Avian Response to Extreme Weather Events

A dissertation proposal submitted by

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Overview

An extreme weather event is an anomalous event that deviates strongly from the normal climate of a region and thereby represents severe conditions, but these events are variably defined. There is no standard definition of what degree of deviation from normal constitutes extreme weather. Further, there are many types of extreme weather, including but not limited to drought, heat wave, and early spring cold snap. The actual parameters that define an extreme event differ among climatic regimes. For example, extreme heat in the southwestern US differs in temperature value from extreme heat in the Arctic. Often, extreme weather events are most usefully identified in terms of their consequences. Thus, it is important to determine at what deviation, and under what conditions, extreme weather events affect a variable of interest.

Extreme weather events are often defined in terms of environmental consequences, or, at what deviation an environmental change of interest would take place. Extreme weather can have direct and indirect effects on biota. A direct effect on an organism would be exceeding a physiological tolerance. For example, a direct effect of drought is plant death due to water stress (Allen and Breshears, 1998). An indirect effect is a response of an organism to an extreme that is mediated by another organism. An example of an indirect effect is a food-mediated response of a predator, whereby prey abundance is decreased by extremes, causing predators to change their behavior (Bolger, et al., 2005).

Extreme weather events affect bird populations, both directly and indirectly. In times of severe drought, birds can forgo a breeding season due to lack of prey availability, an example of an indirect effect (Christman and Thompson III, 2002). Extreme heat can cause juvenile bird mortality, an example of a direct effect (Nisbet, 1975). An unseasonable cold snap can cause birds to abandon nests (Decker and Conway, 2009). Given that extreme weather events are predicted to increase in frequency and intensity (Frich, et al., 2002), I am curious about what deviations birds change their normal behavior, or their breeding season deviates from. In other words, I seek to define extreme weather in the context of avian ecology, in order to understand what conditions cause anomalous avian responses. Using this knowledge, we can better understand how avian populations may respond to a new regime of extreme events in the future.

Since the relationship between extremity of weather event and avian population response remains largely unclear, this dissertation seeks *to quantify both extreme weather events and concurrent avian population declines using large-scale spatial datasets that consist of long-term monitoring records.* In my **first chapter** I will investigate specific extreme weather events associated with an avian response that has been reported in peer-reviewed literature. In this chapter my goal is understand whether both the extreme weather events and avian responses that have been reported for often very local areas can be detected in spatially and temporally extensive datasets of weather and bird abundance. This question matters because if we find we can detect avian response to extreme weather events in these datasets, we can use the values of these extreme weather events as a guide to detect similarly extreme weather events and characterize the avian response in years and locations that have not previously been reported. This investigation can shed insight on the frequency and range of responses among different taxonomic and/or functional groups of birds. This is what I plan to do in my **second chapter**, focusing on the forest songbird guild across the US. Specifically, I will look for extreme weather events, will develop hypotheses about expected responses, and will examine both guild response and species-specific responses. In my **third chapter**, I will refocus, moving to a site- and population-specific analysis. In this chapter I will use a long-term dataset on a population of prothonotary warblers (*Protonotaria citrea*). I will test whether or not the observed extreme weather-avian demographic relationships discovered in Chapters 1 and 2, and also in the literature, are found for this population and site, or if there are important differences per habitat and/or species requirements that produce different trends. This chapter also has the benefit of fine-scale life history data, making it possible to analyze at what stage and specifically how this species is affected by extreme events.

Background

I searched the literature for avian response to drought, heat wave and early spring cold snap. I conducted the search in Google Scholar database through September 2013. I combined members of two sets of key words, in all possible ways. The first set focused on birds and included these terms: “bird”, “birds”, “avian”, “Aves”, “songbird”, “songbirds”, “forest songbird”, “forest songbirds.” The second set focused on different ways to capture extreme events, and included these terms: “heat wave”, “drought”, and “cold snap”. I also included relevant references found within the articles collected by these search terms. The most general search term combination used was “bird” and “extreme event.” Then, search terms for birds, narrowing to a focus on passerines (i.e. songbirds) were each combined with extreme event of interest. Almost certainly, some relevant records were missed.

Defining extreme events in the context of birds

Extreme weather events range from unusually strong wind and/or precipitation, to drought and heat wave, to unseasonable cold snaps, and are defined variably for different purposes. A common mode by which an event draws human attention is by damage or threat to human systems (Meehl, et al., 2000), either directly (Greenough, et al., 2001) or indirectly to e.g. food sources (Rosenzweig, et al., 2001). Thus, weather events are often defined in terms of their consequences; for example heat waves may be defined by the characteristics (e.g. temperature, duration) that make them deadly to humans (Luber and McGeehin, 2008). Yet, extreme weather events can be important drivers of wildlife population fluctuations as well, and may affect a variety of processes, from physiological (Romero, et al., 2000) to behavioral (Parmesan, et al., 2000). There is a rich body of literature documenting the effects of extreme weather on birds (Elkins, 2010), but very often the intensity of the extreme events are not reported quantitatively. Understanding the relationship between weather event quantitative characteristics and avian responses would be valuable for predicting potential future consequences of an increasingly variable climate (Jiguet, et al., 2006).

Extreme events are defined in a variety of ways in the literature. For example, rainfall is the most common variable used for drought. However, various measures of surface water have also been used to capture drought characteristics, such as the May pond index (Derksen and Eldridge, 1980), which measures the number of available breeding ponds for waterfowl. The Everglades National Park hydrologic recording stations categorize water levels relevant to wading birds (Frederick and Ogden, 2001) and have also been used to quantify droughts. In many mountain ecosystems, snowpack is the primary source of spring/summer water supply and governs vegetative regime as well as freestanding water. Thus, drought can be defined as a “snow drought,” indicating below normal winter precipitation.

Extreme weather events are most commonly reported either as raw values or as deviations from average weather variable values. Values that constitute an extreme are sometimes arbitrarily defined, or are a rough estimate of where a behavioral threshold is crossed. For example, 1 SD below normal water level is often sufficient to constitute an extreme event (Frederick and Ogden, 2001). I discovered two other reported deviations describing extreme drought, both approximately 1.6 SD below average rainfall, which correspond to approximately 10 cm and 18 cm below average rainfall in their respective ecosystems of occurrence (Table 1). However, though standard deviation is probably the most useful metric, differences are sometimes also reported. Surface water is usually compared across years in terms of percent change. For example, the May pond index and percentages of seasonal basins containing water are reported in studies of northern pintail (Derksen and Eldridge, 1980).

Duration of extreme conditions is an important consideration in assessing the severity of an event. The minimum reported time period for defining drought conditions in the literature I reviewed was one month, whereas for heat waves only a 1-2 day event is sufficient to cause shorebird chick mortality (Nisbet, 1975). Drought conditions that persisted into the breeding season and affected bird nesting attempts were often characterized by averages including the preceding winter, or an even longer temporal period, such as annual or 4-year average (Bolger, et al., 2005, Christman and Thompson III, 2002, Faaborg, 1982, Verner and Purcell, 1999). Severe snow drought led to a decline in breeding bird species, most notably in deciduous forest (Smith, 1982). Surface water levels upon arrival at a potential breeding ground (i.e. directly preceding a breeding season) determined whether or not northern pintail stayed in North American prairie or continue moving north to find suitable conditions (Derksen and Eldridge, 1980, Henny, 1973). Two papers capture drought conditions exclusively over the span of the breeding season, one documenting community metric changes, and one documenting effects on duckling survival (George, et al., 1992, Krapu, et al., 2006). The use of precipitation averages in a majority of papers describing drought effects likely reflects the fact that prolonged periods of dryness are required to change conditions enough to influence breeding dynamics. However, it is unclear if a drought duration threshold exists above which birds are highly likely to respond, and whether this period length can be defined for different regions and habitat types.

