was to begin assessing climate changes impacting or predicted to impact the health of migratory birds in the jurisdiction of the South Central CASC. We also conducted qualitative interviews of wildlife refuge managers across the region to document how they defined 'health' for migratory birds and what climate-related changes they observed (McPherson & Alger, 2020; not described here). Information gathered from this literature review and the interviews was used to construct conceptual diagrams of each refuge system (Alger, McPherson & Hofmeister, 2024; not described here) that highlighted critical determinants of health for migratory birds, landscape and hydroscape features, and relevant refuge management actions.

For this project, we reviewed the effects of climate variability and change on migratory birds that use the south-central USA as either breeding grounds, wintering grounds, or for stopovers during migration. The migratory birds using our four-state region during part of their life cycle can range hundreds to thousands of miles away from the CASC region across the Central Americas Flyway (Fig. 1). Yet their health throughout their ranges influences their health when using landscapes in these four states. Hence, we approach climate impacts from a holistic system perspective; it is possible to make connections (conceptually, if not empirically) between the health of populations or species and factors such as habitat quality, resource availability, anthropogenic land-use change, and novel direct and indirect effects of a changing climate (e.g. Stephen, 2014) wherever the birds live.

We acknowledge that the scope of work of wildlife managers limits them from tracking study subjects' health and climate change impacts outside of their jurisdiction. New data analytics capabilities (e.g. artificial intelligence, machine learning), however, can support innovations in migratory bird management that infuse dispersed data and knowledge about climate change and health stressors into place-based contexts useful for management decisions.



Fig. 1. Coverage of the Central Americas Flyway (encircled by red dashed line) used for migratory bird conservation and institutional collaborations (Lincoln, 1935; Boere & Stroud, 2006; BirdLife International 2010). Within the USA, the ‘central flyway’ and ‘Mississippi flyway’ (La Sorte *et al.*, 2014) are part of the Central Americas Flyway. Each of the world’s eight main flyways (inset map) represents pathways of groups of related bird species and spans their inbound and outbound migration routes (exemplified by black lines and arrows) between their northern breeding grounds and their southern wintering areas. The domain of the South Central Climate Adaptation Science Center (CASC) is shaded in blue. Figure adapted from BirdLife International (2010) (accessed 25 July 2024). Copyrighted; used with permission.

(3) Climate variability and change

Climate is the statistical representation of all weather observed in a particular area over an extended period of time (typically 30 years or longer), and anthropogenic climate

change has been detected since the start of the Industrial Revolution. Future climate change is projected using global climate models (GCMs) that adequately represent the physics of the atmosphere and, in more recent GCMs, its coupling to

physical processes in the ocean, cryosphere, and biosphere (IPCC, 2021). These numerical models are forced by broad-scale inputs (e.g. concentrations of various greenhouse gases) across different scenarios that represent possible future trajectories of human development and their impacts on the radiative energy input into Earth's atmosphere [e.g. representative concentration pathway (RCP)4.5 adds 4.5 Wm^{-2} of radiative forcing by 2100 relative to pre-industrial forcing]. GCMs output daily or sub-daily data that are aggregated into seasonal or annual products (e.g. total annual precipitation, winter minimum temperature).

The impacts of climate change, however, tend to be most evident at shorter timescales during climate extremes, as manifested by the weather – the atmospheric condition at a particular place and time. Hence, climatologists examine impacts not only from long-term trends but also from extremes, which also can be extracted from GCM output. Lessons learned from extreme events are useful when those events (e.g. droughts, heavy rainfall, heatwaves) are projected to become more frequent with climate change. This review follows that perspective, highlighting climate change signals that manifest as long-term changes (trends) or as climate extremes.

We categorise results from peer-reviewed literature into three main sections: breeding period, wintering (non-breeding) period, and migration, each of which is subdivided by effects on key health determinants according to the framework.

II. BREEDING PERIOD

During the breeding season, birds may build a nest, secure a mate, defend a territory, raise their young, and complete a moult. They may change habitats for different life stages, for example to protect post-fledgling juveniles better. Most migratory birds will arrive at their breeding grounds several weeks before they start laying their eggs, allowing them time to find resources, recover from their flight, build nests, and find a mate. Earlier arrivers generally occupy the best habitat, breed earlier than latecomers, and have the highest nest success rates but they also face higher risks (Newton, 2006), although for some species a combination of habitat quality and site fidelity is used to select territories (e.g. Lanyon & Thompson, 1986). Climate variability and change have negatively affected arrival, nesting, and reproduction in some populations, particularly when complicated by timing mismatches in the phenology of the populations and their food supplies (e.g. availability of seeds or flying insects). Behavioural plasticity – the ability of the bird to change its behaviour in response to environmental or other conditions – can aid some migratory birds in adapting to climate change.

(1) Direct impacts of climate change

Historical climate observations and future projections using GCMs indicate direct effects on near-surface air temperatures

across most land areas, including earlier arrival of spring warmth, later arrival of winter cold, warmer winters, warmer nights, and more days with seasonally extreme heat (IPCC, 2021). Warmer temperatures during late winter or early spring have been associated with earlier arrival of and nest initiation for some migrants (Hurlbert & Liang, 2012). Warmer temperatures on high-latitude breeding grounds also have been related to higher nest survival in prairie-nesting duck species (Drever & Clark, 2007).

(a) Arrival at breeding grounds

Early migrants may be exposed to colder temperatures or more variable weather conditions, leading to higher energy demands, lower food availability, and possible phenological mismatches with food or prey (Mayor *et al.*, 2017). Late arrival can risk poor nesting habitat, lack of available mates, hot extreme temperatures, or resource depletion leading to poor or no reproductive success (Pulido, 2007; Faaborg *et al.*, 2010; Newton, 2006).

For the migratory birds included in this review, in many cases arrival timing to the breeding grounds has changed as breeding grounds warm. Travers *et al.* (2015), for example, compared arrival dates for 83 spring migrant species at their nesting sites near Fargo, North Dakota. The mean value of accumulated growing degree units at time-of-arrival during 1910–1950 occurred 5 days earlier during 2001–2012. On average, the migrants arrived 4.5 days earlier during the 2001–2012 period as compared to 1910–1950, with more than half of the species arriving earlier. Although each bird species experienced this environmental change differently, warmer average temperatures on mid- to high-latitude wintering grounds may have prompted short-distance migrants to leave for breeding grounds earlier. Species arriving from the tropics, where temperature change has been less pronounced (IPCC, 2021), had fewer cues to trigger an early departure (e.g. Usui, Butchart & Phillimore, 2017).

Examples of past late-winter storm systems and low temperatures underscore the risk of early arrival that may lead to higher mortality rates or force reverse migration. For example, Brown & Brown (2000) documented a mass die-off event among cliff swallows (*Petrochelidon pyrrhonota*) in southwestern Nebraska in late May 1996, when a cold front brought unseasonably cold and wet conditions to the area for 6 days. Thousands of birds (an estimated 53–73% of the local population) perished while still nest-building or selecting colonies. These aerial insectivores likely starved because they only could forage when low-flying insects were active. Cliff swallow survivors had later arrival dates, on average, than those that died.

(b) Reproductive success

Climate variability also has been associated with changes in nesting dates and nest distribution. Although climate variability – the natural temporal deviations in the climate from its mean state – results from the internal dynamics of the atmosphere–ocean coupled system (e.g. El Niño, North American Monsoon),

any resulting interannual change in temperature, precipitation, or other atmospheric conditions can help anticipate avian responses to future trends in a warming world. For example, Raquel *et al.* (2019) used data from 164 nesting locations in the Canadian Prairie Pothole Region (southern Alberta, Saskatchewan, and Manitoba) from 1993 to 2011 to examine impacts of climate variability on nest survival of migratory ducks during the breeding season (Mar–Jun) and antecedent wintering season (Dec–Feb). In the study region, El Niño years generally were warmer and drier than other years, and these warmer breeding-season temperatures translated to earlier nesting dates for some species, but not others. Female mallard (*Anas platyrhynchos*), northern shoveler (*Spatula clypeata*), blue-winged teal (*Spatula discors*), and gadwall (*Mareca strepera*) responded strongly to warmer temperatures, but nesting dates in female northern pintails (*Anas acuta*) were only weakly related to temperature, possibly because they were among the earliest migrants to arrive. In contrast to other studies on long-distance migrants, the authors found that the blue-winged teal was more responsive than short-distance migrants in adjusting its nesting date relative to warmer winter conditions in this Canadian nesting region. There was no relationship found, however, between climate conditions and nest survival. Although the frequency of El Niño years remains within the range of natural variability (IPCC, 2021), the warming associated with these events in this region portends migratory bird responses as breeding-season temperatures warm due to climate change.

Birds have changed their period of egg laying as a result of warming temperatures, but plasticity in reproduction is species dependent. Using 50 years of data spanning breeding ranges across the continental USA and southern Canada, Torti & Dunn (2005) studied the effect of temperature on the egg-laying dates and clutch sizes of the American coot (*Fulica americana*), killdeer (*Charadrius vociferus*), American robin (*Turdus migratorius*), eastern bluebird (*Sialia sialis*), red-winged blackbird (*Agelaius phoeniceus*), and song sparrow (*Melospiza melodia*). Within the 1° × 1° latitude–longitude grid boxes used, spring temperatures increased during the 50-year period for locations of nesting killdeer, eastern bluebird, and red-winged blackbird. The killdeer and red-winged blackbird trended to earlier laying dates throughout the period, and the eastern bluebird laid its eggs earlier during the last 20 years of the period. Spring temperatures either did not change or cooled in the grid boxes where the other species laid eggs, and those species did not advance their laying dates. All species except the American coot and song sparrow laid eggs earlier during years with warmer springs. The authors suggested that some species may be less sensitive to temperature fluctuations than others, perhaps as a result of body size or dependency on food type, and this behaviour may result in a future mismatch between resource availability and egg laying.

