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Combined effects of heat waves and droughts on avian communities across the conterminous United States

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Abstract. Increasing surface temperatures and climatic variability associated with global climate change are expected to produce more frequent and intense heat waves and droughts in many parts of the world. Our goal was to elucidate the fundamental, but poorly understood, effects of these extreme weather events on avian communities across the conterminous United States. Specifically, we explored: (1) the effects of timing and duration of heat and drought events, (2) the effects of jointly occurring drought and heat waves relative to these events occurring in isolation, and (3) how effects vary among functional groups related to nest location and migratory habit, and among ecoregions with differing precipitation and temperature regimes. Using data from remote sensing, meteorological stations, and the North American Breeding Bird Survey, we used mixed effects models to quantify responses of overall and functional group abundance to heat waves and droughts (occurring alone or in concert) at two key periods in the annual cycle of birds: breeding and post-fledging. We also compared responses among species with different migratory and nesting characteristics, and among 17 ecoregions of the conterminous United States. We found large changes in avian abundances related to 100-year extreme weather events occurring in both breeding and post-fledging periods, but little support for an interaction among time periods. We also found that jointly-, rather than individually-occurring heat waves and droughts were both more common and more predictive of abundance changes. Declining abundance was the only significant response to post-fledging events, while responses to breeding period events were larger but could be positive or negative. Negative responses were especially frequent in the western U.S., and among ground-nesting birds and Neotropical migrants, with the largest single-season declines (36%) occurring among ground-nesting birds in the desert Southwest. These results indicate the importance of functional traits, timing, and geography in determining avian responses to weather extremes. Because dispersal to other regions appears to be an important avian response, it may be essential to maintain habitat refugia in a more climatically variable future.

Key words: birds (Aves); climate change; drought; extreme weather; heat wave; land surface temperature; mixed effects models; MODIS; North American Breeding Bird Survey; standardized precipitation index; United States.

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Introduction

Episodes of extreme weather can alter biotic communities by affecting survival, reproduction, habitat selection, and resources on which organisms depend. Under a changing climate, extreme weather events such as heat waves and droughts are likely to become more frequent and intense in many locations (IPCC 2007). In much of temperate North America, changes in the interannual variability in temperature and precipitation are predicted to be the most drastic aspects of climate change in the 21st century (Diffenbaugh et al. 2008). Extreme events, which exceed ecological or physiological tolerances of some species, may have greater influence on population persistence than changes in mean conditions (Jentsch et al. 2007). As societies and ecosystems are confronted with a changing climate, it is critical to understand how events such as heat waves and drought affect biodiversity (Archaux and Wolters 2006). However, such an understanding is often limited to individual species, sites, and disturbance events, while a broader perspective that considers communities, diverse regions, and interactions among events is lacking.

Drought has been associated with lower habitat quality (Mueller et al. 2005), higher mortality (Mooij et al. 2002), and reduced reproductive effort (Christman 2002), and can decrease abundance and species richness of avian communities (Albright et al. 2010). Heat waves can also stress avian communities by increasing water requirements (Guthery et al. 2005), eliciting altered behavior on birds (Guthery et al. 2001), and reducing reproduction and survival (Becker et al. 1997, Christman 2002), resulting in altered community structure and lower species richness (Albright et al., *in press*). There is some evidence that the effects of both heat waves and drought vary among birds according to their migratory strategy (Albright et al. 2010), body size (McKechnie and Wolf 2010) and other functional traits (Jiguet et al. 2006), and among regions with differing climate regimes (Albright et al., *in press*).

The timing of disturbances influences their effects on vegetation and ecological communities (Pickett and White 1985). For example, the impacts of drought on primary productivity can depend on whether drought occurs before, during, or after the main period of vegetation growth (Heitschmidt et al. 1999). The timing of events may also be important to birds, because they have different requirements at different times in their annual cycles. Caloric needs may be higher while caring for nestlings (Williams 1988) and prior to and during migration (Jenni-Eiermann and Jenni 1996), which may affect the sensitivity of birds to extreme weather events. The periods of the year during which bird species are most sensitive to heat waves may also depend on the functional characteristics of the species (Albright et al., *in press*).

Heat waves often, but not always, accompany droughts (de Boeck et al. 2010). In most non-polar terrestrial regions, summer temperature anomalies are negatively correlated with precipitation (Trenberth and Shea 2005). A key contributor to this relationship is that low soil moisture associated with drought results in an enhanced ratio of sensible-to-latent heat (the Bowen ratio) leading to greater surface and air temperatures. In Europe, for instance, the extreme heat wave of 2003 was associated with both sustained elevated temperatures and below-normal precipitation (Fischer et al. 2007). However, heat waves may also be accompanied by normal or even above-normal precipitation (Gershunov et al. 2009). Similarly, summer droughts may occur during normal or abnormally cool periods (Trenberth and Shea 2005). For most organisms, the co-occurrence of drought and heat waves may be especially challenging as water requirements are greatly increased when temperatures are elevated. Thus, knowledge of the effects of temperature and precipitation extremes, occurring both separately and in concert, is important for understanding biotic responses to contemporary and future environmental variability.

Here, our goal was to elucidate the fundamental, but poorly understood, effects of heat waves and droughts on avian communities across the conterminous United States at key time periods of the annual cycle of birds (bioperiods): early breeding and post fledging. First, we explored the temporal dimensions of these extreme weather events by asking whether avian assemblages are more responsive during a particular bioperiod and whether the effects of extreme events occurring in consecutive bioperiods are greater than the sum of their effects individually. We hypothesized that especially deleterious effects would follow a sustained period of high temperatures and moisture deficits. While drought and heat waves are often coincident, we also asked whether the effects on avian assemblages vary according to whether these extreme weather events occur in concert or alone (e.g., a drought not accompanied by extremely high temperatures). Because of the increased demand for water at high temperatures, we predicted that periods of coincident heat and drought would be the most influential on avian assemblages. Throughout, we also sought to understand how avian responses vary according to key functional attributes (migratory habit and nest placement) and among ecoregions with differing climatic and physiographic characteristics. We hypothesized that relationships would be most strongly negative in hot and dry regions, which are subject to greater extremes, and that resident and ground-nesting species would be more affected by the extremes than migratory birds and canopy-nesting birds. Our hypothesis regarding resident species was based on their reliance on local resources and their duration of exposure to local conditions. We expected ground-nesting species to be more affected than canopy-nesting species because of the greater temperature extremes experienced at the land surface compared to the vegetation canopy.

Methods

We obtained 2000–2008 data from the North American Breeding Bird Survey (BBS; (USGS 2008) for the conterminous United States, which included 3,418 BBS routes, each 39.5-km in length. Along each route, 50 3-minute point counts are conducted near dawn annually during peak breeding season (most often during June) in which all birds seen or heard within 400 m are recorded. We removed route-years collected by first-year observers and those having inclement weather at the time of the survey (Link and Sauer 1997, Sauer et al. 2004). For each suitable route-year, we summed counts of individual birds for (1) North American landbirds ("ALL") (Rich et al. 2004); (2) three migratory guilds, namely permanent resident birds ("RESIDENT"), temperate or short distance migrant birds ("SHORTDIST"), and Neotropical migrants ("NEOTROP") (Rappole 1995); and (3) a guild composed of ground-nesting birds ("ground") (Pidgeon et al. 2007); (Table 1, complete membership lists in Appendix A). We excluded rare species ($<$30 route-year occurrences over the history of BBS in the conterminous US) and marine or aquatic species, which are poorly sampled by BBS (Bystrak 1981). We assigned each BBS route to one of 17 ecoregions based on a re-aggregation of Bailey's provinces and divisions (Bailey 1995). These modifications were made to maximize physiographic homogeneity within ecoregions while reducing variation in the number of BBS routes among ecoregions (Fig. 1).

Bioperiods and meteorological indicators

For this work, we focused on two bioperiods coinciding with key stages in the annual cycle of most temperate North American landbirds. The early breeding bioperiod corresponded to nest site selection, nest construction, egg laying, and incubation. The post-fledging bioperiod captured the vulnerable stage of young-of-year birds after they have left nests and receive decreasing levels of parental care (Adams et al. 2006). An individual's experiences during both of these bioperiods may determine its immediate survival as well its success during migration and subse-

Table 1. Avian guilds used in the study.