In summary, a challenge to advancing our understanding of the effect of extreme weather on birds is that there are no standard metrics by which deviation from normal weather conditions are reported. Thus, it is difficult to compare severity of events across studies. “Raw differences” in weather metrics cannot be directly compared across eco-regions, because the distribution of weather variables differs among eco-regions. Thus far, in literature on bird response to extreme weather, inclusion of standardized variables is rare, making it difficult to compare extreme event effects across species, time, or geography. Such information could shed light on thresholds for behavioral decision-making.

Literature review of extreme events and birds

Bird absence during times of extremes such as drought have been noted as early as the beginning of the 20th century (Barnard, 1927), accompanied by speculation that the associated lack of food was the proximate reason for the decline (Barnard 1917). Extreme events have been referred to as an “ecological crunch,” that reduces population size (Brown and Brown, 1998), and as a type of disturbance (Canterbury and Blockstein, 1997). The earliest mention of increasing frequency of extreme events in association with birds appears in the observation of a gull colony in which three heat waves occurred in a 6 year period. The earliest explicit link between extreme event and climate change in the context of effects on birds was in regard to the 1988 drought and its effect on grassland birds in the Dakotas (George, et al., 1992). While this extreme event coincided with testimony by James Hansen in 1988 before Congress about changing climate, it was not until approximately 2004 that papers on avian response to extreme events began to discuss the connection between extreme events and climate change commonly.

In the avian literature, the words used to identify extreme events vary widely. From antiquated spellings of key words (e.g. “drouth”) to synonyms for keywords, the inconsistencies can make it difficult to find literature on bird response to extreme events (Hicks, 1935). For example, “aridity” is used to refer to years of snow drought in one paper (French, 1959), though this term is more commonly a descriptor of climate. Cold snaps are synonymous with “cold spells,” but were also referred to as “unseasonable snowstorms,” “cold spring” or “harsh weather.” Drought is a more standard term, but is also referred to as “exceptional dry” or described as “low rainfall.” Heat wave is described variably with the phrases including “higher temperatures,” “record high temperatures,” “temperature variability” and “extremely warm.” The definitions and descriptors used for extreme events vary, but a few that appear often in ecological literature are “prolonged” (Bennett, 1952), “severe” (Barnard, 1917), “exceptional” (Henny, 1973), “extreme” (Derksen and Eldridge, 1980) and “unusual”(Arcese, et al., 1992). These words are used to convey the abnormal nature and the intensity of the observed event, as a qualitative explanation for the avian phenomena observed.

Efforts to synthesize the literature on opportunistic reports of bird response to extreme events have been made. A literature review synthesizing the effects of cold snaps addressed migrant mortality upon arrival at breeding grounds (Newton, 2007). The primary hypothesized mechanism for mortality was disrupted or inaccessible food supply, causing starvation, mostly among passerines, but also in waterfowl. Two literature reviews focusing on the tub and tap hypotheses have been published in recent years (Moreno and Møller, 2011, SÆther, et al., 2004). The tub hypothesis proposes that population fluctuations are due to variation in adult survival during the nonbreeding season, while the tap hypothesis proposes that variation in juvenile recruitment during the breeding season drives fluctuations. Saether et al (2004) categorized the type of population change (including mechanism driving the change as available), and sought to differentiate effects based on birds nestling stage strategy, i.e. whether they are altricial vs. nidifugous. Altricial species are poorly developed at hatching, remain in their nest for a substantial period, and require considerable parental care. Nidifugous species are more advanced in development at hatching and leave their nest shortly after hatching, attended by one or both parents who model foraging and other behavior which juveniles mimic. Saether et al. (2004) suggest that the tub hypothesis (i.e. adult survival) explains the population dynamics of northern temperate altricial species (e.g., barn swallow, *Hirundo rustica*, and garden warbler, *Sylvia borin*) and the tap hypothesis (i.e. juvenile recruitment) explains dynamics of both nidifugous (e.g. Galliformes) and arid land altricial species (e.g. grey-headed junco, *Junco hyemalis* and *Geospiza spp.*). Indeed, support for these categorizations come from two studies not included in the Saether et al. (2004) review; drought in the nonbreeding range was associated with reduced body condition (Sherry and Holmes, 1996), and lower survival of warblers (Probst, 1986). A recent study of adult barn swallows, an altricial species, also points to nonbreeding season mortality as a mechanism for observed population dynamics (Møller, 2011), further support for the tub hypothesis. There are also several examples supporting the tap hypothesis, in which nidifugous juveniles negatively were affected by breeding season extremes (Nisbet, 1975) that are not presented in the Saether et al (2004) review.

However, the simplification of these hypotheses (altricial tub and nidifugous tap) as drivers of population dynamics potentially ignores important ‘tap’ dynamics in altricial bird species’ population dynamics. There are many examples of extreme weather affecting juvenile recruitment of passerines (which are all altricial) (Cox, et al., 2013, Jiguet, et al., 2011, Mattsson and Cooper, 2009). Whether the mechanism is a reduced proportion of the population nesting (Bolger, et al., 2005, Christman and Thompson III, 2002), nest failure and/or egg inviability (Decker and Conway, 2009), or reduced fledging success (Brenner, 1966), is appears that lowered recruitment can be an important driver of population dynamics for altricial species as well as nidifugous species (Faaborg, 1982). Thus, further exploration of the drivers and outcomes of avian population response to extreme events is warranted.

In a review of extreme events in relation to impact on life histories, Moreno and Moller (2011) categorized studies (including mammals) into either juvenile recruitment or adult mortality responses, and related these to extreme versus normal weather years. They reported that both survival rates and reproductive success were about one-third of normal in extreme weather years. However, “extremes” included many types of weather events, from cyclones to high sea-surface temperature. Also, since the subjects of the review included mammals and birds, it was difficult to form further ecological hypotheses for the biota studied, or differentiate mechanisms and patterns that were important to each. While various physiological tolerances can be directly measured, in many cases, it is unknown how weather conditions influence avian behavior. For example, we do not know what specific minimal precipitation threshold causes semi-arid passerine species to forego nesting, though we know that nest building was greatly reduced in times of water stress (Bolger, et al., 2005). It would be beneficial to quantify thresholds and patterns of bird response such as these, in order to understand how birds are likely to respond to a new regime of extreme weather events ushered by climate change.

Trends in avian responses to weather

How birds respond to weather, not specifically restricted to extreme conditions, is captured in studies that record data over a variety of conditions. For example, Florida scrub-jays showed a positive linear relationship between rainfall and clutch size (Woolfenden, 1984). In a central Spain study of sympatric harrier species, which captured range center conditions for Montagu's harrier (*Circus pygargus*) and southern range periphery conditions for hen harrier (*Circus cyaneus*), fledge success similarly showed a positive linear relationship with rainfall for the hen harrier, and hatch success was related to temperature (Garcia and Arroyo, 2001). The same relationship is evident in rufous-crowned sparrow in the US (Bolger, et al., 2005). In a marsh wren (*Cistothorus palustris*) study, clutch size and temperature are inversely related in some populations, and egg inviability increases with increasing temperature (Olsen, et al., 2008). Lowered hatch success with increasing deviation from normal rainfall conditions has been noted for spotted owl and Louisiana waterthrush species (Glenn, et al., 2011, Mattsson and Cooper, 2009).