Similarly, Shave *et al.* (2019) studied purple martins (*Progne subis*) using a 20-year data set to determine whether this long-distance migratory species responded to warmer breeding-ground temperatures by breeding earlier. They found that,

across the breeding range, the date when purple martins laid their first egg was not fixed, shifting earlier in response to spring warming, and the strength of this adjustment (selection for earlier breeding) was largest in the northern part of their breeding range, where temperature changes were greater (i.e. Arctic amplification). In addition, the study showed that purple martins that had earlier laying dates fledged more young than those that delayed egg laying. If individuals that nest earlier at higher latitudes do not migrate earlier during spring migration, however, these songbirds may face a constrained window of time to nest and lay eggs after arrival before temperatures warm beyond their ability to adjust.

Warmer temperatures or unseasonably hot temperatures also can have variable impacts. Using a 36-year data set of house wrens (*Troglodytes aedon*) in central Illinois during the breeding season, Bowers *et al.* (2016) indicated that warmer temperatures were associated with earlier breeding dates and warmer springs with shorter incubation periods and longer nesting duration. Other studies have demonstrated a decline in egg size over time, perhaps as a consequence of warming temperatures in the breeding grounds (e.g. Tryjanowski *et al.*, 2004). Skagen & Adams (2012) found that higher-than-normal mean temperatures on the day prior to laying the first egg resulted in decreased clutch sizes. However, higher average daily maximum temperatures during the breeding season were associated with higher survival of both eggs and nestlings to fledging age, possibly as a result of more insects and greater foraging success.

When faced with warmer temperatures on their breeding grounds, some species will change their geographic location rather than altering their reproductive timeline. Wysner *et al.* (2019) examined nesting behaviour of the western bluebird (*Sialia mexicana*) and ash-throated flycatcher (*Myiarchus cinerascens*) from 1997 to 2017 near the Jemez Mountains and Pajarito Plateau in northern New Mexico. They found that western bluebirds did not breed or hatch earlier, but they nested at higher elevations (average of 5 m per year) as temperatures increased. They noted that these results were consistent with climatic-niche conservatism – a hypothesis that a species will stay in the climate regime of its ancestors over time and space (Wiens *et al.*, 2010). On the other hand, ash-throated flycatchers did not change their elevation or hatching dates overall, and neither species had changes in their clutch sizes. Both species hatched earlier when spring precipitation was higher than normal.

Temperature is not the only climate driver that has influenced timing of egg laying; drought conditions also can influence these dates. For example, Brown & Brown (2014) examined the timing of cliff swallows laying their eggs, measured by the date of colony initiation (i.e. when the first birds settled at a colony site) at sites in southwestern Nebraska. They found that the strongest relationship between climate and the mean date of colony initiation was the Palmer Drought Severity Index (PDSI; Palmer, 1965), with larger negative PDSI values (i.e. more severe drought) associated with earlier colony initiation. The number of nests in a colony was positively related to earlier initiation dates. Hence,

the earlier breeding times over the 30-year study period were explained by increasing drought conditions rather than warming temperatures. More frequent or intense drought is projected by midcentury across much of the USA portion of the Central Americas Flyway (McPherson *et al.*, 2023; Knapp *et al.*, 2023).

Warming temperatures and reduced precipitation in parts of the south-central and southwest USA are expected to increase aridity (McPherson *et al.*, 2023; White *et al.*, 2023) and, thus, present breeding-season challenges for desert and dryland birds. Borgman & Wolf (2016) examined the reproductive success of loggerhead shrikes (*Lanius ludovicianus*) from 2007 to 2012 at Kirtland Air Force Base, southeast of Albuquerque, New Mexico, across a habitat characterised by juniper savanna, plain-mesa sand scrub, and desert grassland. Both residents and migrants used the breeding ground. Although nest initiation dates were significantly earlier for the years with the highest March–April mean maximum temperatures (2011 and 2012), neither temperature nor precipitation appeared to affect clutch size or the number of nestlings fledged. Nest success increased with more precipitation during the preceding winter (December–March) and, to a lesser extent, during the monsoon period (July–September), although they could not attribute this result to more available food. The authors also found significantly more breeding pairs of loggerhead shrikes during years with warmer temperatures and drought; however, they were unable to assess the cause.

(c) Survival

Heat, dry conditions, intense precipitation, and storms also have impacted nest survival in several species of grassland birds and shorebirds in the Great Plains. For example, ferruginous hawks (*Buteo regalis*) in the lowland sagebrush and prairie habitats of Wyoming had fewer fledglings when their territories experienced strong storms during brood rearing in June (Wallace *et al.*, 2016). Conway, Smith & Ray (2005) found that more clutch failures for snowy plovers (*Charadrius nivosus*) resulted from flooding and hail than from predation, and these weather-related causes accounted for almost the same amount of clutch failures for killdeer as predation. Population declines of lesser prairie chickens (*Tympanuchus pallidicinctus*) in Milnesand Prairie Preserve, New Mexico, during droughts were attributed to decreased nesting effort, increased nest abandonment, and decreased recruitment (Fritts *et al.*, 2018). Conrey *et al.* (2016) measured lower survival rates within season following days with either no rain or temperatures at or greater than 35 °C (95 °F). In addition, days with 10 mm of precipitation or more were associated with lower nest survival for ground-nesting horned larks (*Eremophila alpestris*) and thick-billed longspur (*Rhynchophanes mccoweni*) than for shrub- or taller-grass nesting species [i.e. chestnut-collared longspur (*Calcarius ornatus*), lark bunting (*Calamospiza melanocorys*), and western meadowlark (*Sturnella neglecta*)]. The number of hot days, length and intensity of drought, and frequency of heavy precipitation events are expected to increase in the future across most interior lands of the Central Americas Flyway (IPCC, 2021).

For hot, dry conditions, the only physiological mechanism for evaporative heat loss in passerine birds is panting, which is an inefficient cooling method as compared to gular flutter and cutaneous evaporation (e.g. McKechnie *et al.*, 2017). Smaller passerines also have been associated with a higher dehydration risk than larger passerines (Albright *et al.*, 2017). These physiological differences make small passerines particularly vulnerable to future climate change in parts of the south-central and southwest USA, where projections indicate a hotter and drier future (McPherson *et al.*, 2023; White *et al.*, 2023). Grasshopper sparrows (*Ammodramus saviannum*) in southeastern Arizona adapted to their hot, arid breeding grounds by delaying nesting until arrival of the mid-summer monsoon rains (Ruth & Skagen, 2018) and orienting their nests to the north and under grass clumps to reduce heat input (Ruth & Skagen, 2017). Ruth, Talbot & Smith (2020) found that these passerines foraged, nested, and lived on the ground primarily, but during sunny and hot conditions, ground temperatures in open spaces tended to be 15 °C or more hotter than in the shade. When air temperatures exceeded 35 °C, sparrows would abandon their territories; suspend foraging, defence, and advertisement; and seek thermal refugia with other sparrows in shrubs. This behaviour is beneficial temporarily, but a greater intensity and frequency of heatwaves associated with climate change (IPCC, 2021) may prevent birds from conducting their normal activities for longer periods of time, which could lead to deleterious effects.

(2) Indirect impacts of climate change

Climate change is combining with other stressors (e.g. invasive species, overgrazing, polluted runoff) to transform many terrestrial and freshwater landscapes through shifts in ecosystem structure and function, biodiversity loss, tree mortality, and other impacts (McElwee *et al.*, 2023). Although delineations of large-scale ecoregions (e.g. Level II ecoregions; CEC, 2021) remain as defined in recent decades (Fig. 2), changes in habitats have been documented.

Climate variability and extremes can cause abiotic disturbances that affect activities on breeding grounds, from nesting to foraging for food for fledglings. Disturbances include floods from intense rainfall or rapid snowmelt, landslides from excessive precipitation, or wildfire from extreme heat and drought. Climatologists project that extreme heat, drought, intense rainfall, heavy snowfall, and hurricanes will increase in frequency, intensity, or both throughout this century (IPCC, 2021). Extreme cold events are expected to become less frequent but could be more disruptive if they occur after birds arrive at the breeding grounds (Brown & Brown, 2000). Severe storms, hail, local winds, and other relatively small-scale events are more difficult to project into the future and are topics of ongoing research (Seneviratne *et al.*, 2012).