Guild theme	Guild	Short name	Species pool	Description
Avifauna	All landbirds	ALL	369	North American landbirds
Nest location	Ground-nesting	GROUND	105	Nest within 1 m of ground
Migratory habit	Permanent residents	RESIDENT	104	Do not migrate away from breeding range
	Short distance migrants	SHORTDIST	97	Winter north of Tropic of Cancer
	Neotropical migrants	NEOTROP	166	Winter south of Tropic of Cancer

Notes: "Species pool" refers to the number of species in the guild observed and included in the routes in the study area over the period 2000–2008. Guilds within themes are mutually exclusive but not exhaustive, as some birds not assigned a guild may nest across strata or have multiple or unknown migratory habits.

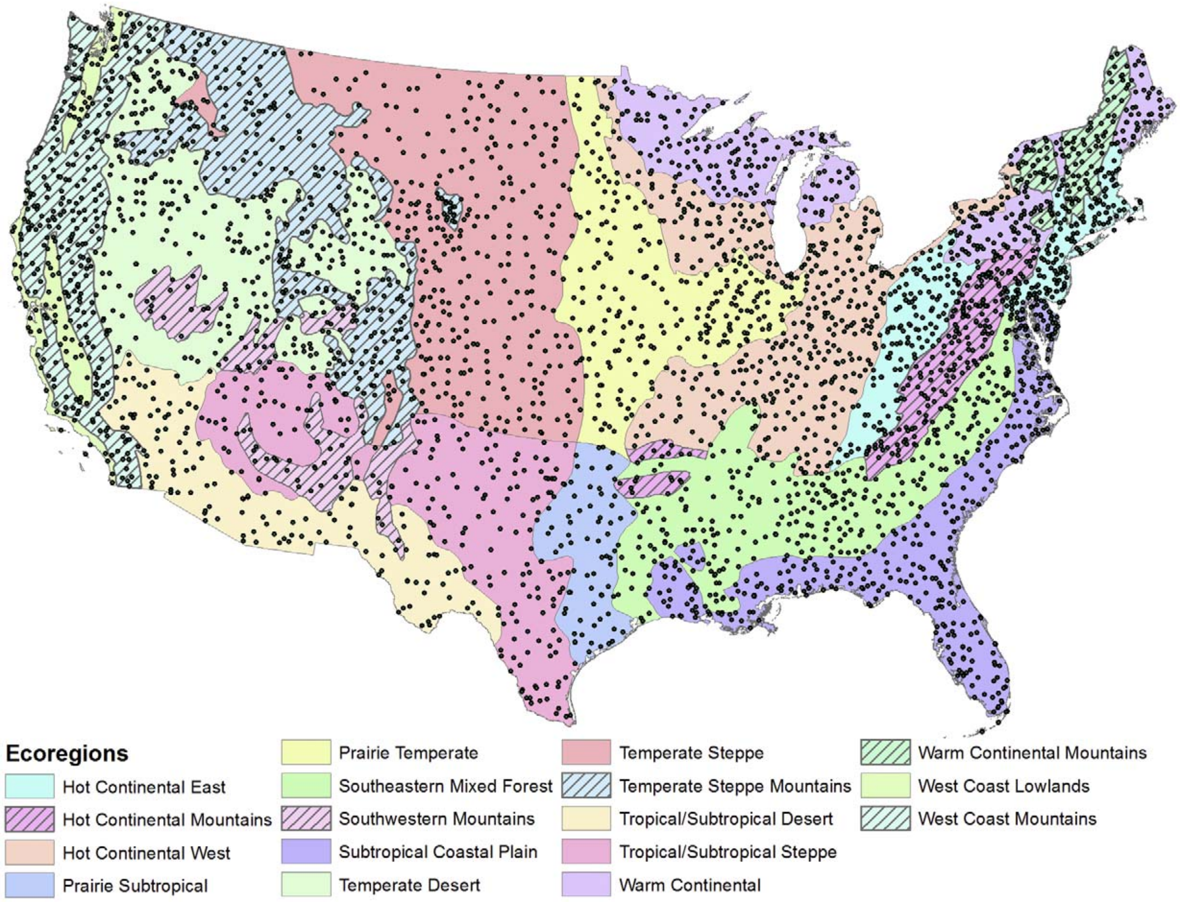

Fig. 1. Ecoregions modified from Bailey (1995) and centroids of BBS routes used in this study.

quent life stages (Merila and Svensson 1997). The exact timing of nesting and fledging varies according to ecoregion, species, and environmental conditions experienced during a given year.

Previous work has documented the predictive utility of standardized precipitation indices (SPI) (Albright et al. 2010) and remotely-sensed daytime land surface temperature (LST) exceedances (Albright et al., *in press*) when modeling avian communities in temperate latitudes. The SPI scales precipitation in units of standard deviations from mean precipitation for each location and time period (McKee et al. 1993). We obtained SPI data from 2000–2008 from the High Plains Regional Climate Center, which consisted of a network of 2427 stations with precipitation measurements from the Applied Climate Information System ⟨http://rcc-acis.org⟩ (Hubbard et al. 2004). Based partially on findings from Albright et al. (2010), we selected the 32-week SPI interval ending in June (~18 Nov–30 June) as an indicator of relevant precipitation for the early breeding bioperiod. We included winter precipitation in this time period, rather than a more narrow spring-time window, because of the influence that winter precipitation can have on spring soil moisture (Entin et al. 2000). We also included an 8-week SPI ending in late August (~2 Jul–26 Aug) as an indicator of precipitation during the post-fledging period. We then produced 1-km gridded SPI maps by interpolating SPI values from the weather stations using inverse distance weighting.

To characterize temperatures experienced by birds, we obtained 2000–2009 8-day composite MOD11C2 daytime land surface temperature data (version 5.0) from the Moderate Resolution Imaging Spectroradiometer (MODIS) flown on the National Aeronautics and Space Administration's Terra satellite. We used the full available historical record of MODIS in order to characterize mean conditions as well as possible for this data source. We excluded data with poor calibration, cloud contamination, or other quality issues, based on MODIS quality assurance information. We subtracted 2000–2009 mean values for each 8-day time period to obtain temperature anomalies for each year and projected the resulting images into Albers equal area projection with 5-km × 5-km cells. We then calculated for the two bioperiods the mean LST exceedance, T_E, which we defined as the average positive anomaly (all negative anomalies are treated as 0). Our rationale for using exceedances was that a cumulative index of high temperatures ignoring temperature variations below the mean would be a better proxy for heat wave conditions (Albright et al., *in press*). Land surface temperature exceedance for the early breeding bioperiod was based on three 8-day MOD11C2 composite periods spanning 2–25 June. Representing the post-fledging bioperiod, we also calculated mean LST exceedance over six 8-day MOD11C2 composite periods spanning 20 Jul–5 Sep. Because of the June timing of the route surveys, we relate the early season bioperiod for both LST and SPI indicators to BBS data from the same year but relate indicators from the post-fledging, which occurs after June, to BBS data during the following year. Although we acknowledge that the temporal windows for some of the metrics may not coincide with the phenology of some species (particularly the June temperature metrics in more southern locations where the breeding cycle occurs earlier), we chose to keep bioperiods consistent to facilitate analysis and comparison over a large area and across a large number of species.

In order to link the LST and SPI datasets to BBS routes, we calculated their spatial means within 20-km-radius buffers around BBS route centroids. In addition to encompassing the entire length of the route, this distance is comparable to ranges of natal dispersal distances reported in the literature (Sutherland et al. 2000, Tittler et al. 2009), indicating that the buffer captures a biologically relevant area.

Analysis

In order to reduce data dimensionality and multicollinearity within bioperiods of SPI and LST data, we centered and standardized the four environmental variables and performed a principal components transformation using the prcomp command in the R language and environment for statistical computing (R Development Core Team 2009). The resulting transformed dataset contained 89% of the original variance in the first three principal components (PCs, Table 2). Furthermore, the loadings from the transformation resulted in highly interpretable principal components. We consider the first component, "PF_STRESS", to describe post-fledging stress because it is loaded heavily on post-fledging T_E and -SPI, while the second, "EB_STRESS", describes early breeding stress because it loads most heavily on T_E and -SPI from this bioperiod. For example, high scores for PF_STRESS indicate unusually hot and dry conditions during the post-fledging bioperiod. The third component, "DRYCOOL", acts as a hybrid, indicative of coincident depressed precipitation and temperatures during both periods, but weighted more heavily on the early breeding season. Thus, a location with high values in DRYCOOL experienced drought conditions accompanied by relatively cool temperatures.