The relationship between weather variables and avian populations varies by ecosystem and taxonomic order. While arid-land birds may not initiate breeding until after rainfall (Burbidge and Fuller, 2007, Dunning Jr, et al., 1999), temperate-ecosystem birds do not exhibit this pattern. This is likely because rainfall is more frequent in temperate systems, and thus not a limiting factor. In arid ecosystems, rainfall may be an indicator of rapidly improving nesting conditions and may stimulate birds to breed (Keast and Marshall, 1954).. In temperate forest ecosystems, unless there is a strong cue indicating unsuitability, birds initiate nesting activities.

In the literature I reviewed, timing of extreme weather events in relation to the annual avian life history cycle had a strong bearing on the type of response incurred (Brown and Brown, 1998, Faaborg, 1982, Probst, 1986). Adult mortality responses were only found for passerine migratory species during non-breeding (winter or in the pre-breeding period) season events. For example, just after return to breeding grounds, a cliff swallow population experienced an approximately 73% decline following a severe cold snap (Brown and Bomberger Brown, 2000). This makes sense in light of the general assertion that among different categories of migration strategy (i.e. permanent resident, short distance and long distance), long-distance migrants are likely the most vulnerable to climate change (Both, et al., 2010).

Juvenile recruitment was affected by both non-breeding and breeding season events (Table 2). A non-breeding season event that could affect juvenile production causes conditions at breeding onset to be unsuitable (Faaborg, 1982). These conditions may persist into the breeding season, which would make them detectable at the time of breeding. An example is the lack of normal precipitation during the winter and spring in Arizona in a La Nina year was associated with lack of leaf out in oak, and no nesting by bridled titmice (Christman and Thompson III, 2002).

In some cases, the same extreme event affects multiple ecosystems. Drought in 1977 appeared in the Sierra Nevada as an absent snowpack, negatively affecting the montane bird community (Smith, 1982), and as lack of water in the prairie potholes of the northern US and southern Canada, causing northern pintail (*Anas acuta*) to migrate on to the Arctic to find suitable habitat conditions for breeding (Derksen and Eldridge, 1980). Similarly, the severe drought affecting the US in 1988 affected both the grassland passerine community (George, et al., 1992) and waterfowl of the upper Midwest (Krapu, et al., 2006). In the Sierra Nevada foot hills during this same time period (1987-1991), house wren (*Troglodytes aedon*) abundance varied directly with the 4-year average of precipitation (Verner and Purcell, 1999). Drought conditions in southern Florida during 1991-1992 led to less nest initiation in the Florida scrub-jay (*Aphelocoma coerulescens*) (Schoech, 1996), and in wading birds in the Everglades (Frederick and Ogden, 2001). The 2003 European heat wave that caused human mortality also caused declines of population growth rates for European breeding birds (Jiguet, et al., 2006).

Both studies of bird response to singular extreme events and studies of an observed relationship between weather variables and avian parameters are useful for determining the nature of the relationship between climate variables and avian response, and potentially elucidating thresholds. Studies that capture deviations over time provide a richer source of information than those that simply compare outcomes in an extreme year to those in a normal year, but the latter type due shed light on conditions that definitively influence avian life history strategies.

A useful way to understand avian response to extreme weather would be to determine the response curve between avian parameters and weather conditions. For this exercise, metrics defining the extremity of an event, or its degree of deviation from normal, can be related to the deviation from normal of avian behavioral or demographic values. Normative weather and associated avian metrics is also necessary for such a response curve. The literature included in this review presents data from abnormal weather years highlighting abnormal avian life history traits in response. Yet, while the values for avian data presented may seem qualitatively severe, in most cases it is difficult to impossible to know how severe the effect was because data from normal conditions are not presented (e.g. normative rates of chick mortality or proportion of first-year birds in a breeding population). Thus, from this literature review we have gathered valuable information regarding weather extremes and avian processes, but data to quantify a relationship or a threshold remains elusive. Future research may clarify these responses, especially if consistent deviation measures are reported.

Table 1: A compilation of definitions of extreme weather events used in published studies on birds. "Time window" is the period of time over which "weather variable value/description" was measured. In the "difference from normal" column, if a value is not calculated in the paper (such as SD), a difference is reported if that data is available. In those cases, the 1st value, representing the extreme conditions, was subtracted from the second value, representing normal conditions. .Deviation column includes data reported in study.

Ecosystem Description	Species or Guild of Study	Weather Variable Value/Description	Time window	Difference from normal	Deviation
Drought					
Grassland, Great plains (George, et al., 1992)	Community	Total rainfall = approx.106 mm (interpreted from graph)	Apr-July (4 mo.) 1988	10.6 cm – 21.4 cm = **-10.8 cm**	**-1.6 SD** precipitation, 34-year average
Dry scrub, Florida (Schoech, 1996)	Florida scrub-jay (*Aphelocoma coerulescens*)	Ave. 2 cm/month (precipitation interpreted from graph)	Nov-Jan (3 mo.) 1991-1992	5.5 cm – 20.75 cm= **-15.25 cm** total	
Mountain, AZ (Christman and Thompson III, 2002)	Bridled titmouse (*Baeolophus wollweberi*)	Ave. 5.4 mm/month (precipitation interpreted from graph)	Dec-May (6 mo.) 1998-1999	32.5 mm – 190 mm = **-15.75 cm** total	
Dry scrub, Puerto Rico (Faaborg, 1982)	Community	Total rainfall = 13.54 cm	Jan-June (6 mo.) 1973	13.54 cm – 29.90 cm = **-16.36 cm**	
Semi-arid, California (Bolger, et al., 2005)	Passerines	Total rainfall = 7.67 cm	Year (measured July-Jun) 2001-2002	7.67 cm – 25.25 cm= **-17.58 cm**	**-1.68 SD**
Foothills,	House wren	29.7 cm average	4-year (July-	29.7 cm –	Ave. annual

Sierra Nevada (Verner and Purcell, 1999)	(*Troglodytes aedon*)	annual precipitation (calculated from reported % from normal)	June) running average of annual precipitation, 1987-1991	47.4 cm = **-17.7 cm**	precipitation 62.6% of long-term mean = **37.4% below**
Mountain, Sierra Nevada (Smith, 1982)	Community	0 cm snow on ground	April 1977	Approx. **-20 cm** equivalent rainfall (assuming 10:1 relationship)	>200 cm snow expected = **>200 cm snow below** normal
Mediterranean, Santa Catalina Island (Langin, et al., 2009)	Orange-crowned warbler (*Oreothlypis celata*)	Total rainfall = 9.1 cm	Nov-Apr (6 mo.) 2006-2007	9.1 cm – 36 cm = **-26.9 cm**	
Mediterranean, Santa Cruz Island (Langin, et al., 2009)	Orange-crowned warbler	Total rainfall = 14.9 cm	Nov-Apr (6 mo.) 2006-2007	14.9 cm - 44.2 cm = **-29.3 cm**	
Freshwater marsh, Everglades (Frederick and Ogden, 2001)	Wading birds	Hydrologic recording station category: “very dry”	Jan. Years listed as “too dry for nesting”: 1932, 1935, 1946, 1990-1992		**<-1 SD**, period-of-record mean minimum monthly stage
Prairie potholes, eastern North Dakota (Krapu, et al.,	Mallard (*Anas platyrhynchos*)	Percentage of seasonal basins containing water ≤ 18%	May-Sept 1988-1992		≤ 18% - >40% = **>22% below**