(a) Climate- and habitat-related trends

Wetland habitats, which already face stresses from urbanisation and agricultural land use, are expected to face additional

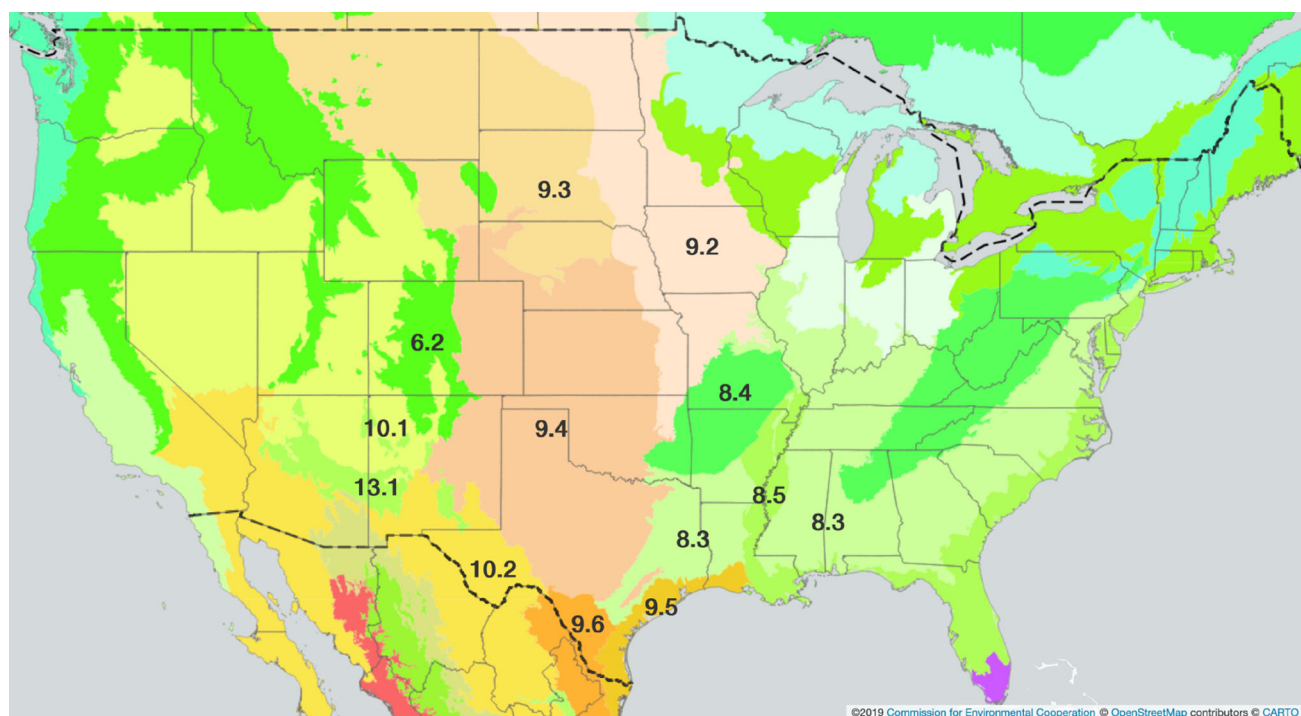


Fig. 2. Level II ecoregions and their associated codes (numeric values), as defined by the Commission for Environmental Cooperation (CEC, 2021). Those most relevant to the south-central USA include the Western Cordillera (code 6.2), Southeastern USA Plains (8.3), Ozark, Ouachita-Appalachian Forests (8.4), Mississippi Alluvial and Southeast USA Coastal Plains (8.5), Temperate Prairies (9.2), West Central Semi-Arid Prairies (9.3), South Central Semi-Arid Prairies (9.4), Texas–Louisiana Coastal Plain (9.5), Tamaulipas–Texas Semi-Arid Plain (9.6), Cold Deserts (10.1), Warm Deserts (10.2), and Upper Gila Mountains (13.1). Map created from the CEC North American Environmental Atlas using overlays from OpenStreetMap (under the Open Data Commons Open Database License). Copyrighted; used with permission.

challenges from climate change. Friggens & Finch (2015) applied an ecological niche model and climate projections [using three GCMs and one emissions scenario – Special Report on Emissions Scenarios (SRES) A2] to examine how changes in riparian habitats of the Rio Grande Basin in New Mexico might affect the breeding grounds of three Neotropical migrants: Lucy’s warbler (*Leiothlypis luciae*), southwestern willow flycatcher (*Empidonax traillii eximius*), and western yellow-billed cuckoo (*Coccyzus americanus*). Over time (1970–2013, 2020–2040, 2050–2070, and 2080–2100), suitable riparian habitat reduced in areal extent and was fragmented to higher elevations and wetland sites. Within the Rio Grande basin south of Albuquerque, New Mexico, woodland and forested habitats were projected to be replaced by semi-desert grassland and Chihuahuan Desert scrublands, reducing cottonwood-willow (Family: Salicaceae) habitats that all three species use for nesting. The authors noted that Bosque del Apache National Wildlife Refuge (NWR) and the wetlands surrounding Elephant Butte and Caballo reservoirs were expected to host suitable breeding habitats until the end of the 21st century.

Changes in upland forest habitats of New Mexico (and the Southwest USA) also have been rapid in the past few decades, with increasing risk of larger and more intense fire (Woolman *et al.*, 2022), insect infestations (Allen *et al.*, 2010), and drought

(Levesque & Hamann, 2022). In the drought of 2000–2002 across the Southwest USA, for example, stress on piñon pine (*Pinus edulis*) resulted in high mortality, as piñon engraver beetle (*Ips confusus*) attacked the trees and wildfire burned forests (Fair, Hathcock & Bartlow, 2018). Fair *et al.* (2018) found that, during the first half of June (breeding season), there were substantial reductions in bird richness, diversity, and abundance from 2003 to 2013, after mass mortality of piñon pine in the Pajarito Plateau, Los Alamos County, New Mexico. They hypothesised that some species moved to higher elevations nearby where tree mortality was lower, perhaps hindering future regeneration of the forest (and allowing non-native weeds to expand into these openings) because birds help re-seed piñon pines. In a three-year study of nest sites in piñon–juniper woodlands of Rattlesnake Canyon Habitat Management Area, San Juan County, New Mexico, Francis, Ortega & Hansen (2011) found that black-chinned hummingbirds (*Archilochus alexandri*) and gray flycatchers (*Empidonax wrightii*) (among others) nested in junipers (*Juniperus* spp.) disproportionately more than piñon pines even without any differences for nesting success. Both studies may signal an aversion to piñon pines because of their sensitivity to drought and insects, resulting in a large annual variation in piñon pine abundance (Breshears *et al.*, 2005).

Although most research has documented habitat trends in the past, there are studies that use output from GCMs as input to ecological models to project how a species may respond to habitat shifts in the future. For example, Bonnot *et al.* (2018) used a combination of an individual-based (i.e. agent-based) model and a dynamic-landscape meta-population model to project changes in reproduction of the Acadian flycatcher (*Empidonax virens*) in the Southeastern USA Plains and Ozark/Ouachita-Appalachian Forests ecoregions (Fig. 2) of the southern U.S. Midwest. Results indicated that both nest success and annual productivity declined in all future warming scenarios tested (i.e. RCP2.6, RCP4.5, and RCP8.5) using three GCMs [i.e. GFDL-CM3 (Delworth *et al.*, 2006); MRI-CGCM3 (Yukimoto *et al.*, 2012); CanESM2 (von Salzen *et al.*, 2013)]. Differences in the scenarios emerged after 2050. Productivity decreased by up to 30% in comparison to 2010–2020 levels in the warmest scenario (RCP8.5), resulting in a reduction of nest success by more than 60% and a productivity of less than one fledgling per female by 2100. Results signalled that the local population of this species in this region of temperate, hardwood forest could decline from an estimated 4 million breeding females in 2010 to near-extinction by 2100 in the warmest scenario. The models did account for how Acadian flycatchers re-nest after a failure, but also assumed that snake (i.e. the bird's main predator) populations will continue to increase unabated with warming – an assumption that may not be realistic.

(b) Climate variability and post-disturbance changes

Many of these studies examine interannual climate variability or extreme climate events to understand relationships among biological attributes and climate variables. For example, Skagen & Adams (2012) studied the impact of climate variability on the breeding performance of lark buntings, which breed in the central and northern Great Plains and winter in Texas, northern Mexico, and southern parts of Arizona and New Mexico. They found that a lower-than-normal precipitation total for April, May, and June (i.e. dry conditions) reduced clutch size, nest survival, and productivity (number of young fledged per successful nest). The authors conversely proposed that more precipitation led to larger food supplies and, thus, larger clutches, less time foraging, more time for parents to defend their nests, and better rates of fledgling success.

Warmer air has a greater moisture-carrying capacity than cooler air, increasing the risk of intense or extended rainfall events and associated flooding in a warmer world (Marvel *et al.*, 2023). Floods, whether initiated from extreme or greater-than-normal rainfall locally or upstream, have been associated with habitat changes that are especially troublesome for ground-foraging or understory-nesting bird species (e.g. Reiley, Benson & Bednarz, 2013). In addition to longer-term habitat alterations, flooding can cause acute crises including nest failure, territory abandonment, changes in the abundance of food and prey, and declines in litter, shrubs, and other understory matter in forests

(Klaus, 2004; Hoover, 2006; Benson & Bednarz, 2010; Reiley *et al.*, 2013). Swainson's warblers (*Limnothlypis swainsonii*) breed in bottomland hardwood forests across the lower basin of the Mississippi River and southeast USA, and they forage in understory litter (eBird, 2022) that is subject to occasional flood disturbance. Reiley *et al.* (2013) used data from 2004 to 2010 to assess species changes following major floods in early spring 2008 that affected breeding-ground habitats in the White River NWR and Saint Francis National Forest of Arkansas. They found that although the body condition of sampled Swainson's warblers increased from pre-flood to post-flood, this unpredicted result was most likely associated with more food availability on wintering grounds because of La Niña rains across the Caribbean and Central America. On their breeding grounds, however, apparent survival declined at both study sites in all years after the flood. The researchers were unsure whether the decline resulted from mortality, dispersal to other habitats, or lower abundance from causes at their wintering locations.

Projected to increase in frequency or intensity in the future (IPCC, 2021), heatwaves also can cause declines in reproductive success and increases in stress and mortality (Christman, 2002; Guthery *et al.*, 2005). When they co-occur, heatwaves and drought have resulted in a reduction of bird abundance by more than 15% predominantly due to relocation and adult mortality (Albright *et al.*, 2010a). Albright *et al.* (2010a) found the largest decline in abundance occurred in short-distance migrants during the post-fledgling period, perhaps because they were able to disperse to other habitats more readily. Reductions in abundance for ground-nesting birds were larger than those for total landbird abundance across most regions, especially in the Warm Deserts ecoregion (Fig. 2).