To quantify the relationship between the temperature metrics and avian abundance, rescaled as ln(abundance + 1), we developed a series of linear mixed effect models using the nlme package within R (Pinheiro et al. 2008). We

Table 2. Contributions and cumulative variance of the raw variables to principal component axes.

Raw variable	PC1–PF_STRESS	PC2–EB_STRESS	PC3–DRYCOOL	PC4
Post-fledging LST exceedance	0.707	–0.055	–0.267	0.652
Early breeding LST exceedance	–0.039	–0.705	–0.649	–0.284
Post-fledging SPI	–0.697	0.099	–0.339	0.624
Winter/early breeding SPI	0.116	0.700	–0.627	–0.323
Cumulative proportion of variance (%)	37.7	71.9	88.5	100

included a fixed effect for ecoregion to account for broad scale variation in abundance among the 17 different ecoregions. We included an *environmental metric* × *ecoregion* interaction term, which allowed fixed effects of the environmental stressors to be estimated for each ecoregion. We also included a random effect for BBS route. Similarly, different BBS observers possess different skill levels in detecting birds, which may result in biased estimates of abundance and richness (Sauer et al. 1994), prompting us to treat observers as random effects nested within BBS routes. Finally, we added a continuous time autoregressive component to account for temporal autocorrelation (no residual spatial autocorrelation was encountered). The resulting general model for predicting abundance, *y*, was:

$$y = \beta_{0i} + \beta_{1i}X_{jk} + b_j + b_k + e(t)$$

where the β_{0i} and β_{1i} were the intercept and slope vectors for the specified fixed effects at ecoregion i, X_{jk} was a matrix of PC transformed variables at route j observed by observer k, b_j and b_k were random effects for route j and observer k, and $e(t)$ was a continuous time autoregressive process of order 1.

To investigate the influence of different bioperiods and different types of extreme weather, we included ecoregion-specific fixed effects for PF_STRESS, EB_STRESS, and DRYCOOL ("main effects model"). We also considered a model that additionally included an interaction between PF_STRESS and EB_STRESS to determine whether the effects of extreme weather during successive bioperiods were, for example, greater than their effects individually ("interaction model"). For each guild, we compared these two competing models using Akaike's information criterion (AIC) (Akaike 1974), calculating change in AIC (Δ_i), and examining ecoregion-specific coefficients. As a rule of thumb, $\Delta_i < 2.0$ indicates a similar level of support as the "best" model (Burnham and Anderson 2002).

Because of the log scaling and variation in baseline abundance among the regions, coefficients estimated from these models were difficult to compare and interpret. To better understand the magnitude and variation of observed relationships between the predictor variables and avian assemblages across ecoregions, we produced a series of model predictions based on different types of extreme conditions. We first extracted the 99th percentile from each of the three PC-transformed variables to obtain nominal 100-year extreme events. We then used the coefficients obtained from the fitted models to estimate the percentage change in avian abundance predicted to occur in response to each of the 100-year events.

Results

During the nine years of this study, total bird abundance on routes ranged from 10 to 7134 individuals. Abundance was highest in the north central and lowest in the inland southwestern portions of the conterminous US. Short distance migrants were the most abundant guild (median = 249 individuals per route) and permanent residents were the least (median = 64).

The main effects models garnered much more support from the data than models incorporating bioperiod interactions, as indicated by comparison of Δ_i. The within-guild Δ_i values for the interaction models were ALL: 16.57, GROUND: 8.77, RESIDENT: 13.08, SHORTDIST: 1.66, NEOTROP: 27.01. As such, subsequent results and discussion will focus on main effects-only models. Coefficients estimated from this model for all landbirds included numerous significant terms and considerable variation among ecoregions (Table 3).

The effects of drought and heat waves on landbird abundance differed considerably among the bioperiods. The estimated effect of stress during the post fledging bioperiod (PF_STRESS) was negative in every ecoregion, but the effect of extreme weather associated with the early breeding period (EB_STRESS) was as likely to be positive as negative. The magnitude of the abundance changes varied considerably among bioperiods, as illustrated by the modeled changes in abundance following events of equivalent likelihood (Fig. 2, Appendix B). The largest modeled declines in overall avian abundance were associated with EB_STRESS, and included those in the temperate (–11.0%) and subtropical deserts (–23.1%) of the West. Although there was considerable variation in effect size among functional guilds, the pattern of consistently negative effects of PF_STRESS and varying effects of EB_STRESS generally held regardless

Table 3. Ecoregion-specific coefficients (multiplied by 100) estimated for main effects model of overall avian abundance and 95% confidence intervals.

Ecoregion	PF_STRESS	EB_STRESS	DRYCOOL
HotContiEast	–0.41 ± 0.89	1.27 ± 1.59	–1.34 ± 1.49
HotContiMtn	–0.06 ± 1.04	**2.38 ± 1.55**	–1.17 ± 1.51
HotContiWest	**–0.95 ± 0.61**	–0.06 ± 0.74	0.00 ± 0.95
PrairieSubtrop	**–1.22 ± 1.12**	0.47 ± 1.56	–1.82 ± 2.50
PrairieTemp	**–0.94 ± 0.91**	**1.55 ± 0.97**	–1.10 ± 1.47
SEMixedForest	–0.56 ± 0.67	–0.31 ± 0.86	–1.44 ± 1.54
SWMountains	–1.03 ± 1.29	–0.88 ± 1.34	–1.19 ± 2.89
SubCoastPlain	–0.63 ± 0.87	–0.47 ± 1.10	–1.68 ± 1.82
TempDesert	–0.94 ± 1.27	**–3.32 ± 0.83**	**1.94 ± 1.65**
TempSteppe	**–0.78 ± 0.64**	**–1.88 ± 0.56**	–0.06 ± 1.26
TempStpMtns	**–0.92 ± 0.79**	**1.27 ± 0.74**	0.28 ± 1.44
TropSubDesert	**–3.62 ± 1.41**	**–7.47 ± 1.33**	**3.14 ± 2.78**
TropSubSteppe	**–1.44 ± 0.69**	**–1.08 ± 0.75**	–0.70 ± 1.69
WarmConti	–0.75 ± 0.93	–0.05 ± 1.14	–0.49 ± 1.26
WarmContiMtn	–1.22 ± 1.31	1.01 ± 1.86	–0.89 ± 1.48
WestLowlands	–2.50 ± 2.34	0.70 ± 2.11	–0.45 ± 2.29
WestMtns	–1.04 ± 1.21	0.30 ± 1.17	**–1.81 ± 1.17**

Note: Values in boldface indicate significant effects ($P < 0.05$).

of guild (Fig. 2; Appendices B–F). As with landbirds overall, the largest declines within specific guilds were in association with of EB_STRESS.

Avifauna response to DRYCOOL was both mixed and muted, with only two ecoregions (Temperate Desert and Tropical/Subtropical Desert) having significantly negative coefficients and one region (West Coast Mountains) having a significant positive coefficient. 100-year extreme conditions for DRYCOOL had only modest modeled changes in avian abundance, with a maximum decline of 5.5% occurring in the TropSubDesert ecoregion. This mixed and muted pattern generally held among the functional guilds. However, there were some cases in which abundance changes were greater in association with 100-year DRYCOOL events than for stress in either of the bioperiods. This was most notable in the ground nesting guild in the WestMtns and Prairie Subtropical ecoregions, which saw GROUND increases of 8.9% and 6.6%, respectively (Appendix B).

The distinct response of ground nesting birds to DRYCOOL is but one example of a large amount of variation in avian responses according to functional traits. Ground nesting birds appeared the most susceptible to large declines in association with extreme weather events during either of the bioperiods, having larger declines (including a 35.9% decline in the TropSubDesert ecoregion) than any other guild and comparatively few increases in abundance (Appendix C). Among migratory guilds (Appendices D–F), short distance migrants had the largest modeled declines, although Neotropical migrants were the only group to not include any significant positive responses to the 100-year events. Permanent residents were notable for the range of modeled responses, which included both large negative and positive changes, depending on ecoregion.

As noted above, the relationship between the environmental variables and avian abundance varied considerably among the ecoregions. Although declines in abundance were the only significant response to post fledging stress, the magnitude of declines varied considerably, with the largest declines occurring in the Southwest. A notable exception to this geographic trend was the relatively large, 10.6% modeled decline in ground nesting birds following 100-year PF_STRESS event in the Warm Continental Mountains ecoregion in the northeastern U.S. In contrast to PF_STRESS, EB_STRESS produced a wide range of significant positive and negative changes in avian abundance. Ecoregions that experienced abundance increases following EB_STRESS were concentrated in northern and mountainous areas, while declines were concentrated in the West and Southwest. In particular, the TropSubDesert ecoregion stood out as having the largest and most consistent declines.