2006)					
Prairie potholes, Dakotas & Montana (Derksen and Eldridge, 1980)	Northern pintail (*Anas acuta*)	May pond index	May 1977		**21-41% below** 10-year average
Prairie wetland, Canada (Henny, 1973)	Northern pintail	May pond index	May 1977		**47% below** prior year, **42% below** 1955-76 average
Heat wave					
Beach, MA (Nisbet, 1975)	Common tern (*Sterna hirundo*)	Air temperature daily > 38°C	8-9 July 1973		
Beach, CA (Salzman, 1982)	Western gull (*Larus occidentalis*)	Air temperature in shade near 38°C, heat wave defined as 32°C	9 June 1979	38°C - 24°C = **14°C**	9 heat waves (≥32°C) possible over 62 year temp record

Table 2. Mechanisms that affect juvenile recruitment, compared between extreme drought or heat and normal years. Where the data is available, the 1st value was recorded in drought, and the second in normal conditions, to calculate deviance in extreme years. These records are roughly ranked by severity of avian response observed.

Study & Species	Weather	Breeding (producing a clutch)	Nest building	# nests	Fledglings	Chick survival	Nest success
Florida scrub-jay (*Schoech 1996*)	Drought	83.8% - (95.6+97.7%)/2 = -12.85%					

Common tern (*Nisbet 1975*)	Heat wave					Average 18% across colony, age and cover dependent	
Western gull (*Salzman 1982*)	Heat wave					Average 37% mortality	
Semi-arid passerines (*Bolger et al 2005*)	Drought		6.7% - 88.4% = -81.7%	1.44	0.07-2.37 = -2.3		1.8% - 47.7% = -45.9%
Bridled titmouse (*Christman 2002*)	Drought (La Nina)		53%- 100% = -47%		0.4-4.4 per breeding pair = -4	41.4% - 100% = -58.6%	23% - 85% = -62%
OCWA (Santa Cruz Is.) (*Langin et al 2009*)	Heat wave	94%	100%		11%		
Orange-crowned warbler (Catalina Island) (*Langin et al 2009*)	Drought	2%	11%		0		
Tropical forest birds (*Faaborg 1982*)	Drought	No active breeding observed, juveniles were 6% of following year population					

Wading birds (*Frederick and Ogden 2001*)	Drought	No nesting

Chapter 1

Introduction

My review of the literature revealed general bird response themes including forgone or reduced breeding effort, relocation for the breeding season, and the death of juvenile birds. These different responses were not equally distributed through the breeding season, but occurred with specific timing. When drought conditions occurred during migration, reduced adult body condition or delayed arrival at breeding grounds were observed consequences (Tøttrup, et al., 2012). If drought is dire enough by the time of e.g. territory establishment, species may move to more suitable conditions or forgo breeding, due to differing evolved life history characteristics. For example, northern pintail have moved to the Arctic when surface water is too scarce within their normal breeding range (Henny, 1973). On the other hand, an example of a forgone breeding season without movement was observed in four passerine species during an extreme drought year (Bolger, et al., 2005). If a stochastic event happened after hatching, juveniles recruitment may be reduced, as was the case in a population of Louisiana waterthrush exposed to precipitation anomalies (Mattsson and Cooper, 2009).

I wanted to determine which characteristics of the reported weather events were most strongly related to bird response. I hypothesized that the extremity of the event would be a strong predictor of bird response, that is, how greatly the event deviated from normal climatic conditions. Unfortunately, this information was not often available, or at least not in a form that was comparable across studies. One question that remains unclear is whether climatic thresholds are related to bird responses, and if so, what these thresholds are. Since even in cases of weather stress and extremely reduced breeding effort, there was no observation of population-wide abortion of breeding behavior, there is likely a gradient of avian response across a range of weather conditions. It would be instructive to better understand the nature of that relationship, to be able to predict avian response based on given climatic conditions. This would illuminate past population dynamics, as well as response to future climatic events.

The observed avian responses to extreme events ranged from single-species breeding behavior to community metrics, depending on the focus of the study. For example, bridled titmice in the Chiricahua mountains largely failed to produce young during a La Nina year (Christman and Thompson III, 2002). In a different study, researchers detected breeding bird density declines within the 15 most common species encountered at a North Dakota field site, concurrent with declines in species richness and diversity by conducting line-transect surveys during a drought year (George, et al., 1992). These localized studies provide interesting observations of avian population response under extreme conditions, which lead to questions and hypotheses about patterns of response under similar conditions, and what specific conditions or weather parameters trigger a given response.

In order to determine whether or not a pattern of response exists, both long-term weather and avian survey data are needed. Most studies included in the literature review are from limited-term projects. Further, data from spatially separated populations would be desirable in order to test the generality of the response to extreme weather. Thus, I am curious as to whether or not the North American Breeding Bird Survey (BBS) captures the observed localized population changes associated with these weather events that have been documented in the literature. I will look for bird population responses in BBS data that corresponds to the published response, and concurrently examine weather data from the record of nearby stations in order to calculate deviations from normal climate. It will be interesting to see if these relationships do hold in the larger-scale data, and can be generalized and observed in places other than the prior study locales. Thus, my goal is to determine whether or not observed, localized avian responses to extreme weather are evident in concurrent but larger-scale, standardized citizen science efforts; namely, BBS data. Also, I want to assess the strength of relationship between standardized precipitation index (SPI) and standardized temperature index (STI) and BBS data, to determine whether or not these weather metrics are good predictors of avian population and community trends.

Methods

Data

The BBS has been conducted since 1966, and is designed to capture breeding bird abundance in natural areas across the conterminous US. Each participant covers 24.5 miles per survey route, and all birds seen and heard during each 3-minute stop (conducted every 0.5 miles) is counted. Since the data is also spatially recorded, it is possible to examine habitat associations and distributions by analyzing land cover along the route, and this data may be applied to answer questions related to e.g. efficacy of protected areas. There may be many drivers of population trends observed in BBS, and there has been much research published regarding analysis and interpretation of this dataset (Holmes and Sherry, 1988). Similar surveys from other countries have been used to relate avian population trends to extreme events (Jiguet, et al., 2006).