Drought is perhaps the most studied of climate disturbances in the south-central USA. Extreme drought has affected migratory bird species richness and abundance (e.g. Albright *et al.*, 2010a), reproductive success (e.g. Christman, 2002), and food quantity and quality (e.g. Kim *et al.*, 2008). As semi-arid lands in the southern Great Plains become drier (Seager *et al.*, 2018) due to climate change, more frequent and intense droughts are expected in the future (Overpeck & Udall, 2020). Cady *et al.* (2019) examined the impacts of drought on 10 common species in the southern Great Plains, including American robin, dickcissel (*Spiza americana*), grasshopper sparrow, horned lark, lark sparrow (*Chondestes grammacus*), mourning dove (*Zenaidura macroura*), scissor-tailed flycatcher (*Tyrannus forficatus*), and western kingbird (*Tyrannus verticalis*). They found that impacts over a 16-year period were related to bird species, drought timing, and drought spatial extent. Drought conditions during June negatively affected both American robins and western kingbirds, likely because of reduced availability of soft-bodied invertebrates (in hard soils) and flying insects. Scissor-tailed flycatcher, horned lark, dickcissel, and grasshopper sparrow species were most impacted by year-long drought conditions, perhaps as a result of reduced quantity or quality of plants and seeds. Dickcissels expanded their range northward during long, dry conditions

and also colonised previously unoccupied habitats within their core range.

For raptors, lower abundance of prey during drought affects the timing of nest initiation, brood size, and body condition. For example, Porro *et al.* (2020) studied nest initiation dates for burrowing owls (*Athene cunicularia*) across the central and southern Great Plains and northern Mexico from 1989 to 2017 and found that the probability of delayed nest initiation was higher when there were drought conditions (and, conversely, earlier initiation during wet conditions) on the wintering grounds or migratory stopover sites. Drought on wintering grounds may decrease food resources whereas drought during migration may impose additional energy requirements that necessitate more or longer stopovers. Although burrowing owls are opportunistic eaters, drought may limit rodents, reptiles, and insects, contributing to a decrease in all available prey. Similarly, Cruz-McDonnell & Wolf (2016) examined changes in a breeding population of burrowing owls in Kirtland Air Force Base, New Mexico, from 1998 to 2013 to determine if aridity and air temperature played roles in a significant population decline from 2008 to 2013 (from 49 breeding pairs to 1). Over the period there were trends indicating smaller broods and worsening body condition in both adults and nestlings. Changes in population size during the study period were associated with a combination of air temperature and precipitation changes, primarily through lower winter precipitation totals leading to reduced food supply during May and June. In addition, productivity and nest success declined as temperatures increased, precipitation decreased, and droughts became more severe. The authors suggested that their results might be attributed to reduced abundance of prey during drought and increased physiological stress, as temperatures exceeded 33 °C regularly during the nesting season.

Fires during drought conditions can have positive effects on available habitats for nesting years later. In March 2006, for example, intense wildfires burned more than 360,000 ha of shortgrass and mixed-grass rangelands in Roberts, Gray, and Donley Counties, Texas, resulting in a substantial reduction in woody vegetation (Roberts, Boal & Whitlaw, 2017). Comparing burned and unburned nesting sites for May–August of 2007 and 2008, Roberts *et al.* (2017) found that nesting success for most bird species was greater in burned areas than unburned sites, with few differences in nest placement between the two landscapes. These burned landscapes may have provided greater heterogeneity (as recovery from wildfire varies among vegetative species) that served more purposes during nesting than their unburned counterparts.

III. WINTERING (NON-BREEDING) PERIOD

As compared to the breeding season, less is known regarding how the climate affects migratory birds during wintering, primarily because of a lack of consistent data over space and

time (Faaborg *et al.*, 2010; Andersson *et al.*, 2015). Available studies on wintering, however, do indicate that migrants that use the highest-quality wintering habitats start their spring migration earlier, arrive earlier on breeding grounds, secure a good nesting site, and have higher breeding success (Newton, 2006).

(1) Climate- and habitat-related trends

Climate change has been suggested to affect the duration of wintering directly for some species, although this topic remains understudied and some results are inconclusive. Foster, Amos & Fuiman (2010), for example, examined the migration phenology of several coastal birds at Mustang Island, Texas, from 1978 to 2005. Birds using the barrier island during the winter included the double-crested cormorant (*Phalacrocorax auritus*), eared grebe (*Podiceps nigricollis*), and herring gull (*Larus argentatus smithsonianus*). Migrants wintering there stayed for less time over the 27-year period, although there was no correlation between local temperature and either arrival date, departure date, or stopover duration. Meehan *et al.* (2021), on the other hand, examined changes in the winter abundance of 16 species of dabbling and diving ducks that migrate through the eastern USA for winters from 1969–1970 to 2018–2019. Trends in species abundance were positive at higher latitudes and in inland or high-elevation areas. For 12 of the species, relative abundance trends were related to mean winter temperature, with warmer temperatures associated with decreasing abundance.

For long-distance migrants that winter in tropical regions, where climate variability tends to be less than that in temperate or cold climates (IPCC, 2021), long-term changes in temperature and precipitation could introduce novel climates that impact avian habitats (García-López & Allué, 2013), indirectly affecting avian health. La Sorte, Fink & Johnston (2018) projected the location and frequency of novel climates potentially encountered by 77 passerine migrant species that winter primarily in Central and South America and breed in North America. They applied the highest radiative forcing scenario (RCP8.5) and compared the late-century projections (2091–2100) to the 2007–2016 historical period. Interannual variability was higher and projected novel conditions were fewer for the temperate latitudes. Species that migrate east of the Rocky Mountains and winter closer to the equator were more likely to experience novel climates during the non-breeding season and the autumn transition to southward migration.

Studies have shown that the different rates of winter warming with latitude are resulting in alterations in the distribution of migratory birds during their non-breeding period. For example, from 1986 to 2010, observations of wintering bald eagles (*Haliaeetus leucocephalus*) decreased in the south-central USA (−2.2% in Arkansas; −0.9% in Louisiana; −1.7% in New Mexico; −1.2% in Oklahoma; −3.5% in Texas) and increased in most northern and Atlantic Coast states (by over 5% in some states) (Eakle *et al.*, 2015). These results are consistent with warming patterns and earlier

lake-ice breakup (Lopez, Hewitt & Sharma, 2019), increasing the availability of food during the winter.

Some migratory birds use similar climate regimes during both breeding and non-breeding seasons ('niche followers') while others ('niche switchers') use different climate regimes during their annual cycle (Nakazawa *et al.*, 2004). For example, Peña-Peniche, Ruvalcaba-Ortega & Rojas-Soto (2018) applied ecological niche modelling to examine the annual cycle of Baird's sparrow (*Centronyx bairdii*) from its breeding grounds in the northern USA and southern Canada to its wintering grounds in the Chihuahuan Desert in southwestern Texas and northwestern Mexico. They found that although Baird's sparrows continued to use grasslands year-round, the climate regimes used by the sparrows during breeding and wintering seasons largely did not overlap. In fact, more precipitation increased sparrow density during wintering but warmer temperatures increased sparrow density during the breeding season.

Changes in precipitation appear to be the largest driver of health and population changes for migrants wintering in subtropical or tropical climates. Using data from eBird and spatial modelling, La Sorte *et al.* (2017) estimated spatial patterns of 21 passerine species that wintered primarily in Central America's tropical and subtropical forests and migrated northward to temperate forests for breeding. They computed that species richness and bird density were greater on the wintering grounds than on the breeding grounds and that species stayed on the wintering grounds for about 200 days, on average. Increased warming was projected to affect the breeding grounds substantially more than the wintering grounds, possibly causing changes in the distribution of breeding populations or trophic mismatches. Wintering grounds, however, were expected to have considerably less precipitation during boreal summer, which might degrade the quality of these habitats for wintering.

(2) Climate variability and post-disturbance changes

The impacts of climate variability at a species' wintering ground can carry over to affect the species during migration or breeding (and *vice versa*) (e.g. Sæther, Sutherland & Engen, 2004). For instance, from 1961 to 2013, above-average winter precipitation in the Mississippi Alluvial Valley was associated with higher mid-continent breeding populations of mallards during the subsequent breeding season (Osnas *et al.*, 2016). The linkage between more precipitation during wintering and larger populations on breeding grounds was thought to result from an increase in high-quality foraging habitat, generated by occasional flooding of bottom-land hardwood forests (Sedinger & Alisauskas, 2014). These carryover effects, however, may be conflated with lag effects whereby climate variables such as temperature and precipitation may cause delayed responses in avian populations (e.g. melting of snow and ice may follow a heatwave).

Several studies show a positive feedback between conditions in winter habitats and spring breeding success (Fig. 3),

as documented by Faaborg *et al.* (2010). When winter habitats experience drought, dominant males force females and younger birds to lower-quality habitats where they suffer from poorer physical condition by spring. The healthiest adults can leave for, and arrive at, the breeding grounds earlier and enjoy higher reproductive success by outcompeting later arrivals for the best breeding-ground habitats. For example, American redstarts (*Setophaga ruticilla*) that experienced significant declines in food abundance (e.g. during dry years) on wintering grounds in Jamaica gained fat, perhaps to avoid starvation, but lost pectoral muscle – their main flight muscles. The food-reduced redstarts also delayed their departure date by an average of 3 days, which significantly reduced their reproductive success (Tonra, Marra & Holberton, 2013).