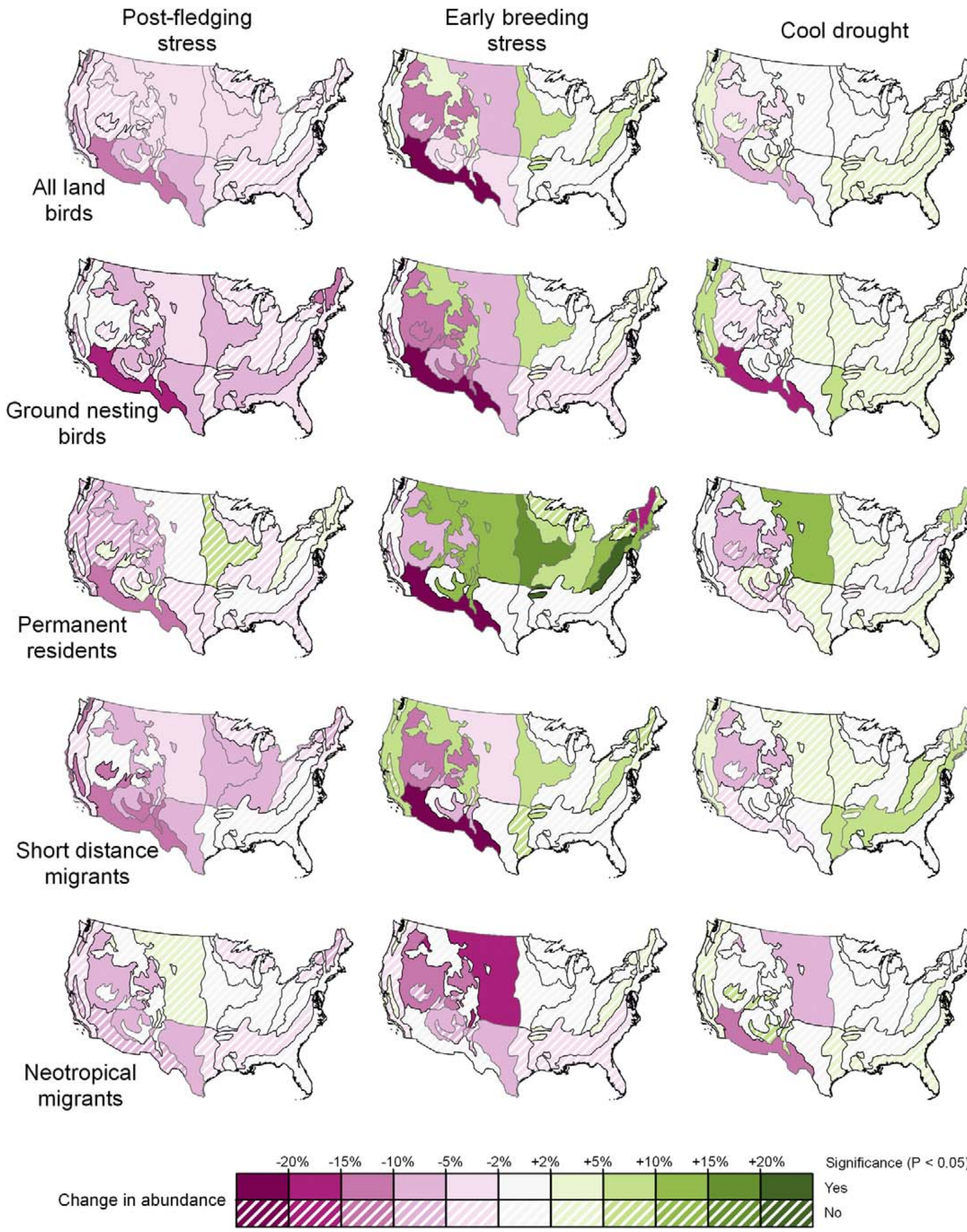

Fig. 2. Maps of modeled changes in community abundances of five different avian assemblages (rows) for three different 100-year extreme events based on principal component axes used in this study (columns). The maps show percent change in abundance increases (green) and decreases (magenta), with non-significant ($P > 0.05$) changes shown with cross-hatching.

Discussion

The co-occurrence of drought and heat waves wielded strong influence on avian abundance in the conterminous U.S. over our 9-year study period. Modeled responses to periods of extreme weather, with avian abundance changing by more than 15% in many cases, appeared more dramatic than found in previous studies in the central U.S. examining drought and heat waves separately (Albright et al. 2010, *in press*). Extreme weather occurring in both post-fledging and early nesting periods influenced avian communities, but in different ways. PF_STRESS consistently produced negative responses, but both declines and increases in abundance were of greater magnitude following EB_STRESS. July and August temperatures (used in PF_STRESS), which are generally the highest of the year, are often used in physiological studies of avian thermal stress (Guthery et al. 2001, McKechnie and Wolf 2010), so there is reason to expect this period to be highly influential. However, because of the timing of surveys associated with the BBS, there is a much longer lag between the post-fledging bioperiod and the dates of avian data collection used in this study. So, while heat and drought occurring during the early breeding period may influence habitat selection, survival, and induce post-migratory movements among adult birds, this approximately 10-month lag could dampen the effects of PF_STRESS due to the intervention of mortality during migration, density dependence, and other factors (Robinson et al. 2007). We found little support for bioperiod interactions, refuting our hypothesis that effects would be greater following successively occurring PF_STRESS and EB_STRESS events than the sum of their effects individually.

In contrast to the jointly occurring droughts and heat waves described above, droughts accompanied by relatively cool temperatures (and by corollary, heat waves with relatively abundant precipitation) were associated with relatively minor changes in avian abundance. There is a strong biophysical basis for increased water requirements of individual birds under high ambient temperatures (Williams and Tieleman 2005). Thus, it is not surprising that even extreme drought, if accompanied by cooler temperatures, would not affect avian abundance as much as a more common hot drought. An explanation for the number of positive responses to drought and heat is not clear.

Our findings reinforce and extend the importance of functional characteristics in differentiating the response of birds to extreme weather. Most striking was the wide variation among migratory guilds in response to extremes associated with EB_STRESS. In a number of ecoregions, the response to EB_STRESS by permanent residents was much more positive than that by Neotropical migrants. For the most part, these regions tended to be either mountainous or northern, suggesting an influence of winter snowfall (snow water equivalent is included in SPI) on avian community dynamics. The increased abundances associated with dry conditions could thus indicate less of a snow pack to challenge resident birds' access to resources (Albright et al. 2010). Although no migratory guild responded positively, extreme weather during the post-fledging period was most influential in reducing abundance of short distance migrant birds, which may make decisions about dispersal during this period, potentially influencing their selection of habitat during the following breeding season. Following this logic, the reduced abundance measured by BBS would reflect a tendency among short distance migrant birds to avoid routes that experienced hot and dry conditions during the previous post-fledging period. Among Neotropical migrants, this effect may be overwhelmed by high mortality rates from migration to and from their wintering grounds (Sillett and Holmes 2002). Considering nest location, we found that declines among ground nesting birds associated with drought and heat waves were nearly always larger than those among landbirds overall across the entire study region. The declines in the deserts of the Southwest were even stronger than found in a study focusing on land surface temperature alone (Albright et al., *in press*) and the extension of this ground nesting effect to heavily forested regions of the East was not expected. Unless heavily thinned, temperatures under forest canopies at ground level tend to be less extreme than at the top of the canopy (Rambo and North 2009).

This study covered a much greater diversity of ecoregions than any previous study. While some aspects of the influence of ecoregional variation on the response of birds to drought and heat have already been discussed, a few others merit emphasis here. The effects of drought and heat waves were felt more strongly in the subtropical deserts of the Southwest than in any other region, despite the likely temporal mismatch between the temperature metrics and the reproductive cycle of most species in this region. This suggests that these extremes can have large effects on observed populations even outside of the periods in breeding phenology to which we hypothesized avian species would be especially sensitive. Not only is this region subject to extremely high temperatures that can exceed physiological limits of birds (McKechnie and Wolf 2010), it is considered a climate change hot spot that is predicted to see increasing interannual variability in precipitation (Diffenbaugh et al. 2008). On the other hand, more modest avian responses were found in other regions, including much of the lowland portion of the eastern US. While we have already discussed the tendency of some functional groups to respond positively to early breeding stress in northern and mountainous areas, we also uncovered surprisingly negative responses by ground-nesting and resident birds in the WarmContiMtn region encompassing the northern Appalachian Mountains, for which an explanation remains elusive.