We relied on standardized indices to quantify how unusual the extreme events reported in the literature were given climate conditions at each site. The Standardized Precipitation Index (SPI) is a simple and widely used measure of drought (McKee et al. 1993). One advantage of this index over other drought measures is that the measurement timescale can be readily adjusted to the study system in question (Guttman 1998). The Standardized Temperature Index (STI) is an

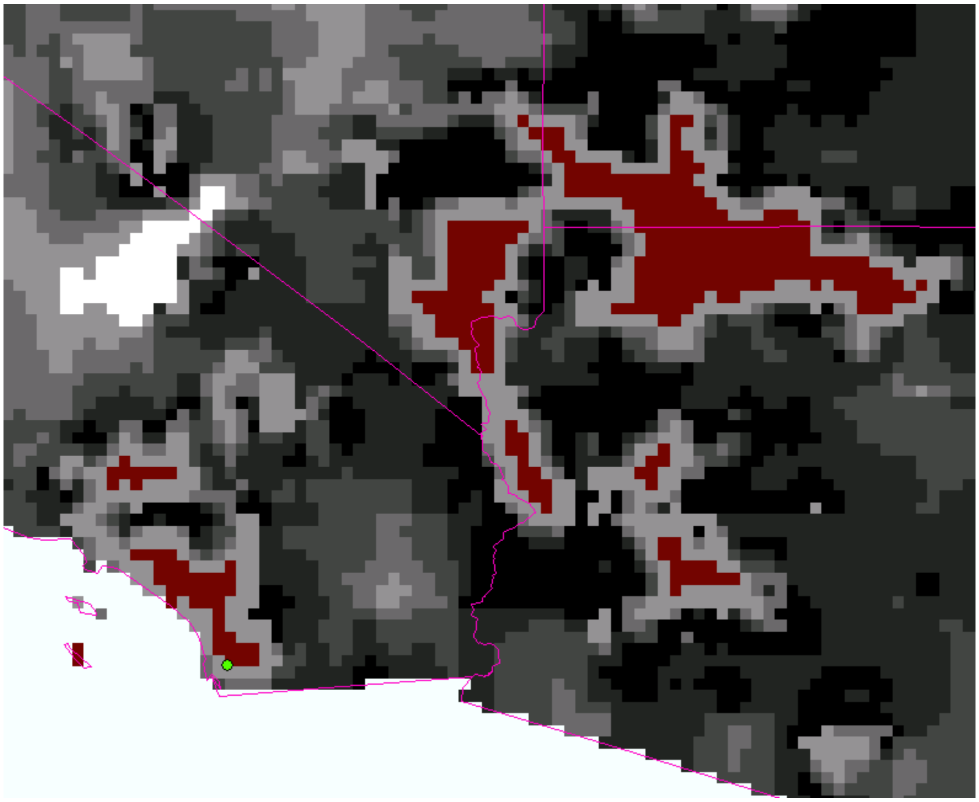

Figure 1. Map of SPI values for 2002, comparing annual precipitation (July-Jun) to the available time record. An extreme drought is evident (red) in the San Diego area, and is reflected in arid passerine community breeding failure.

analogous measure for temperature (Allstadt et al. in prep). To calculate these indices, we located a weather station near the recorded event with at least a 30-year record including the year when the event was recorded. Where possible, we used the weather stations mentioned in the original study. On an annual basis, we calculated the total precipitation and average temperature for the time periods mentioned in the study as an extreme event. We then fit a distribution to these annual values, using a Pearson-III distribution for SPI (Guttman 1999) and the generalized normal distribution for STI (Allstadt et al. in prep). The resulting percentiles corresponding to each year were converted to standard deviations from a standard normal distribution for familiarity and to accommodate assumptions of common statistical analysis. These standard deviations indicate how unusual the precipitation or temperature patterns were in a given year, with negative values for SPI indicating a drought (Figure 1), and positive values for STI (Figure 2) indicating a heat wave.

Analysis

I aim to determine the mathematical nature of the relationship between BBS abundance and weather variables. I will investigate whether or not the singular extreme events and concurrent avian responses reported in the literature are adequately reflected in the weather station data (SPI and STI) and BBS data (abundance), respectively (Table 1). If these responses are well captured in these coarser datasets, there will be further evidence that the datasets are useful to represent the relationship between birds and extreme events. Thus, this data can be used to investigate extremes and bird responses elsewhere. Once this relationship is determined, it will ideally become apparent at which deviations either significant or extreme bird responses occur. Though this may not be a binary threshold, these values can be used to understand where we can “see” avian responses at the resolution of our data.

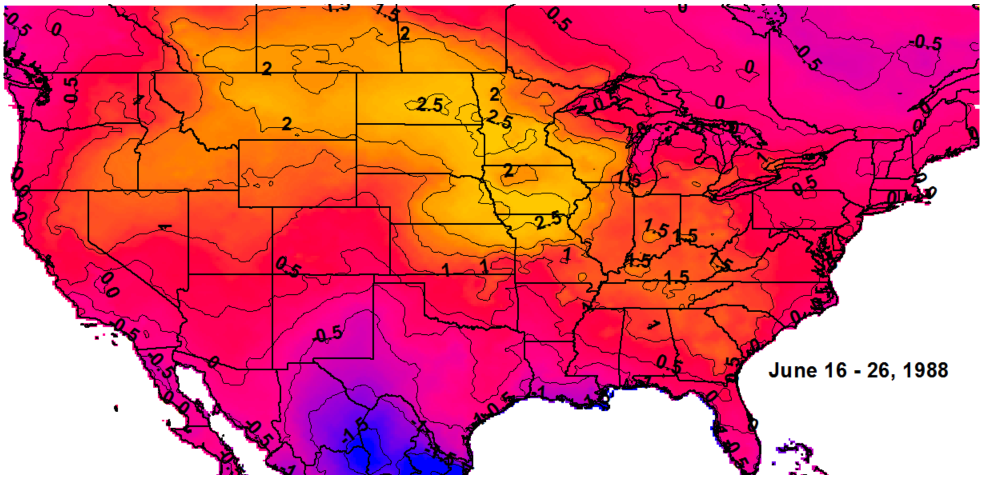

Figure 2. Map of STI values, highlighting the extreme temperatures that accompanied the 1988 drought of the Midwest. This extreme event was reported to affect grassland birds (George, et al., 1992) and mallards (Krapu, et al., 2006) in North Dakota, and house wrens in the Sierra Nevada foothills (Verner and Purcell, 1999)

Table 1. The availability of BBS data at the locations of studies of extreme events affecting birds.

Author, extreme event	BBS route #(s)	BBS route name(s)	Spp.
George et al. 1992, drought	64032	GORHAM	Sharp-tailed grouse, upland sandpiper, mourning dove, eastern kingbird, horned lark, Sprague's pipit, clay-colored sparrow, field sparrow, vesper sparrow, lark sparrow, Baird's sparrow, grasshopper sparrow, western meadowlark, brewer's blackbird, brown-headed cowbird
(Christman and Thompson III, 2002), drought	6133, 6033, 6901	PORTAL, SUNIZONA, RUCKER	Bridled titmouse
Bolger et al. 2005, drought	14091, 14050	POWAY, SAN YSIDRO	Wrentit, spotted towhee, California towhee, Rufous-crowned sparrow
Langin et al. 2009, drought	14099, 14135	S CATALINA, S CRUZ I	Orange-crowned warbler
Verner & Purcell 1999, drought	14022, 14191	BASS LAKE, ONEALS	House wren, Bewick's wren
Nisbet 1975, heat wave	47004, 47001	WELLFLEET, E DENNIS	Common tern
Schoech 1996, drought	25024	CHILDS	Florida scrub-jay

I will model the relationship between weather variables (SPI/STI) and avian abundance (BBS), and quantify the strength of this relationship at the route level.

Expected results

I plan to test whether responses of birds to extreme weather characterized in BBS data mirror those observed in the localized published studies. Of this analysis, I expect an estimate of abundance declines using BBS data in response to severity of an event. I also hope that this response can be described in clear mathematical relationships between weather variables and route-level abundance. There may be interesting qualitative differences in response among species, such as higher or lower tolerance to anomalous conditions, or differences in temporal response, such as sensitivity to different scales of extreme events. Also, the patterns of response may differ per species, such as a positive linear relationship between SPI and abundance for some species vs. a logarithmic or exponential relationship for others.