Changes in precipitation at wintering sites have been linked to changes in the physical condition of migrating birds, although research typically examined interannual precipitation differences rather than long-term trends. For example, using geolocation devices, several studies have shown that some species use multiple overwintering locations, possibly moving as food availability changes alongside seasonal rainfall patterns (Jahn *et al.*, 2013; Kardynal & Hobson, 2017; Mancuso *et al.*, 2021). Moon & Haukos (2006) studied northern pintails that wintered across parts of the USA, including the Playa Lakes region of the southern Great Plains, and documented that differences in body mass in wintering females were not associated with survival rates during a relatively wet year. Those pintails wintering during a dry year (when water was in fewer than 1% of the playas), however, exhibited a strong, positive relationship between body mass and survivability from October to March.

Spatial differences in winter-habitat moisture also affect body mass and spring migration timing. Smith, Reitsma & Marra (2010) found that daily differences in body-mass gain between wet habitats (i.e. mangrove) and dry habitats (i.e. dry forest) were insignificant for the northern waterthrush (*Parkesia noveboracensis*) in Puerto Rico; however, the accumulation of these differences from January to April was significant. Food availability was higher in the wet habitats, generally occupied by territorial males. Males that established these higher-quality home ranges recovered better from migration-related depletion of fat reserves and loss of protein mass in muscle tissue. The reverse was true in the dry habitats, leading to delays in spring migration departure that the authors attributed to delays in fattening.

Hurricanes also affect populations of wintering birds in the south-central USA. For instance, Stroud *et al.* (2019) used 22 years of paired data for lesser scaup (*Aythya affinis*) and molluscs to study the impact of hurricanes on the abundance of the wintering birds at Lake Pontchartrain, Louisiana. Hurricane-driven storm surges deposit a thick layer of sediment on the bottom of the lake, changing lake salinity and dissolved oxygen levels and causing mass mortality of molluscs – a major food source for the lesser scaup. The authors found that the year following a hurricane, however, the small- to medium-sized clams that were preferred by

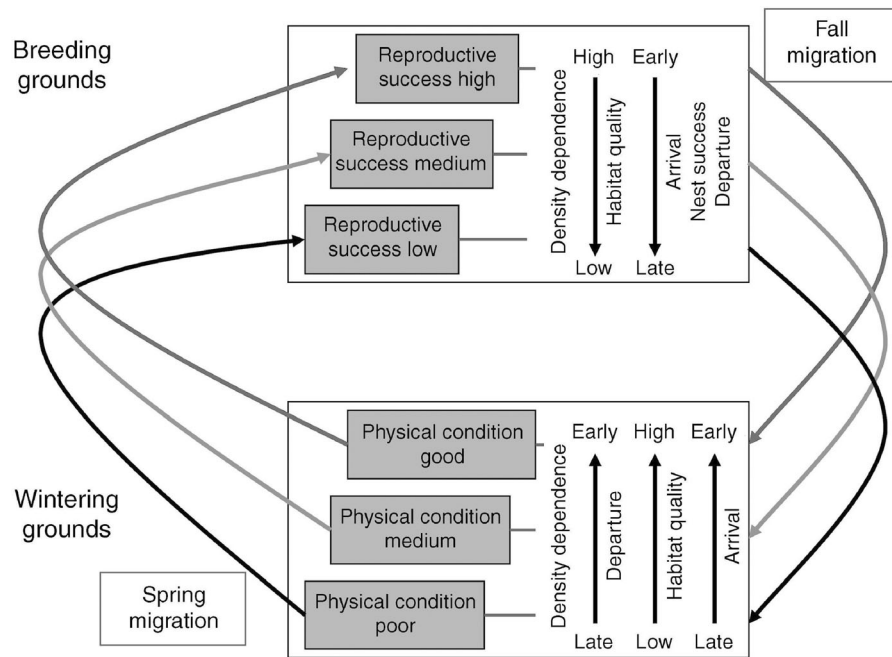


Fig. 3. Conceptual model illustrating a positive feedback between the habitat quality of a migrant's wintering grounds and its reproductive success in its breeding grounds. From Faaborg *et al.* (2010). Copyright 2010 by the Ecological Society of America; used with permission.

the birds had high levels of spawning. Hence, lesser scaup abundance declined during years with a nearby hurricane landfall and increased during the subsequent year.

IV. SPRING AND AUTUMN MIGRATION

Migration demands significant time (weeks to months) and the high amount of energy expended translates into a need for increased nutritional intake *en route*. Some populations that rest and refuel at stopover sites with high densities of other migrants competing for resources may have a reduced survival rate (Newton, 2006). Climate change has impacted stopover habitats, as atmospheric patterns change and new temperature and precipitation patterns alter the phenology of food sources (Parmesan *et al.*, 2022). Resource availability for migrating species is further challenged by changes in land use/cover due to agricultural production, urbanisation, deforestation, alteration of riparian habitats, and water management (Carlisle *et al.*, 2009). Whereas resident species receive year-round cues of weather and habitat conditions because of the proximity of their breeding and non-breeding grounds, migrants do not receive such information from afar. The risks are even greater for migrants that must develop exceptional reserves to cross long stretches with minimal or no food (e.g. Gulf of Mexico, Sonoran Desert) and for waterfowl and shorebirds crossing areas with limited wetlands, lakes, or reservoirs (e.g. Great Plains) (Newton, 2006). Hence,

mortality can be many times higher during migration than during other seasons (Sillett & Holmes, 2002; e.g. Carlisle *et al.*, 2009).

For many bird species, annual migration pathways are somewhat flexible depending on ground-resource availability for stopovers and winds in the lower troposphere, presumably to reduce energy consumption, flight time, or both (Alerstam, 1979; Marra *et al.*, 2005). Migratory birds that work to minimise their total flight time tend to refuel quickly at as few stopovers as possible, requiring high-quality forage conditions at refuelling sites (Gómez *et al.*, 2017). Migrants that try to minimise their total energy expended during migration tend to reduce their fuel loads both in transit and at the stopover sites; thus, they avoid long stretches of unsuitable stopovers (e.g. seas, deserts) and stop more often to refuel than those minimising their total flight time (Gómez *et al.*, 2017).

Water, food, and shelter change during and after extreme climate events (e.g. drought), some of which are projected to become more frequent, more intense, or both under most climate scenarios (IPCC, 2021). Environmental conditions during spring migration have been shown to affect arrival timing and body condition on breeding grounds, population density, nest success, and clutch size (Carlisle *et al.*, 2009). Large-scale, collaborative networks that track the migration of birds have helped to increase understanding of migratory patterns and the conditions that migrants experience; however, much is still unknown about weather impacts, food availability, parasites, diseases, and prey along migration routes (Bairlein, 2003).

(1) Direct impacts of climate change

(a) Timing of migration

Warmer temperatures have been the most obvious climate change over the past several decades worldwide (IPCC, 2021) and will impact ecosystems for decades to come (Sala *et al.*, 2000). This warming has extended the growing season across most of North America, providing an opportunity for spring food supplies to become available earlier. Satellite remote-sensing data indicate that ‘green-up’ has shifted earlier for many high- and mid-latitude locations (Badeck *et al.*, 2004; Park, Jeong & Peñuelas, 2020).

Numerous studies have shown timing changes in species migrations associated with a warming climate. For spring migration, the timing of both passage over or arrival at high-latitude locations is trending earlier overall, although annual variations (e.g. cold *versus* warm spring) affect some migrating species (e.g. Smith, Mabey & Moore, 2009). For instance, Jorgensen & Brown (2017) determined that whooping cranes (*Grus americana*) that migrate between Wood Buffalo National Park, Alberta, Canada, and Aransas NWR, Texas, migrate an average of 22 days earlier in spring and 21 days later in autumn than in the 1940s. Andersson *et al.* (2022) examined waterfowl data during January–March and October–December from 1955 to 2008 at 21 NWRs across Kansas, Nebraska, New Mexico, Oklahoma, and Texas. They demonstrated that some species advanced their date of peak spring-migration abundance, corresponding to warmer temperatures, and that these earlier dates were more likely as latitude increased. For autumn, delayed migration occurred twice as often as earlier migration. Similarly, Buskirk (2012) studied the migration timing over 15 or more years of 14 raptor species that migrated through the central USA; they documented earlier spring migration, especially for short-distance migrants, and later autumn migration for most raptor species. Research also has identified that some migrants do not travel as far as they once did – sometimes called ‘short-stopping’ – and these range shifts are occurring at an unprecedented rate (Elmberg *et al.*, 2014).

Not all migrating species are exhibiting earlier spring arrival, however. In fact, within the same species, arrival times at different locations may trend differently. Senner (2012) compared changes in arrival dates for two populations of Hudsonian godwits (*Limosa haemastica*) during 2008–2010: one that passed through the central USA during April to breed at Beluga River, Kenai Peninsula Borough, Alaska, and one that passed through the central USA during May to breed near Churchill, Manitoba, Canada (on the western shore of Hudson Bay). The southern Alaska location is warmed and moderated by the northern Pacific Ocean; thus, spring arrives earlier and more consistently than it does for the Manitoba location, with its high climate variability. The researcher found that the Alaskan population arrived about 9 days earlier than it did in the early 1970s whereas the Manitoban population arrived about 10 days later. They attributed the earlier Alaska arrival to warmer spring temperatures combined with a long-distance, non-stop flight from the population’s last stopover in Kansas or

Nebraska, using timing cues from prior years. Conversely, spring temperatures have cooled near Hudson Bay, and the Manitoban population have their last stopover as far north as southern Manitoba, gaining knowledge of local weather conditions near their breeding grounds before their last flight leg.