While our study was not focused on identifying mechanisms associated with the changes in avian abundances we described, it provides some insight. We can considered three broad processes by which environmental stresses, such as drought and heat waves, affect avian abundance: (1) adult survival, (2) reproduction and recruitment, and/or (3) dispersal. While the effects of each of these in response to PF_STRESS could be detected by our study, changes in survival and dispersal are the only possible responses to EB_STRESS detectable in BBS data collected during June of the same year. Given that some of the strongest responses were associated with this early breeding bioperiod, it appears that changes in adult mortality and dispersal are the predominant processes behind the observed changes in abundance in our study. The relative contribution of adult mortality and dispersal remains an important question. During times of extreme weather, normally philopatric birds may disperse to other regions, which serve as refugia. While there is evidence of this occurring in response to drought (Martin et al. 2007), the literature does not provide examples of this during heat waves, which are a more suddenly-developing phenomenon. It is possible that birds may be limited in their ability to undertake a demanding dispersal under duress to avoid the consequences of a heat wave, especially when the spatial scale of the heat wave is broad. More common in the literature are examples of heat wave-induced mortality (e.g., Finlayson 1932, Becker et al. 1997).

Our results highlight both important implications and questions for a more climatically variable future. Drought and heat waves influence avian community structure across a broad range of ecoregions, but reductions in avian abundance were the greatest in the arid Southwest. Because the arid Southwest is predicted to experience among the greatest increases in interannual temperature and precipitation variability, this finding merits special attention. While understanding the response to these events at the scale of one year is an important step, understanding the longer term demographic consequences of altered variability regimes is an important emerging question. Theory and modeling studies suggest reduced population growth rates in more variable climates (Boyce et al. 2006). The degree to which this expresses itself on real landscapes will be an interesting future discovery. The potential of birds undertaking energetically-costly migrations to be especially susceptible to extreme events such as heat waves and drought also deserves further study. Finally, we caution that because of our identification of dispersal as a key response to environmental extremes in this work, management and conservation decisions should consider the importance of suitable refugium areas even if they are used infrequently.

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Appendix A

Classification of species by functional group. Due to intraspecific variation, not all species were assigned a migratory habit or nesting location.

Scientific name	Common name	Migratory habit			Nest location
		Resident	Shortdist	Neotrop	Ground
Ortalis vetula	Plain Chachalaca	X			
Bonasa umbellus	Ruffed Grouse	X			
Centrocercus urophasianus	Greater Sage-Grouse	X			
Centrocercus minimus	Gunnison Sage-Grouse	X			
Falcipennis canadensis	Spruce Grouse	X			
Lagopus lagopus	Willow Ptarmigan		X		
Lagopus muta	Rock Ptarmigan		X		
Lagopus leucura	White-Tailed Ptarmigan	X			
Dendragapus obscurus or *fuliginosus*	Blue Grouse	X			
Tympanuchus cupido	Greater Prairie-Chicken	X			X
Tympanuchus pallidicinctus	Lesser Prairie-Chicken	X			X
Meleagris gallopavo	Wild Turkey	X			X
Oreortyx pictus	Mountain Quail	X			
Callipepla squamata	Scaled Quail	X			
Callipepla californica	California Quail	X			
Callipepla gambelii	Gambel's Quail	X			
Colinus virginianus	Northern Bobwhite	X			X
Cyrtonyx montezumae	Montezuma Quail	X			
Coragyps atratus	Black Vulture	X			
Cathartes aura	Turkey Vulture		X		
Gymnogyps californianus	California Condor	X			
Pandion haliaetus	Osprey		X		
Chondrohierax uncinatus	Hook-Billed Kite				
Elanoides forficatus	Swallow-Tailed Kite			X	
Elanus leucurus	White-Tailed Kite	X			
Rostrhamus sociabilis	Snail Kite	X			
Ictinia mississippiensis	Mississippi Kite			X	
Haliaeetus leucocephalus	Bald Eagle		X		
Circus cyaneus	Northern Harrier		X		X
Accipiter striatus	Sharp-Shinned Hawk		X		
Accipiter cooperii	Cooper's Hawk		X		
Accipiter gentilis	Northern Goshawk	X			
Buteogallus anthracinus	Common Black-Hawk		X		
Parabuteo unicinctus	Harris's Hawk	X			
Buteo lineatus	Red-Shouldered Hawk		X		
Buteo platypterus	Broad-Winged Hawk			X	
Buteo nitidus	Gray Hawk		X		
Buteo brachyurus	Short-Tailed Hawk		X		
Buteo swainsoni	Swainson's Hawk			X	
Buteo albicaudatus	White-Tailed Hawk	X			
Buteo albonotatus	Zone-Tailed Hawk			X	
Buteo jamaicensis	Red-Tailed Hawk		X		
Buteo regalis	Ferruginous Hawk		X		
Buteo lagopus	Rough-Legged Hawk		X		
Aquila chrysaetos	Golden Eagle		X		
Caracara cheriway	Crested Caracara	X			
Falco sparverius	American Kestrel		X		
Falco columbarius	Merlin			X	
Falco femoralis	Aplomado Falcon	X			
Falco rusticolus	Gyrfalcon		X		
Falco peregrinus	Peregrine Falcon			X	
Falco mexicanus	Prairie Falcon		X		
Patagioenas leucocephala	White-Crowned Pigeon		X		
Patagioenas flavirostris	Red-Billed Pigeon		X		
Patagioenas fasciata	Band-Tailed Pigeon			X	
Zenaida asiatica	White-Winged Dove		X		
Zenaida macroura	Mourning Dove		X		
Columbina inca	Inca Dove	X			
Columbina passerina	Common Ground-Dove	X			
Leptotila verreauxi	White-Tipped Dove	X			

Continued.

Scientific name	Common name	Migratory habit: Resident	Shortdist	Neotrop	Nest location: Ground
Aratinga holochlora	Green Parakeet				
Rhynchopsitta pachyrhyncha	Thick-Billed Parrot		X		
Amazona viridigenalis	Red-Crowned Parrot	X			
Coccyzus americanus	Yellow-Billed Cuckoo			X	
Coccyzus minor	Mangrove Cuckoo	X			
Coccyzus erythropthalmus	Black-Billed Cuckoo			X	
Geococcyx californianus	Greater Roadrunner	X			
Crotophaga ani	Smooth-Billed Ani	X			
Crotophaga sulcirostris	Groove-Billed Ani		X		
Tyto alba	Barn Owl		X		
Otus flammeolus	Flammulated Owl			X	
Megascops kennicottii	Western Screech-Owl	X			
Megascops asio	Eastern Screech-Owl	X			
Megascops trichopsis	Whiskered Screech-Owl	X			
Bubo virginianus	Great Horned Owl	X			
Bubo scandiacus	Snowy Owl		X		
Surnia ulula	Northern Hawk Owl		X		
Glaucidium gnoma	Northern Pygmy-Owl				
Glaucidium brasilianum	Ferruginous Pygmy-Owl	X			
Micrathene whitneyi	Elf Owl		X		
Athene cunicularia	Burrowing Owl			X	
Strix occidentalis	Spotted Owl	X			
Strix varia	Barred Owl	X			
Strix nebulosa	Great Gray Owl		X		
Asio otus	Long-Eared Owl		X		
Asio flammeus	Short-Eared Owl		X		X
Aegolius funereus	Boreal Owl	X			
Aegolius acadicus	Northern Saw-Whet Owl		X		
Chordeiles acutipennis	Lesser Nighthawk			X	X
Chordeiles minor	Common Nighthawk			X	X
Chordeiles gundlachii	Antillean Nighthawk				
Nyctidromus albicollis	Common Pauraque	X			
Phalaenoptilus nuttallii	Common Poorwill		X		X
Caprimulgus carolinensis	Chuck-Will's-Widow			X	X
Caprimulgus ridgwayi	Buff-Collared Nightjar			X	
Caprimulgus vociferus	Whip-Poor-Will			X	X
Cypseloides niger	Black Swift			X	
Chaetura pelagica	Chimney Swift			X	
Chaetura vauxi	Vaux's Swift			X	
Aeronautes saxatalis	White-Throated Swift			X	
Cynanthus latirostris	Broad-Billed Hummingbird		X		
Hylocharis leucotis	White-Eared Hummingbird				
Amazilia beryllina	Berylline Hummingbird				
Amazilia yucatanensis	Buff-Bellied Hummingbird		X		
Amazilia violiceps	Violet-Crowned Hummingbird		X		
Lampornis clemenciae	Blue-Throated Hummingbird		X		
Eugenes fulgens	Magnificent Hummingbird		X		
Calothorax lucifer	Lucifer Hummingbird			X	
Archilochus colubris	Ruby-Throated Hummingbird			X	
Archilochus alexandri	Black-Chinned Hummingbird			X	
Calypte anna	Anna's Hummingbird	X			
Calypte costae	Costa's Hummingbird			X	
Stellula calliope	Calliope Hummingbird			X	
Selasphorus platycercus	Broad-Tailed Hummingbird			X	
Selasphorus rufus	Rufous Hummingbird			X	
Selasphorus sasin	Allen's Hummingbird			X	
Trogon elegans	Elegant Trogon		X		
Megaceryle torquata	Ringed Kingfisher	X			
Megaceryle alcyon	Belted Kingfisher			X	
Chloroceryle americana	Green Kingfisher	X			
Melanerpes lewis	Lewis's Woodpecker		X		
Melanerpes erythrocephalus	Red-Headed Woodpecker		X		
Melanerpes formicivorus	Acorn Woodpecker	X			
Melanerpes uropygialis	Gila Woodpecker	X			
Melanerpes aurifrons	Golden-Fronted Woodpecker	X			
Melanerpes carolinus	Red-Bellied Woodpecker	X			