Significance

I hope to better understand the “signal” in both bird and weather data that will allow us to investigate other places and times where these events may have occurred that have not been reported in the literature. Understanding mathematical relationships between weather and avian variables will lend to predictive capabilities outside the system studied. Scientifically, this work is applicable to broader questions related to biotic response to climate change. The frequency and severity of extreme events is predicted to increase with climate change, so if the BBS and weather station records prove as useful tools to understand those changes, then we can use the past record of response to better understand how birds will react to a more variable climate across eco-regions. Methodologically, if BBS captures known avian population responses at the route level, its precision can be further validated. Any differences per species will be used to form ecological hypotheses that also may be generalizable based on life history traits, but at least would give clearer insight into how ecological response may be specific.

Chapter 2

Introduction

Based on published observations, it is reasonable to hypothesize that in cases of extreme weather during the breeding season, forest songbird productivity may be reduced in proportion to the extremity of the event. For example, in cases of severe drought, some forest songbirds may choose not to breed for a season (Christman and Thompson III, 2002, Faaborg, 1982). Nestling survival may also be negatively impacted by a sufficient dearth of precipitation during the breeding season (Mattsson and Cooper, 2009). Effects may differ by ecosystem (Şekercioğlu, et al., 2012) and migratory habit (Bauchinger, et al., 2011). Though direct water stress to birds is a concern in extreme environments like the Sahara (Schmaljohann, et al., 2007), the effects of drought may also appear indirectly via lower food availability (Hahn, et al., 2008), altered predator-prey dynamics (Sperry and Weatherhead, 2008) and/or habitat change (Canterbury and Blockstein, 1997). Given these observed, local responses of forest songbirds to extreme weather, this guild seems sensitive to weather variability, and thus potentially a good subject for community and species-specific analyses. Impacts of extreme weather may be seen as lower population abundance in the year of or following an extreme event (Jiguet, et al., 2006), or lower numbers of juveniles within that year's population, within datasets designed to capture these metrics (Faaborg, 1982).

I predict that extreme events during the breeding season will lower forest songbird productivity. Though ecological requirements are similar across species in this guild, niche is by definition, fundamentally different per species. Therefore, it is possible that extreme events will affect species within a guild differently. Some may be more severely affected than others, or the pattern of response may differ with respect to specific physiological tolerances or life history traits. For example, some forest songbirds are obligate riparian species (Mattsson and Cooper, 2009), while others are more generalist within forested habitats. In this case, both habitat restriction and species dependence on water could lead to differential response to extremes per species. Effects of extreme events may not only correspond to lowered abundance of highly affected species, but may be reflected in changes in species richness and diversity within the forest songbird guild. There may be also patterns of response that affect the entire guild. Thus, in order to determine how extreme events affect forest songbirds at the guild and species levels, I will examine a suite of weather variables to describe extreme weather events in relation to species abundance, as well as community metrics. I aim to determine the strength of the relationship between these extreme weather metrics and forest songbird response variables, which weather predictors perform best in the models, and the mathematical nature of the response. Thus, I will determine if species respond differently, or respond to different suites of variables, and if there are coherent response patterns across the guild. I will use these models to draw methodological and ecological conclusions about the observed results.

Methods

Study Area

I will investigate these phenomena within the conterminous U.S.

Data

The BBS is a citizen science effort designed to capture year-to-year trends in bird populations and communities. The BBS covers 39.4 km per survey route, and all birds seen and heard during each 3-minute stop is counted. Since the data has a spatial component, it is possible to examine habitat associations and distributions by analyzing land cover along the route, and this data may be applied to answer questions related to e.g. efficacy of protected areas. Similar surveys from other countries have been used to relate avian population trends to extreme events (Jiguet, et al., 2006).

The MAPS program is a mist-netting effort, often conducted in wildlife refuges, that involves operating mist nets during each of 10 periods over the course of the breeding season. The first time period (May 1-10) is designed to capture adult birds upon (if migratory) return to the breeding grounds, and can thus include transients if the sampling is performed early during the period. As the season progresses, the goal is to capture breeding adults across the sample area, and then capture their offspring as they fledge later in the season. From this data, variables such as the juvenile-to-adult ratio can be calculated as a measure of productivity. The spatial area of each MAPS station is much smaller than the BBS, but the temporal resolution is finer, lending to demographic information about the bird communities sampled.

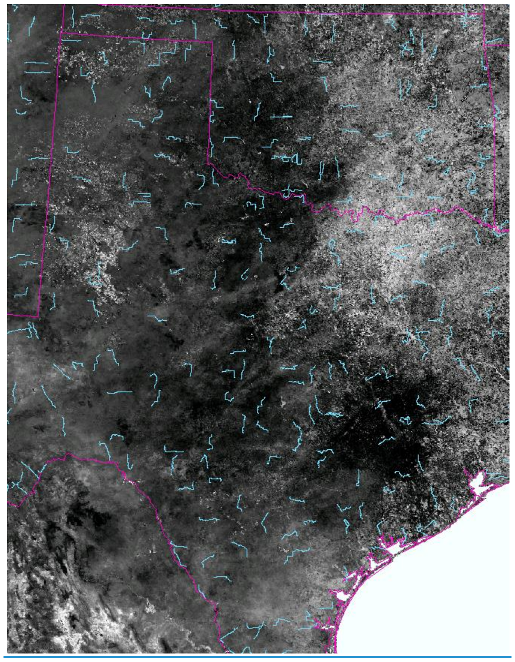

Figure 1. NDVI anomaly of May 2011, with BBS routes (light blue lines). Anomalies were calculated by computing the mean value per pixel for 2003-2011 and subtracting this mean from each observation. The image is displayed in grayscale, so negative anomalies are represented by darker colors, while positive anomalies are lighter. This image thus visualizes a vegetative drought in Texas, as compared with average values of NDVI for May over the MODIS time record.

Moderate Resolution Imaging Spectroradiometer (MODIS) captures variables such as land surface temperature (LST) and spectral data that can be used to calculate normalized difference vegetation index (NDVI). Lower NDVI indicates reduced vegetative vigor. It has been used as an indicator of drought (Peters et .. 2002), and I plan to use this index to capture vegetative conditions that may be important to birds (Figure 1).

difference vegetation index (NDVI). Lower NDVI indicates reduced vegetative vigor. It has been used as an indicator of drought (Peters, et al., 2002), and I plan to use this index to capture vegetative conditions that may be important to birds (Figure 1).

I plan to investigate the use of the land surface temperature product MYD11A2 (1 km spatial resolution, 8-day compositing period) and the NDVI product MYD13A3 (1 km spatial resolution, monthly compositing period) as suitable proxies for heat wave and drought, respectively. The time periods are especially suitable given the findings of Ch. 1: 8-day is the minimum compositing period for reliable spatial coverage of the desired area, and thus was chosen to best approach the short-term heat wave phenomena that can affect birds during the breeding season. Meanwhile, the minimum time period in the literature used to describe drought was one month (Frederick and Ogden, 2001), so this seemed like an appropriate compositing period ecologically, and with respect to maximizing quality of data incorporated into the imagery without sacrificing meaningful temporal information.

Analysis

I will average anomalies calculated per pixel within 20 km of each BBS route, and thus relate bird abundance to anomalous weather at the route level. I will simultaneously investigate the relationships of weather variables to BBS abundance, in order to determine the best predictors of avian response. I will examine plots of these variables to determine the nature of relationships (linear, logarithmic, etc.), in order to understand the mathematical nature of the relationship between weather and avian population response. I plan to use a model selection technique (i.e. AIC) to determine what the best predictors of route-level abundance are for the guild of forest songbirds, and per species within that guild. I will thereby develop species-specific and community models of avian abundance as related to a larger suite of weather-related variables (SPI/STI, NDVI, LST, etc.), and determine whether or not the best predictors for community-level metrics are the same for individual species within the forest songbird guild.