In some cases, the timing of mid-migration segments has not changed. For example, Horton *et al.* (2019) used weather radar and eBird datasets to quantify the timing of spring migrants arriving on the USA coast of the Gulf of Mexico, an important stopover for many Neotropical migrants. From 1995 to 2015, despite significant changes in vegetative greenness, the timing of peak arrival on the Gulf Coast remained constant for short- and long-distance migrants alike. Earlier arrivals on breeding grounds likely arose from quickening the remainder of their northward flight. Marra *et al.* (2005) showed that long-distance migrants increased their rate of migration northward from the Louisiana Gulf Coast during warm years, shortening the duration of their intracontinental voyage and timing passage with leaf and insect emergence.

(b) Use of winds

Birds generally migrate with supporting winds and in fair weather. Precipitation, strong headwinds, and clouds tend to suppress migration and delay take-off; long delays can cause migrants to take off into unsuitable winds (Shamoun-Baranes, Liechti & Vansteelant, 2017). Shamoun-Baranes *et al.* (2017) summarised that individual birds decide when to fly, where to fly, and how to fly for migration in response to weather conditions based on their type of flight, sex, experience, and physiological condition.

Soaring birds take advantage of convective thermals from daytime heating of Earth’s surface, moving from one thermal to another, at times several kilometres high during maximum daytime heating (Shamoun-Baranes *et al.*, 2017). Supportive horizontal winds at flight level aid these migrants to achieve higher daily ground speed and flight range. Large birds that expend vast amounts of energy flapping tend to use soaring strategies that maximise daytime thermal updrafts and rising motion along mountain slopes or in low-pressure systems to gain height and reduce energy consumption. For example, Gutierrez Illan *et al.* (2017) documented that although American white pelicans (*Pelecanus erythrorhynchos*) actively sought faster tailwinds in both spring and autumn migrations, they mainly used thermal updrafts during spring migration to arrive earlier at their breeding grounds. When clouds suppress thermals, soaring birds tend to delay departures. Generalist fliers (who can choose flapping or soaring) may reduce energy consumption by using a soaring strategy during the day and flapping during the early morning or after sunset (Shamoun-Baranes *et al.*, 2017). Warming surface temperatures associated with climate change are expected to support deeper thermals that should reduce energy consumption during migration.

Horizontal winds are more important than vertical winds for birds that flap their wings to migrate (Shamoun-Baranes *et al.*, 2017). Tailwinds increase the likelihood that birds will

take off from stopovers and may be particularly important for long-distance flights to reduce energy expenditure. During flight, migrants adjust their altitude depending on changes of wind speed or direction with height. For example, using radar data along the USA–Mexico border from Texas to Arizona in 2005–2006, Felix, Diehl & Ruth (2008) found that migrants generally flew lower and faster during spring migration than during autumn migration. Spring migrants tended to concentrate at altitudes with consistent winds from the south (i.e. southerlies); autumn migrants rarely had northerlies to support migration, and these were more likely at higher altitudes. Regional shifts in wind speed and direction with climate change may lead to deviations in what were historical flight paths.

Spatial differences in winds can cause seasonal differences in flight paths, or loop migration. For example, a low-level jet with strong southerly winds, especially during the night, is common during the spring across the south-central USA, sometimes extending into the northern Great Plains or Upper Midwest. During spring migration, these winds aid inbound migration to breeding grounds, especially for nocturnal migrants and birds that use flapping flight. With tailwinds sometimes exceeding 35 m s^{-1} , birds can achieve airspeeds over 200% greater than that of unassisted flight by using the low-level jet (Wainwright, Stepanian & Horton, 2016). During autumn migration, however, these strong southerlies hinder outbound migration, causing many birds to delay flight until winds weaken, fly at heights above or below the jet-speed maximum, or displace their route from that of springtime. Using geolocators, Delmore, Fox & Irwin (2012) tracked migratory routes of the Swainson's thrush (*Catharus ustulatus*) from northwest South America to British Columbia, Canada, finding that the birds flew along the Great Plains during spring migration but as far east as Illinois and Alabama during autumn migration. Although birds could climb to a height above the low-level jet, temperature and moisture content decrease substantially with height, causing the birds to expend more energy. On rare occasions that the low-level jet switched from southerly to northerly during autumn, migrant density increased tenfold (Wainwright *et al.*, 2016). Research using an ensemble of GCMs project that the Great Plains low-level jet will intensify and expand further north during spring and autumn (Zhou *et al.*, 2021), likely affecting migratory flight paths and durations.

High winds or heavy precipitation can affect bird survival during migration (Fig. 4). Tens of thousands of exhausted migrating songbirds, particularly warblers, died during a cold front passage (followed by high winds and unseasonably cold temperatures) in early May 1951 as they flew into buildings, poles, and utility wires across Nueces and Cameron Counties, Texas (James, 1956). King (1976) documented a similar event in early May 1974 when about 5,000 migrating passerines and shorebirds washed ashore on Galveston Island, Texas, after a severe storm. In early April 1993, a passing cold front with thunderstorms was implicated in the deaths of about 40,000 migrating birds of 45 species near Grand Isle, Louisiana (Wiedenfeld & Wiedenfeld, 1995).

Inland, Loss *et al.* (2020) reported an unusually high number of collisions of early-migrant American woodcocks (*Scolopax minor*) with buildings in Minneapolis, Minnesota, during late-March to mid-April storm events with strong north winds and exceptionally heavy snowfall.

(2) Indirect impacts of climate change

(a) Climate- and habitat-related trends

Stopover habitats along migration pathways are important to provide food, water, rest, and shelter to migrating birds. An estimated 38 shorebird species and 25 waterfowl species employ Great Plains wetlands as stopover sites during spring migration (Skagen, 1997; Smith, 2003; Jorgensen, 2004). In the Central Americas Flyway (Fig. 1), ephemeral lakes – prairie potholes (northern Great Plains) and playa lakes (southern Great Plains) – also serve as important habitats during migration because upwards of 90% of the region's original wetlands were drained for agriculture (Mitsch & Hernandez, 2013). Safe passage at stopovers is critical for species survival, with migration dangers including less-predictable weather and habitat conditions, high energetic requirements, disease, starvation, and predation (Newton, 2006). There are over 100 USA NWRs along the Central Americas Flyway that serve as protected stopover sites or wintering grounds for waterfowl (Andersson *et al.*, 2018).

Some migratory species breed across broad areas but migrate in narrow corridors, making the stopover habitats in those corridors especially important. For example, the breeding grounds of Canada warblers (*Cardellina canadensis*) extend from Manitoba to Nova Scotia (Canada) and southward through New England; however, most migration routes converge to hug the coasts along the northwest and western Gulf of Mexico (Louisiana, Texas, and Mexico), through Central America, and into northwest South America (Roberto-Charron *et al.*, 2020). Similarly, although wintering areas of flammulated owls (*Psiloscops flammeolus*) were distributed across Mexico, Linkhart, Fox & Yanco (2016) noted that migration routes converged across the Trans-Pecos region of Texas and eastern New Mexico, where ponderosa pine (*Pinus ponderosa*) was more common.

Changes in migration pathways have been attributed, in part, to climate change. Pearse *et al.* (2018) examined the migration corridor of the Aransas–Wood Buffalo population of whooping cranes from 1942 to 2016, using telemetry data from 58 birds from 2010 to 2016. Ninety-five per cent of the observations were within a corridor width ranging from 170 km in central Texas to 407 km at the USA–Canada border. They attributed width differences to the availability of natural and manmade lakes and wetland habitats, with fewer but more permanent lakes/wetlands for stopovers in the central and southern Great Plains. Over time, the authors detected an eastward shift in the migration path from Oklahoma to Saskatchewan, mostly from decreasing use of locations west of the corridor's historical median path. The authors proposed that this shift resulted from western



Fig. 4. Specimens of hundreds of migratory birds that died during a strong cold front in New Mexico on 8–9 September 2020. The National Weather Service reported winds over 25 m s^{-1} across portions of north-central New Mexico, and temperatures plummeted 25°C over 2 days. Researchers found signs of starvation and dehydration in the migratory insectivores (McCullough, 2020). Photograph courtesy of the University of New Mexico (Jenna McCullough). Copyrighted; used with permission.

precipitation declines (e.g. Seager *et al.*, 2018), altering food availability.

In a subsequent study, Pearse *et al.* (2020) found that although the spring and autumn migration corridor of the whooping cranes had high fidelity over the years 2010–2016, the stopover locations did not (with the exception of Salt Plains NWR, Quivira NWR, and Cheyenne Bottoms Wildlife Area). The lack of site fidelity was attributed to high precipitation variability throughout the Great Plains that induced variability in wetland habitats. Migration timing and the number of stopovers were consistent over the years. Migration duration, however, was substantially longer for autumn (average of 45 days) than spring (average of 29 days), likely because the cranes had higher fuel reserves from wintering and needed fewer extended stopovers as they migrated northward.

Surviving migration requires timing stopovers with food availability (Newton, 2006). Climate variability and related phenology shifts can affect stopover habitats and their food supplies, thus affecting migration timing and migrant health (Schmaljohann, Eikenaar & Sapir, 2022). Mass gain during stopovers depends on the density of migrants and the abundance of food [e.g. Kelly, DeLay & Finch (2002) for Wilson's warblers (*Wilsonia pusilla*) in Bosque del Apache NWR]. Migrants can increase their rate of fuel deposition at stopovers where food supplies are enhanced by nearby cropland waste (Newton, 2006), but the availability and timing of this high-quality food also changes with climate variability (Kerr *et al.*, 2022).