Continued.

Scientific name	Common name	Migratory habit			Nest location
		Resident	Shortdist	Neotrop	Ground
Sphyrapicus thyroideus	Williamson's Sapsucker		X		
Sphyrapicus varius	Yellow-Bellied Sapsucker			X	
Sphyrapicus nuchalis	Red-Naped Sapsucker			X	
Sphyrapicus ruber	Red-Breasted Sapsucker		X		
Picoides scalaris	Ladder-Backed Woodpecker	X			
Picoides nuttallii	Nuttall's Woodpecker	X			
Picoides pubescens	Downy Woodpecker	X			
Picoides villosus	Hairy Woodpecker	X			
Picoides arizonae	Arizona Woodpecker	X			
Picoides borealis	Red-Cockaded Woodpecker	X			
Picoides albolarvatus	White-Headed Woodpecker	X			
Picoides dorsalis	American Three-Toed Woodpecker	X			
Picoides arcticus	Black-Backed Woodpecker	X			
Colaptes auratus	Northern Flicker		X		
Colaptes chrysoides	Gilded Flicker				
Dryocopus pileatus	Pileated Woodpecker	X			
Camptostoma imberbe	Northern Beardless-Tyrannulet		X		
Contopus cooperi	Olive-Sided Flycatcher			X	
Contopus pertinax	Greater Pewee		X		
Contopus sordidulus	Western Wood-Pewee			X	
Contopus virens	Eastern Wood-Pewee			X	
Empidonax flaviventris	Yellow-Bellied Flycatcher			X	X
Empidonax virescens	Acadian Flycatcher			X	
Empidonax alnorum	Alder Flycatcher			X	X
Empidonax traillii	Willow Flycatcher			X	
Empidonax minimus	Least Flycatcher			X	
Empidonax hammondii	Hammond's Flycatcher			X	
Empidonax wrightii	Gray Flycatcher			X	
Empidonax oberholseri	Dusky Flycatcher			X	
Empidonax difficilis	Pacific-Slope Flycatcher			X	
Empidonax occidentalis	Cordilleran Flycatcher			X	
Empidonax fulvifrons	Buff-Breasted Flycatcher		X		
Sayornis nigricans	Black Phoebe	X			
Sayornis phoebe	Eastern Phoebe			X	
Sayornis saya	Say's Phoebe			X	
Pyrocephalus rubinus	Vermilion Flycatcher			X	
Myiarchus tuberculifer	Dusky-Capped Flycatcher		X		
Myiarchus cinerascens	Ash-Throated Flycatcher			X	
Myiarchus crinitus	Great Crested Flycatcher			X	
Myiarchus tyrannulus	Brown-Crested Flycatcher		X		
Pitangus sulphuratus	Great Kiskadee	X			
Myiodynastes luteiventris	Sulphur-Bellied Flycatcher			X	
Tyrannus melancholicus	Tropical Kingbird		X		
Tyrannus couchii	Couch's Kingbird	X			
Tyrannus vociferans	Cassin's Kingbird			X	
Tyrannus crassirostris	Thick-Billed Kingbird		X		
Tyrannus verticalis	Western Kingbird			X	
Tyrannus tyrannus	Eastern Kingbird			X	
Tyrannus dominicensis	Gray Kingbird			X	
Tyrannus forficatus	Scissor-Tailed Flycatcher			X	
Pachyramphus aglaiae	Rose-Throated Becard				
Lanius ludovicianus	Loggerhead Shrike			X	
Lanius excubitor	Northern Shrike		X		
Vireo griseus	White-Eyed Vireo			X	X
Vireo bellii	Bell's Vireo			X	X
Vireo atricapilla	Black-Capped Vireo			X	
Vireo vicinior	Gray Vireo			X	
Vireo flavifrons	Yellow-Throated Vireo			X	
Vireo plumbeus	Plumbeous Vireo			X	
Vireo cassinii	Cassin's Vireo			X	
Vireo solitarius	Blue-Headed Vireo			X	
Vireo huttoni	Hutton's Vireo	X			
Vireo gilvus	Warbling Vireo			X	
Vireo philadelphicus	Philadelphia Vireo			X	
Vireo olivaceus	Red-Eyed Vireo			X	
Vireo flavoviridis	Yellow-Green Vireo			X	

Continued.

Scientific name	Common name	Migratory habit			Nest location
		Resident	Shortdist	Neotrop	Ground
Vireo altiloquus	Black-Whiskered Vireo			X	
Perisoreus canadensis	Gray Jay	X			
Cyanocitta stelleri	Steller's Jay	X			
Cyanocitta cristata	Blue Jay		X		
Cyanocorax yncas	Green Jay	X			
Cyanocorax morio	Brown Jay				
Aphelocoma coerulescens	Florida Scrub-Jay	X			X
Aphelocoma insularis	Island Scrub-Jay	X			
Aphelocoma californica	Western Scrub-Jay	X			
Aphelocoma ultramarina	Mexican Jay	X			
Gymnorhinus cyanocephalus	Pinyon Jay	X			
Nucifraga columbiana	Clark's Nutcracker	X			
Pica hudsonia	Black-Billed Magpie	X			
Pica nuttalli	Yellow-Billed Magpie	X			
Corvus brachyrhynchos	American Crow		X		
Corvus caurinus	Northwestern Crow	X			
Corvus imparatus	Tamaulipas Crow				
Corvus ossifragus	Fish Crow		X		
Corvus cryptoleucus	Chihuahuan Raven	X			
Corvus corax	Common Raven	X			
Eremophila alpestris	Horned Lark		X		X
Progne subis	Purple Martin			X	
Tachycineta bicolor	Tree Swallow			X	
Tachycineta thalassina	Violet-Green Swallow			X	
Stelgidopteryx serripennis	Northern Rough-Winged Swallow			X	
Riparia riparia	Bank Swallow			X	
Petrochelidon pyrrhonota	Cliff Swallow			X	
Petrochelidon fulva	Cave Swallow		X		
Hirundo rustica	Barn Swallow			X	
Poecile carolinensis	Carolina Chickadee	X			
Poecile atricapillus	Black-Capped Chickadee	X			
Poecile gambeli	Mountain Chickadee	X			
Poecile sclateri	Mexican Chickadee	X			
Poecile rufescens	Chestnut-Backed Chickadee	X			
Poecile hudsonica	Boreal Chickadee	X			
Poecile cincta	Gray-Headed Chickadee	X			
Baeolophus wollweberi	Bridled Titmouse	X			
Baeolophus inornatus	Oak Titmouse	X			
Baeolophus ridgwayi	Juniper Titmouse	X			
Baeolophus bicolor	Tufted Titmouse	X			
Baeolophus atricristatus	Black-Crested Titmouse	X			
Auriparus flaviceps	Verdin	X			
Psaltriparus minimus	Bushtit	X			
Sitta canadensis	Red-Breasted Nuthatch		X		
Sitta carolinensis	White-Breasted Nuthatch	X			
Sitta pygmaea	Pygmy Nuthatch	X			
Sitta pusilla	Brown-Headed Nuthatch	X			
Certhia americana	Brown Creeper		X		
Campylorhynchus brunneicapillus	Cactus Wren	X			
Salpinctes obsoletus	Rock Wren		X		X
Catherpes mexicanus	Canyon Wren	X			X
Thryothorus ludovicianus	Carolina Wren	X			X
Thryomanes bewickii	Bewick's Wren		X		X
Troglodytes aedon	House Wren			X	
Troglodytes troglodytes	Winter Wren		X		X
Cistothorus platensis	Sedge Wren		X		X
Cistothorus palustris	Marsh Wren			X	X
Cinclus mexicanus	American Dipper	X			X
Regulus satrapa	Golden-Crowned Kinglet		X		
Regulus calendula	Ruby-Crowned Kinglet			X	
Phylloscopus borealis	Arctic Warbler				
Polioptila caerulea	Blue-Gray Gnatcatcher			X	
Polioptila californica	California Gnatcatcher	X			
Polioptila melanura	Black-Tailed Gnatcatcher	X			
Polioptila nigriceps	Black-Capped Gnatcatcher				
Luscinia svecica	Bluethroat				