I will also calculate the juvenile-to-adult ratio for species within the forest songbird guild, and relate this metric to the same set of weather variables and proxies for extreme events. This analysis will also likely be performed in a regression framework as appropriate for the data. Thus, I will determine the relationship between a suite of weather variables and juvenile-to-adult ratio, as a metric of productivity.

Expected Results

This will shed light on how avian populations respond to varying weather conditions, and whether or not important thresholds to weather exist. Best ranked models will reveal the best weather predictors per species and for the guild, leading to an understanding of what is important climatically for forest songbirds.

Significance

If suitable models are found, we will be better able to predict forest songbird response to anomalous weather conditions, which may have implications for adaptive management. Further, differential responses would reveal species-specific needs and vulnerabilities. If a species responds more severely to weather anomalies than e.g. another congener, it may be at higher risk in a more variable climate scenario. Thus, this knowledge can reveal urgency for a certain species conservation plan, and can be incorporated into future management and prioritization planning. Also, guild responses would potentially be applicable to holistic forest management.

Chapter 3

Introduction

Prothonotary warblers (*Protonotaria citrea*) are dependent on ecosystems that are characterized by standing or slow-moving water. These ecosystems include seasonally flooded bottomland hardwood forest, bald cypress (*Taxodium distichum*) swamps, riparian areas or forested lakes (Petit, 1989). Prothonotary warblers may indeed be indicators of wooded wetland habitat quality, as reflected by their presence and density (Hoover, 2009). However, in some areas a novel situation has been imposed by human-altered hydrology, which may act as an ecological trap (Hoover, 2008). Channelization of rivers can cause faster drainage of prothonotary warbler habitat, which cannot be anticipated by the birds (Hoover, 2009). Drainage results in lower habitat quality, because prothonotary warblers have adapted in many ways to utilize water, and exhibit highest productivity in flooded habitats (Hoover, 2003). Nests are usually placed in cavities directly over water, which deters predators (Hoover, 2006). Older nestlings and fledglings have adapted to be able to “row” with their wings in order to traverse water surfaces if needed after leaving the nest, which enhances survival. Drier sites are often occupied by immature males, who experience lower pairing success than males in flooded sites.

Nests are susceptible to parasitism by brown-headed cowbirds, which sometimes destroy existing nests in order to force re-nesting by host prothonotary warblers, and promote subsequent cowbird egg acceptance (Hoover and Robinson, 2007). Offspring from parasitized nests often return to their natal area to breed, which increases their susceptibility to parasitism (Hoover and Hauber, 2007). Parents that raise cowbird nestlings provision at a higher rate, and produce smaller warbler nestlings than those whose nests are not parasitized (Hoover and Reetz, 2006).

Given that prothonotary warblers respond to standing water, drought could significantly alter their breeding habitat, and thus potentially affect breeding success (Smith, et al., 2010). Depending on the severity of the event, drought could restrict available habitat by lowering the amount of surface water, with potential consequences including lower nestling success or lower territory density. It is also possible that a population might forgo a breeding season, as has been documented for the cavity-nesting songbird, bridled titmouse (*Baeolophus wollweberi),* during severe drought (Christman and Thompson III, 2002). Since prothonotary warblers are wetland-dependent, it is possible that nesting will not be initiated until water levels are sufficient, or may be delayed in years with lower-than-normal water levels. If a breeding season is delayed due to unsuitable weather, there is evidence that later fledge dates are associated with reduced juvenile survival (McKim-Louder, et al., 2013).

Extreme heat can also decrease habitat quality, and anomalously high temperatures during incubation can cause inviable eggs (Olsen, et al., 2008). If an extreme heat event occurs after hatching, nestling mortality may be high. In fact, there is a report of prothonotary warbler nestlings dying during a “hot afternoon” (Walkinshaw, 1953). Depending on the timing of the extreme heat event, second clutches may be more affected than first clutches (Møller, 2011).

When high temperature and drought occur concurrently, the stress on wetland-associated species can be compounded. High temperatures combined with low water are likely to more negatively affect prothonotary warblers than the occurrence of one weather extreme alone. Protracted drought may also alter vegetative communities, potentially even causing tree mortality (Allen and Breshears, 1998). Thus, a prolonged drought may change a forested wetland composed of cypress, tupelo, etc. to a drier forest type, composed of trees that are less tolerant to flooding.

The effect of extreme weather on bird populations may ultimately be mediated by available food supply. The breeding-season diet of both adults and nestlings is primarily caterpillars, midges (Chironomidae), and spiders (Petit, et al., 1990). Prothonotary warblers also respond to outbreaks of mayflies (Ephemeroptera), and opportunistically forage on aquatic organisms such as dragonflies (Odonata), mollusks and isopods (Isopoda) (Petit 1999). Hovering and fly-catching behaviors increase when feeding nestlings (Petit, et al., 1990). Since several potential prothonotary warbler prey items are dependent on water, prey population (e.g. midges, odonates, mollusks, isopods, mayflies) fluctuations in response to drought may be the determinant of prothonotary warbler response (Gray, 1993). Thus, many prothonotary warbler prey species directly or indirectly depend on water levels within the habitat, and thus prey availability may be the primary proximal mechanism determining prothonotary warbler population trends in relation to weather.

Extreme weather has also been shown to affect bird and nest predators (Catling, 1988). For example, prey switching occurs as prey dynamics change in times of extremes (Sperry and Weatherhead, 2008). Thus understanding the indirect effects on prothonatory warblers and other species nesting in the wooded wetland ecosystem could yield important insights into the role that predation may have on this community as extreme weather frequency increases in the future.

I hope to determine whether or not prothonotary warbler nest success is negatively affected by extreme weather conditions, and if so, at what nest stage success is most affected. I would like to characterize weather conditions that cause a decline in various stages of breeding, if the data is available. If possible, I will do this by determining the nature and strength of relationship between weather variables (e.g. precipitation, temperature, etc.) and breeding parameters (e.g. clutch size, # inviable eggs, nestling survival, fledge success). I predict that drought conditions, if severe enough, will delay clutch initiation. If indeed drought conditions delay onset of breeding, I predict a lower first-year survival rate of the juveniles hatched during a drought year. If extreme weather occurs after breeding activities have commenced, I expect to see various responses based on the nesting stage during which they occur. For example, if a heat wave occurs during incubation, I expect a higher incidence of egg inviability or nest abandonment. If extreme weather occurs after hatching, nestling survival may be reduced. Thus, my goal is to assess the contribution of extreme weather to nest success, with both coarse and fine measures of prothonotary warbler breeding effects.

Methods

Study Area

A long-term (1994 to present) prothonotary warbler dataset has been collected by Jeff Hoover and Wendy Schelsky in the Upper Cache River watershed in Southern Illinois. The study area is 192-km^2, and includes floodplain forest, forested sloughs and backwaters, and deep-water hardwood swamps. A nest-monitoring study of this spatial and temporal range is rare. Prothonotary warblers nest in tree cavities and artificial nest boxes, which allows for monitoring and control of several variables (Hoover, 2003).