Synchronisation of plant green-up and insect emergence may explain the timing of some migratory species. La Sorte & Graham (2021) examined relationships between a satellite vegetation greenness index and the abundance of 230 North American migratory bird species in seven dietary guilds from

2006 to 2018. Herbivores, granivores, herbivore–granivores, omnivores, and carnivores generally were synchronised to changes in vegetation greenness during both spring and autumn migration, with the relationship being strongest for herbivores. Relationships were weakest for migrating insectivores and for carnivores migrating across western North America. Similarly, using both satellite and citizen science data sets, Mayor *et al.* (2017) calculated the rates of change between spring green-up and arrival of 48 North American passerine species at their breeding grounds from 2001 to 2012. Twenty-five species advanced their arrival dates as mean spring green-up occurred earlier; however, for nine species, the interval between spring green-up and breeding-ground arrival increased significantly. Species in temperate forests of the eastern USA had the largest lags from the earlier green-up dates; those in the western USA had the smallest lags.

Stopover duration generally is inversely related to the abundance of food supplies (Newton, 2006). Renfrew *et al.* (2013) used geolocators to track bobolinks (*Dolichonyx oryzivorus*) from three disparate breeding grounds (Oregon, Nebraska, and Vermont) as they migrated to South America. During autumn migration, the bobolinks made multiple, long stopovers in grasslands, timing the stops with high or increasing values of primary productivity, as measured by satellite reflectances (Renfrew *et al.*, 2013). Because bobolinks continue to eat grains while wintering (i.e. niche-followers), the precipitation-induced 'green wave' (Drent, Ebbinge & Weijand, 1978; Owen, 1980) of seasonal changes in primary productivity across South America appeared to be important.

Climate change is expected to reduce available water in some years, reducing the areal extent of ephemeral wetland habitats. For example, Londe *et al.* (2022) examined

depressional-wetland inundation in a four-county area of north-central Oklahoma to find that spring inundation occurred in 7 of 15 years during the recent past, but projected a reduction to 3–4 springs over 15 years by mid-century. It is unknown whether these changes would result in more dispersed migrants or if the fewer remaining large-scale wetland habitats would need to support more birds, potentially introducing disease threats or increasing resource competition. Drought conditions that reduce wetland extent, for example, also have been associated with outbreaks of avian cholera, as birds occupy limited habitats more densely (Samuel, Botzler & Wobeser, 2007).

Along the Gulf Coast, warming winters support the expansion of mangroves into salt marshes (Fig. 5), fundamentally changing the vegetation structure and reducing open areas for migratory birds to roost or forage safely (Kelleway *et al.*, 2017). Nearctic migratory shorebirds, in particular, may be affected, as the coastal salt marshes generally provide multiple levels of protection from both avian and ground-based predators *via* long visual distances, and large pools of relatively open water (Kelleway *et al.*, 2017). Clear line-of-sight roosts are more available in salt marshes than encroaching mangroves, and some endangered or threatened species, such as the whooping crane, do not use mangrove habitats (Kelleway *et al.*, 2017).

Carryover effects of environmental conditions (Fig. 3) during wintering affect the timing of spring migration. In a study of migration timing of Swainson's thrush, González-Prieto, Bayly & Hobson (2020) used an automated wildlife tracking system to understand the relationship between wintering habitats in the eastern Andes of Colombia and both the departure date for and duration of spring migration. Thrushes using shade-grown coffee (warmer, drier, and lower-quality) habitats during wintering departed earlier than those using native forest (moister, cooler, and higher-

quality) habitats. The later-departing thrushes migrated at a faster pace than early departees [also found for grey-cheeked thrushes (*Catharus minimus*) (Gómez *et al.*, 2017)], possibly because they left with more fuel reserves and did not need as many or as lengthy stopovers. Interannual differences in departure dates coincided with winter precipitation amount, with the earliest departures during the drier winter and the latest departures during the wetter winter. The authors hypothesised that thrushes left wintering grounds earlier when habitats were of lower quality (i.e. coffee plantations, drier years), contrary to Faaborg *et al.* (2010).

Precipitation-fed playa wetlands in the central and southern Great Plains provide important habitats for wetland-dependent migratory birds. Albanese, Davis & Compton (2012) and others have noted that large clusters of high-density wetland habitats in the southern Great Plains provide a visual cue for migratory shorebirds to select stopover locations. Migrants tended to select stopover sites based on the broad-scale availability of these wetland habitats rather than any microhabitat characteristics (Albanese & Davis, 2013). Unfortunately, these habitats are threatened by drought and increased evaporation caused by warmer temperatures, as well as by agricultural land use, polluted runoff, declining aquifer levels, land cover change, transforming hydrology, and sedimentation (Johnson *et al.*, 2012).

Future projections for species abundance or distribution have been used to examine spring migration. Reese & Skagen (2017) applied output from global climate models to species distribution models for 14 migratory shorebirds (from three families) that use Great Plains' wetlands as stopovers to examine the impact of mid-century climate change (2041–2070 *versus* 1981–2010) on probabilities of occurrence. They found overall slight increases in probability of occurrence of most shorebirds during spring migration across the central Great Plains by mid-century, with decreases for

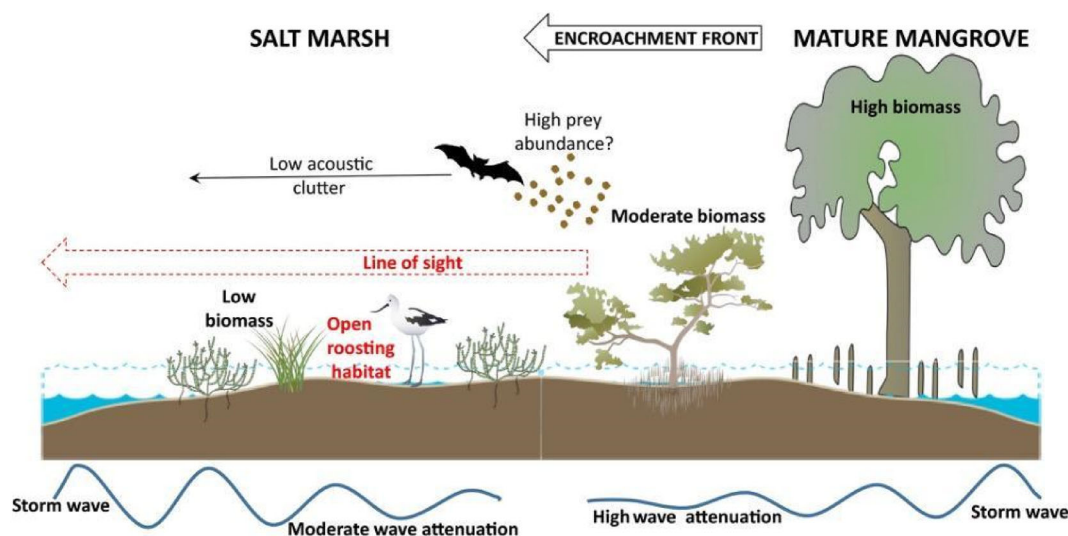


Fig. 5. Conceptual diagram of how mangrove encroachment into coastal salt marshes can change the structure and function of habitats (Source: Kelleway *et al.*, 2017). Copyright 2017 John Wiley & Sons Ltd.; used with permission.

mountain plovers (*Charadrius montanus*) and long-billed curlews (*Numenius americanus*) throughout the migration period. From late April to mid-May, there also were declines in probability of occurrence for marbled godwits (*Limosa fedoa*), willets (*Tringa semipalmata*), and Wilson's phalaropes (*Phalaropus tricolor*). The largest positive changes in distribution occurred for shorebirds in eastern (i.e. moister) portions of the Great Plains and for long-distance migrants.

(b) *Climate variability and post-disturbance changes*

Great Plains wetlands change substantially during dry years because much of the region is semi-arid (Fig. 6). Webb *et al.* (2010) examined use of wetlands in the Rainwater Basin, (south-central) Nebraska, by wetland birds during spring migration through the Great Plains in below-normal precipitation years: 2002, 2003 (driest), and 2004 (moistest). Most of the available wetlands were semi-permanent during those years, likely because the substantially drier-than-normal conditions reduced more ephemeral water bodies. They observed almost half as many birds in the driest year as compared to the other 2 years, perhaps as a result of shorter stop-over times. Dabbling ducks maintained a strong relationship to landscapes with the highest wetland area (within 10 km) even when the overall number of available wetlands in the region was lowest. These landscapes may have provided a wider variety of shelter and forage favourable to surface-feeding waterfowl in comparison to ducks that dive for food below the surface. Species richness also increased with higher percentages of wetland area in the landscape. Shorebird abundance was highest on wetlands with intermediate vegetation coverage and decreased as water depth increased.

Natural and manmade fires can interact with climate variability to provide spatially distinct microclimates for avian species. For example, recently burned landscapes in tallgrass prairie have been found greatly to enhance the abundance during spring migration of killdeer, upland sandpiper (*Bartramia longicauda*), and American golden-plover (*Pluvialis dominica*) – short- to long-distance migratory shorebirds (Hovick *et al.*, 2017).

The blackened soils of these burned areas are locally warmer than soils in unburnt areas, leading to a greater abundance of invertebrates for food. Yet the conditions necessary for prescribed burns for management of these habitats are expected to alter with climate change (Yurkonis *et al.*, 2019).