Continued.

Scientific name	Common name	Migratory habit			Nest location
		Resident	Shortdist	Neotrop	Ground
Oenanthe oenanthe	Northern Wheatear				
Sialia sialis	Eastern Bluebird		X		
Sialia mexicana	Western Bluebird		X		
Sialia currucoides	Mountain Bluebird		X		
Myadestes townsendi	Townsend's Solitaire		X		X
Catharus fuscescens	Veery			X	X
Catharus minimus	Gray-Cheeked Thrush			X	X
Catharus bicknelli	Bicknell's Thrush			X	
Catharus ustulatus	Swainson's Thrush			X	X
Catharus guttatus	Hermit Thrush			X	X
Hylocichla mustelina	Wood Thrush			X	
Turdus grayi	Clay-Colored Robin				
Turdus migratorius	American Robin		X		
Ixoreus naevius	Varied Thrush		X		
Chamaea fasciata	Wrentit	X			X
Dumetella carolinensis	Gray Catbird			X	
Mimus polyglottos	Northern Mockingbird	X			
Oreoscoptes montanus	Sage Thrasher			X	X
Toxostoma rufum	Brown Thrasher		X		
Toxostoma longirostre	Long-Billed Thrasher	X			
Toxostoma bendirei	Bendire's Thrasher		X		
Toxostoma curvirostre	Curve-Billed Thrasher		X		
Toxostoma redivivum	California Thrasher	X			
Toxostoma crissale	Crissal Thrasher	X			X
Toxostoma lecontei	Le Conte's Thrasher	X			X
Motacilla alba	White Wagtail				
Anthus cervinus	Red-Throated Pipit				
Anthus rubescens	American Pipit			X	
Anthus spragueii	Sprague's Pipit			X	X
Bombycilla garrulus	Bohemian Waxwing		X		
Bombycilla cedrorum	Cedar Waxwing			X	
Phainopepla nitens	Phainopepla			X	
Peucedramus taeniatus	Olive Warbler		X		
Vermivora pinus	Blue-Winged Warbler			X	X
Vermivora chrysoptera	Golden-Winged Warbler			X	X
Vermivora peregrina	Tennessee Warbler			X	X
Vermivora celata	Orange-Crowned Warbler			X	X
Vermivora ruficapilla	Nashville Warbler			X	X
Vermivora virginiae	Virginia's Warbler			X	X
Vermivora crissalis	Colima Warbler			X	
Vermivora luciae	Lucy's Warbler			X	
Parula americana	Northern Parula			X	
Parula pitiayumi	Tropical Parula		X		
Dendroica petechia	Yellow Warbler			X	
Dendroica pensylvanica	Chestnut-Sided Warbler			X	X
Dendroica magnolia	Magnolia Warbler			X	
Dendroica tigrina	Cape May Warbler			X	
Dendroica caerulescens	Black-Throated Blue Warbler			X	
Dendroica coronata	Yellow-Rumped Warbler			X	
Dendroica nigrescens	Black-Throated Gray Warbler			X	
Dendroica chrysoparia	Golden-Cheeked Warbler			X	
Dendroica virens	Black-Throated Green Warbler			X	
Dendroica townsendi	Townsend's Warbler			X	
Dendroica occidentalis	Hermit Warbler			X	
Dendroica fusca	Blackburnian Warbler			X	
Dendroica dominica	Yellow-Throated Warbler			X	
Dendroica graciae	Grace's Warbler			X	
Dendroica pinus	Pine Warbler		X		
Dendroica kirtlandii	Kirtland's Warbler			X	
Dendroica discolor	Prairie Warbler			X	X
Dendroica palmarum	Palm Warbler			X	X
Dendroica castanea	Bay-Breasted Warbler			X	
Dendroica striata	Blackpoll Warbler			X	
Dendroica cerulea	Cerulean Warbler			X	
Mniotilta varia	Black-And-White Warbler			X	X
Setophaga ruticilla	American Redstart			X	

Continued.

Scientific name	Common name	Migratory habit			Nest location
		Resident	Shortdist	Neotrop	Ground
Protonotaria citrea	Prothonotary Warbler			X	
Helmitheros vermivorum	Worm-Eating Warbler			X	X
Limnothlypis swainsonii	Swainson's Warbler			X	X
Seiurus aurocapilla	Ovenbird			X	X
Seiurus noveboracensis	Northern Waterthrush			X	X
Seiurus motacilla	Louisiana Waterthrush			X	X
Oporornis formosus	Kentucky Warbler			X	X
Oporornis agilis	Connecticut Warbler			X	X
Oporornis philadelphia	Mourning Warbler			X	X
Oporornis tolmiei	Macgillivray's Warbler			X	X
Geothlypis trichas	Common Yellowthroat			X	X
Wilsonia citrina	Hooded Warbler			X	X
Wilsonia pusilla	Wilson's Warbler			X	X
Wilsonia canadensis	Canada Warbler			X	X
Cardellina rubrifrons	Red-Faced Warbler			X	
Myioborus pictus	Painted Redstart		X		
Basileuterus rufifrons	Rufous-Capped Warbler				
Icteria virens	Yellow-Breasted Chat			X	X
Piranga flava	Hepatic Tanager			X	
Piranga rubra	Summer Tanager			X	
Piranga olivacea	Scarlet Tanager			X	
Piranga ludoviciana	Western Tanager			X	
Piranga bidentata	Flame-Colored Tanager				
Sporophila torqueola	White-Collared Seedeater	X			
Arremonops rufivirgatus	Olive Sparrow	X			X
Pipilo chlorurus	Green-Tailed Towhee			X	X
Pipilo maculatus	Spotted Towhee		X		X
Pipilo erythrophthalmus	Eastern Towhee		X		X
Pipilo fuscus	Canyon Towhee	X			X
Pipilo crissalis	California Towhee	X			X
Pipilo aberti	Abert's Towhee	X			
Aimophila carpalis	Rufous-Winged Sparrow	X			X
Aimophila cassinii	Cassin's Sparrow		X		X
Aimophila aestivalis	Bachman's Sparrow		X		X
Aimophila botterii	Botteri's Sparrow	X			X
Aimophila ruficeps	Rufous-Crowned Sparrow	X			X
Aimophila quinquestriata	Five-Striped Sparrow	X			
Spizella arborea	American Tree Sparrow		X		
Spizella passerina	Chipping Sparrow			X	
Spizella pallida	Clay-Colored Sparrow			X	X
Spizella breweri	Brewer's Sparrow			X	X
Spizella pusilla	Field Sparrow		X		X
Spizella atrogularis	Black-Chinned Sparrow		X		X
Pooecetes gramineus	Vesper Sparrow			X	X
Chondestes grammacus	Lark Sparrow			X	X
Amphispiza bilineata	Black-Throated Sparrow		X		X
Amphispiza belli	Sage Sparrow		X		X
Calamospiza melanocorys	Lark Bunting			X	X
Passerculus sandwichensis	Savannah Sparrow			X	X
Ammodramus savannarum	Grasshopper Sparrow			X	X
Ammodramus bairdii	Baird's Sparrow			X	X
Ammodramus henslowii	Henslow's Sparrow		X		X
Ammodramus leconteii	Le Conte's Sparrow		X		X
Ammodramus nelsoni	Nelson's Sharp-Tailed Sparrow		X		X
Ammodramus caudacutus	Saltmarsh Sharp-Tailed Sparrow		X		X
Ammodramus maritimus	Seaside Sparrow		X		X
Passerella iliaca	Fox Sparrow		X		X
Melospiza melodia	Song Sparrow		X		X
Melospiza lincolnii	Lincoln's Sparrow			X	X
Melospiza georgiana	Swamp Sparrow			X	X
Zonotrichia albicollis	White-Throated Sparrow		X		X
Zonotrichia querula	Harris's Sparrow		X		
Zonotrichia leucophrys	White-Crowned Sparrow			X	X
Zonotrichia atricapilla	Golden-Crowned Sparrow		X		
Junco hyemalis	Dark-Eyed Junco		X		X
Junco phaeonotus	Yellow-Eyed Junco	X			

Continued.