Data

Prothonotary warblers

Nest boxes have been placed within suitable habitat, and monitored from nest building to fledging. Thus, nest progress at all stages has been recorded, providing data on clutch initiation, clutch size, probable cause of failure/nestling mortality/unviable eggs, hatching, nestling survival and fledging (Hoover, 2003). Additionally, >95% of the population has been banded, allowing for monitoring of year-to-year dynamics such as site fidelity and survival. Such fine-scale data on this population of prothonotary warblers provides the opportunity to investigate the effects of short-term temporal weather variability on various breeding processes. Further, experiments have been designed that may yield interesting comparative results in extreme vs. normal years. For example, certain nest boxes have been built with predator exclusion, making it potentially possible to tease apart the independent effects of predation and weather on nest success.

Weather

To assess weather conditions, I plan to do a comparison between directly measured conditions within the ecosystem and available weather sources, such as local weather station data and remote sensing products, in order to determine what the best measure of weather is for the bottomland hardwood study site. Weather variables of interest include maximum air temperature, deviation of maximum air temperature from normal (or anomaly), amount of precipitation, and precipitation anomaly. I would like to deploy iButtons® and Phenocams in order to gather fine-scale data on weather and vegetation at the site (Wolaver and Sharp, 2007). Phenocams are cameras that capture phenological data locally, and can be monitored remotely (for example, visit University of New Hampshire's website). Both of these technologies have been developed to capture local ground conditions, and can be compared to coarser datasets. Thus, I hope to compare data from these field site devices to both nearby weather station data and remotely sensed (i.e. MODIS) weather data and its proxies. Weather station data is often considered the "ground measure" of weather conditions, and captures variables such as temperature and precipitation. Yet, unless the station is on site, its measurements can vary significantly from those of interest. Further, if there are not many stations available, data can be skewed by faulty calibration, or lost in missing days of observations. Remote sensing data can provide smoother and more standardized coverage, but is subject to its own equipment and observation limitations. MODIS observes many wavelengths, and NASA provides products calculated from those observations, such as land surface temperature (LST) and normalized difference vegetation index (NDVI). Vegetative vigor is measured by NDVI, and thus lower-than-normal NDVI can indicate drought. There is a tradeoff between spatial and temporal resolution for satellite imagery, meaning that e.g. more frequent observations often require lower spatial resolution. Also, cloud cover often precludes the use of daily observations, so in using e.g. MODIS data, 8-day composites are much more often reliable. I plan to “ground-truth” the MODIS products MYD11A2 and MYD13A3, in order to determine what coarse-scale datasets available best characterize weather conditions at the site, and use the resulting datasets to characterize weather or related variables of importance for the longer-term time record.

Overall seasonal average temperature and water conditions, as well as smaller time windows within the breeding season, will be calculated. As mentioned above, a one-day temperature anomaly extreme enough may kill nestlings, so daily temperature anomaly, considered with timing of occurrence in the breeding season, may predict nest failure. Also, if available, water depth within the flooded forest could be an important drought metric. These values will be compared to the long-term average conditions, in order to determine degree of weather anomaly for a breeding season, both in terms of value difference and standard deviation.

Analysis

I plan on working in a regression or mixed effect modeling framework, as appropriate to the data, in order to determine associations between nest success and weather. Initial scatterplots will shed light on the shape of the relationships, and help me to determine the most appropriate modeling framework, and will give insights into the existence of potential physiological, breeding behavior or success thresholds in relation to weather.

The response variables I plan to analyze are clutch size, number of nestlings, number of fledglings per nest, and juvenile survival. The independent variables will be precipitation, precipitation anomaly, NDVI anomaly, water depth (if available), temperature, and temperature anomaly, from both weather station and MODIS data, or whatever subset proves to be most appropriate to this system. Overall season averages of weather variables will be related to total productivity, and smaller time window weather conditions will be related to breeding onset and temporal productivity.

I plan to relate weather conditions at arrival of males on breeding grounds (anomaly of average precipitation or water deficit, where applicable, from beginning of the year to time of male arrival on breeding grounds) to territory density, and timing of nest and clutch initiation. Then, I will examine both temperature and precipitation anomaly after clutch initiation in relation to clutch size and hatch success. I will relate temperature and precipitation anomaly during the nestling phase to fledge success and nestling mortality/survival probabilities.

As mentioned above, a comparison between predator-excluded and predator-allowed nest boxes may be possible with this dataset. I would like to 1) investigate whether or not predation pressure differs between extreme and normal years and 2) if possible, determine the effects of extreme weather on nest success, independent of predators. Since cause of mortality is estimated, it may be possible to report variation in predation pressure between extreme and normal years.

Expected Results

I predict that weather will be strongly correlated with different breeding activities, based on the timing and severity of the event. Overall productivity will likely be lower in summers where both heat and drought were extreme. Also, I predict that clutch production will only commence when conditions are suitable, e.g. when there is enough available water. I expect that clutch production will be delayed during anomalously hot and dry weather.

Significance

This will expand on the literary record and further test the trends emerging from the collection of studies that capture avian response during times of extreme weather. This study will aid in determining if this system fits in with emerging trends, or exhibits a response other than what has been recorded in different systems. Either type of response will aid in predicting ecological response to future extremes.

Overall Significance

This work will result in a deeper understanding of how extreme weather events affect birds. Scientifically, I will contribute to avian ecology by quantifying how avian populations respond to extreme climate events across broad scales. Nationwide investigations of avian response to weather have not been done. Through this analysis, we can better predict how birds will respond in the future at the population level (McKechnie and Wolf, 2010). I hope to estimate at what deviations from normal bird populations are likely to undergo a significant decline, and to be able to measure these conditions using remote sensing imagery and large-scale weather datasets. By examining a specific population of prothonotary warblers, I hope to gain understanding of the population level processes affected by climatic deviations for this species. However my findings about the prothonotary warbler population will be used to develop hypotheses of response pattern for species with similar life history traits

Methodologically, this work will further our understanding of the applicability of remote sensing data to conservation problems. By using the latest MODIS products in tandem with large-scale data on bird occurrence and abundance, I will not only quantify relationships between the remotely-sensed independent and the avian response variables, but will also measure how well satellite imagery captures weather phenomena that influence birds. I will determine whether previously established relationships are characterized similarly, or not, when analyzed using updated imagery products. Thus, we may discover that variables captured by newer sensors have different predictor capability than previously used data sources. By deploying local sensing devices such as iButtons and Phenocams, I will learn more about the relationship between ground conditions and bird response, and the relationship between ground conditions and satellite imagery in forested wetlands. Forested wetlands may not be well-characterized by NDVI because of the background water signal, so it will be instructive to attempt to quantify this relationship. If remote sensing and large-scale weather datasets prove useful for characterizing weather phenomena that affect birds, these datasets can be further investigated and used to tackle conservation issues.

Climate change has the potential to equal land use/land cover change in its impact on biotic communities. Thus, traditional methods of land preservation and habitat management will be incomplete without accounting for the effects of climate change on ecosystems. In contributing to better understanding of patterns of response to climate by birds, my work will provide information needed for management decisions. Vulnerability assessments to climate change are becoming standard in considering species conservation issues at the federal, state and local levels (Klein and Nicholls, 1999). For example, state natural resources management agencies are developing adaptation plans (e.g., WICCI (http://www.wicci.wisc.edu/). I believe my work here will contribute to understanding species' vulnerability to climate change, and since the results will be at the nationwide scale, will provide context for state level and regional level decisions.

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