El Niño–Southern Oscillation (ENSO) is a pattern of normal (i.e. neutral phase), warmer-than-normal (El Niño phase), or cooler-than-normal (La Niña phase) sea-surface temperatures in the central and eastern equatorial Pacific Ocean that affects large-scale temperature and precipitation patterns across the globe, particularly during autumn and winter. ENSO impacts have been examined in relation to migratory stopovers of long-distance migrants across the Americas. Paxton *et al.* (2014), for example, assessed the physical condition, timing, and abundance of Nearctic–Neotropical migrants stopping on their way north to refuel in Cameron Parish, Louisiana, from late March to early May 1993–1996 and 1998–2010. They compared migrants from South America, where El Niño is associated with warmer and drier conditions, to those from the Caribbean or Central America, where temperature and moisture changes are minimal during ENSO events. Results indicated that El Niño conditions were related to lower-than-normal vegetation greenness in South America but little interannual difference in the Caribbean–Central America. Consistent with these differences, the energetic condition (as measured by subcutaneous fat) of South American migrants [red-eyed vireo (*Vireo olivaceus*), gray-cheeked thrush, and Swainson's thrush] was lower during El Niño years but that of Caribbean–Central American migrants [wood thrush (*Hylocichla mustelina*), ovenbird (*Seiurus aurocapilla*), hooded warbler (*Setophaga citrina*), indigo bunting (*Passerina cyanea*), and Kentucky warbler (*Geothlypis formosa*)] was unchanged across all years. The energetic condition of South American migrants was not significantly different for La Niña (cooler and wetter than normal) and neutral-phase years. Also, the migrants from South America were twice as abundant in the North American coastal stopover locations during El Niño years as other years, possibly indicating that their fuel

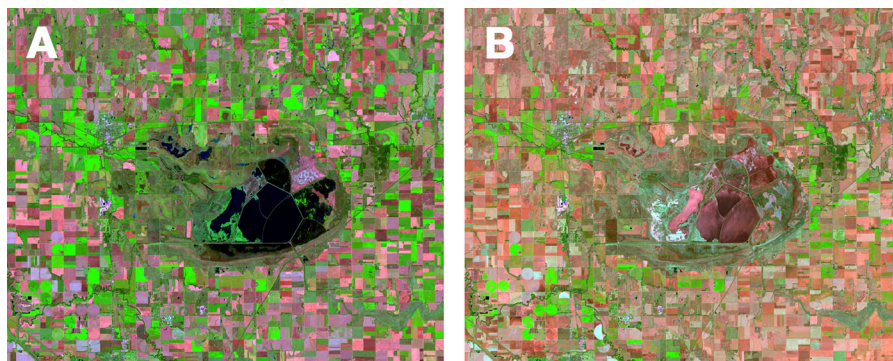


Fig. 6. Imagery from Landsat 8 on (A) 22 October 2021 and (B) 25 October 2022 displaying the difference in open-water habitat (dark blue) in the Cheyenne Bottoms Wetlands of central Kansas during an autumn (2021) with near-average precipitation and an autumn (2022) with extreme drought. These wetlands serve as an important stopover for migratory waterfowl and shorebirds. Images courtesy of USGS EarthShots.

stores were so low after crossing the Gulf of Mexico that they could not fly further inland where there was higher-quality habitat. This premise is further supported by the fact that there were not substantial differences in the interannual timing of stopovers, indicating that the over-wintering birds from South America likely did not remain on their non-breeding grounds until they reached the same physical condition as normal, thus arriving at the coast in a more depleted state.

Droughts affect migratory bird populations differently than resident birds. Across 15 states in the central USA (bounded by Montana, New Mexico, Texas, and Wisconsin), Albright *et al.* (2010b) found that avifauna abundance and richness were related to drought conditions during and one-year-prior to both mid-April and late June. Although permanent residents responded positively to drought, short-distance migrants and, to a greater extent, long-distance migrants were negatively affected in both abundance and species richness (e.g. decreasing about 13% and 6%, respectively, for Neotropical migrants). The difference between migrants and residents possibly resulted from the fact that migrants could bypass an area with severe drought conditions, thereby reducing species abundance and species richness in drought-affected areas.

Groundwater-fed saline lakes, or salinas, in west Texas and eastern New Mexico also support a variety of migrating shorebirds. As compared to playa lakes, salinas historically have been wetter because they were recharged by groundwater (e.g. Ogallala aquifer), but flow from springs has been reduced by groundwater depletion (Heintzman *et al.*, 2017). Now many salinas are predominantly recharged by precipitation, causing them to be hydrologically and ecologically different wetlands. In a study of 45 salinas in eastern New Mexico, Andrei *et al.* (2008) found that shorebirds used lakes with lower salinity (< 40 g/l) and higher abundance of invertebrates. Lakes with salinities of 40 to 120 g/l only had brine shrimp (*Artemia* spp.) and brine flies (*Ephydra* spp.); lakes with salinities over 120 g/l had no invertebrates. With increased evaporation resulting from warming temperatures, it is expected that salinities of ephemeral lakes across the south-central USA will increase over time, potentially reducing food resources for migrating birds.

Some species of Neotropical migrant passerines migrate a substantial distance southward in late summer before moulting (i.e. moult-migration), likely to take advantage of a growing food supply that occurs across parts of Arizona, New Mexico, and northern Mexico during the North American Monsoon (Rohwer, Butler & Froehlich, 2010; Jahn *et al.*, 2013; Contina *et al.*, 2019). Carlisle *et al.* (2009) list numerous western avian species that do or may undertake moult-migration in this region. When drought conditions occur, however, these migrants tend to be more abundant in riparian habitats or may choose to bypass the region and moult on their wintering grounds (Pyle *et al.*, 2009). Limited (and sometimes conflicting) studies on how the North American Monsoon may evolve with climate change (White *et al.*, 2023) currently preclude evaluation of its future impacts on migratory activities.

Many migratory birds that breed in the south-central USA rely on stopover habitats across multiple Latin American countries. Eastern kingbirds (*Tyrannus tyrannus*), western kingbirds, and scissor-tailed flycatchers, for example, breed in grasslands and mixed-grass prairies across the southern Great Plains and winter in or near Bolivia/Peru, Guatemala, and Nicaragua, respectively (Jahn *et al.*, 2013). Using miniature solar geolocators, Jahn *et al.* (2013) first tracked western kingbirds from southwest Oklahoma in late July to the Sonoran Desert region, where they stayed for 2 months, likely to moult during monsoon season while food was abundant. As monsoon season ended, the western kingbirds moved to central Mexico for a month and finally to their wintering grounds until late April, likely moving as regions received more rainfall and had abundant food supplies. The research team noted that the fruit-eating eastern kingbirds delayed their departure until late August/early September and their moult until they reached their wintering grounds in the southern Amazon Basin, where fruit was plentiful by September. On the other hand, scissor-tailed flycatchers moulted in Oklahoma during a late-summer peak in insect abundance, then migrated southward in early October.

Not all weather-related disturbances have negatively affected migrating birds across the region, however. For example, hurricanes can damage or destroy trees across the Chenier Plain, where bands of remnant beach ridges stretch along the Gulf Coast and inland areas from Galveston, Texas, to Vermilion Bay, Louisiana (Owen, 2008). In southwest Louisiana, remnants of forests remain – the first forested land that spring migrants encounter after the energy-depleting journey across the western Gulf of Mexico (Yong & Moore, 1997; Moore, 1999). Major hurricanes Rita (in 2005) and Ike (in 2008) stripped leaves, fruit, vines, and branches from the sugar hackberry (*Celtis laevigata*) and live oak (*Quercus virginiana*) forest at a study site in Johnson Bayou, Louisiana (Lain *et al.*, 2017). Lain *et al.* (2017) determined that there was no significant change in migrant songbird (about 30 species) abundance, likelihood of stopover, or rate of mass gain from pre-storm to post-storm even though food supplies (including arthropods) had declined. In fact, eastern kingbirds and yellow warblers (*Setophaga petechia*), which prefer more open habitat, increased in abundance post-storm. The authors proposed that the migrants used different foraging techniques to make the most of the hurricane-damaged area.

V. CONCLUSIONS

- (1) Climate change and associated extremes are expected to have direct, indirect, carryover, and time-lagged effects on migratory birds.
- (2) Studies have examined individuals, populations, species, and communities, including changes in phenology, abundance, richness, distribution, clutch sizes, habitats, and resources.

Many of the studies examine historical changes or use climate extremes (e.g. drought years, ENSO) as proxies for what future changes may be expected.

(3) Climatologists regularly work across spatial and temporal scales ranging from regional to global and weeks to decades in their analyses of how and why climate is changing in a given location. This review follows this tradition, incorporating impacts during breeding, wintering, and migratory seasons of migratory birds that use the south-central USA at some time in their life cycle.

(4) Many migratory birds that use the south-central USA during part of their life cycle have changed their behaviours as a result of long-term temperature changes. Short-distance migrants tend to adjust their timing of migration, arrival at breeding grounds, nesting, and egg-laying to warmer temperatures more than do long-distance migrants, leading to earlier spring activities and later autumn activities. Increased temperatures also have caused changes in nesting in montane forests and sheltering behaviour for thermal refugia in grassland habitats.

(5) Hydroscares and habitats change interannually across this region because of high natural precipitation variability, causing annual differences in species abundance and richness, migration stopover locations and fuel load, nest success, territory abandonment, and abundance of food and prey. More frequent or intense drought as well as heavier rainfall events are expected to cause additional stresses on migratory birds in this region.

(6) Despite avian species being perhaps the most comprehensively studied non-human species in their response to climate, much is still unknown. New technologies such as biologging and weather radar supply valuable data for examining how atmospheric conditions influence bird migration behaviours. Researchers also are connecting niche or species distribution modelling with future climate projections to develop spatially explicit predictions of species change.

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