Scientific name	Common name	Migratory habit: Resident	Shortdist	Neotrop	Nest location Ground
Calcarius mccownii	Mccown's Longspur		X		X
Calcarius lapponicus	Lapland Longspur		X		
Calcarius pictus	Smith's Longspur		X		
Calcarius ornatus	Chestnut-Collared Longspur		X		X
Plectrophenax nivalis	Snow Bunting		X		
Plectrophenax hyperboreus	Mckay's Bunting		X		
Cardinalis cardinalis	Northern Cardinal	X			
Cardinalis sinuatus	Pyrrhuloxia	X			
Pheucticus ludovicianus	Rose-Breasted Grosbeak			X	
Pheucticus melanocephalus	Black-Headed Grosbeak			X	
Passerina caerulea	Blue Grosbeak			X	X
Passerina amoena	Lazuli Bunting			X	X
Passerina cyanea	Indigo Bunting			X	X
Passerina versicolor	Varied Bunting			X	
Passerina ciris	Painted Bunting			X	
Spiza americana	Dickcissel			X	X
Dolichonyx oryzivorus	Bobolink			X	X
Agelaius phoeniceus	Red-Winged Blackbird		X		X
Agelaius tricolor	Tricolored Blackbird	X			X
Sturnella magna	Eastern Meadowlark		X		X
Sturnella neglecta	Western Meadowlark		X		X
Xanthocephalus xanthocephalus	Yellow-Headed Blackbird			X	X
Euphagus carolinus	Rusty Blackbird		X		
Euphagus cyanocephalus	Brewer's Blackbird			X	
Quiscalus quiscula	Common Grackle		X		
Quiscalus major	Boat-Tailed Grackle	X			
Quiscalus mexicanus	Great-Tailed Grackle	X			
Molothrus bonariensis	Shiny Cowbird				
Molothrus aeneus	Bronzed Cowbird		X		
Molothrus ater	Brown-Headed Cowbird			X	
Icterus spurius	Orchard Oriole			X	
Icterus cucullatus	Hooded Oriole			X	
Icterus pustulatus	Streak-Backed Oriole				
Icterus bullockii	Bullock's Oriole			X	
Icterus gularis	Altamira Oriole		X		
Icterus graduacauda	Audubon's Oriole	X			
Icterus galbula	Baltimore Oriole			X	
Icterus parisorum	Scott's Oriole			X	
Leucosticte spp	Unid. Rosy-Finch		X		
Pinicola enucleator	Pine Grosbeak		X		
Carpodacus purpureus	Purple Finch		X		
Carpodacus cassinii	Cassin's Finch		X		
Carpodacus mexicanus	House Finch		X		
Loxia curvirostra	Red Crossbill		X		
Loxia leucoptera	White-Winged Crossbill		X		
Carduelis flammea	Common Redpoll		X		
Carduelis hornemanni	Hoary Redpoll		X		
Carduelis pinus	Pine Siskin		X		
Carduelis psaltria	Lesser Goldfinch		X		
Carduelis lawrencei	Lawrence's Goldfinch	X			
Carduelis tristis	American Goldfinch		X		
Coccothraustes vespertinus	Evening Grosbeak		X		

Appendix B

Predicted changes in abundance following 100-year extreme events: All landbirds.

Ecoregion	PF_STRESS	EB_STRESS	DRYCOOL
HotContiEast	–1.47 ± 3.14	4.53 ± 5.66	2.42 ± 2.71
HotContiMtn	–0.22 ± 3.71	**8.67 ± 5.73**	2.11 ± 2.73
HotContiWest	**–3.39 ± 2.14**	–0.21 ± 2.54	–0.01 ± 1.69
PrairieSubtrop	**–4.34 ± 3.82**	1.65 ± 5.41	3.31 ± 4.53
PrairieTemp	**–3.38 ± 3.15**	**5.58 ± 3.53**	2.00 ± 2.65
SEMixedForest	–2.01 ± 2.38	–1.07 ± 2.95	2.62 ± 2.79
SWMountains	–3.68 ± 4.44	–3.03 ± 4.43	2.16 ± 5.17
SubCoastPlain	–2.27 ± 3.06	**–1.63 ± 3.71**	3.06 ± 3.30
TempDesert	–3.38 ± 4.37	**–10.98 ± 2.56**	**–3.42 ± 2.81**
TempSteppe	**–2.81 ± 2.24**	**–6.38 ± 1.81**	0.11 ± 2.24
TempStpMtns	**–3.32 ± 2.75**	**4.56 ± 2.67**	–0.49 ± 2.54
TropSubDesert	**–12.41 ± 4.42**	**–23.05 ± 3.50**	**–5.48 ± 4.61**
TropSubSteppe	**–5.14 ± 2.37**	**–3.70 ± 2.50**	1.26 ± 3.03
WarmConti	–2.69 ± 3.25	–0.16 ± 3.91	0.88 ± 2.25
WarmContiMtn	–4.35 ± 4.48	3.61 ± 6.53	1.60 ± 2.66
WestLowlands	**–8.72 ± 7.47**	2.48 ± 7.31	0.80 ± 4.05
WestMtns	–3.73 ± 4.16	1.07 ± 4.05	**3.30 ± 2.14**

Note: Values in boldface indicate significant effects ($P < 0.05$).

Appendix C

Predicted changes in abundance following 100-year extreme events: Ground-nesting birds.

Ecoregion	PF_STRESS	EB_STRESS	DRYCOOL
HotContiEast	–2.52 ± 4.15	–0.14 ± 7.15	3.51 ± 3.64
HotContiMtn	–1.67 ± 4.86	2.79 ± 7.16	3.04 ± 3.67
HotContiWest	–2.13 ± 2.87	–1.93 ± 3.31	1.33 ± 2.28
PrairieSubtrop	–3.09 ± 5.12	–4.80 ± 6.73	**8.85 ± 6.32**
PrairieTemp	**–5.72 ± 4.08**	**5.37 ± 4.68**	3.12 ± 3.54
SEMixedForest	**–6.84 ± 3.00**	–3.12 ± 3.82	2.08 ± 3.70
WMountains	–4.15 ± 5.87	**–10.77 ± 5.45**	–0.12 ± 6.73
SubCoastPlain	**–4.24 ± 3.98**	–2.99 ± 4.87	2.62 ± 4.38
TempDesert	–0.16 ± 6.00	**–13.51 ± 3.30**	–3.51 ± 3.73
TempSteppe	**–4.52 ± 2.93**	**–9.40 ± 2.35**	2.15 ± 3.03
TempStpMtns	**–6.13 ± 3.57**	**6.21 ± 3.62**	1.64 ± 3.45
TropSubDesert	**–18.47 ± 5.44**	**–35.85 ± 3.93**	**–15.06 ± 5.54**
TropSubSteppe	**–7.96 ± 3.04**	**–9.01 ± 3.16**	–0.21 ± 3.96
WarmConti	–2.39 ± 4.33	–0.88 ± 5.15	0.47 ± 2.98
WarmContiMtn	**–10.62 ± 5.58**	2.73 ± 8.58	0.54 ± 3.50
WestLowlands	–6.99 ± 10.08	–5.10 ± 8.87	3.25 ± 5.52
WestMtns	–1.37 ± 5.70	–0.30 ± 5.29	**6.59 ± 2.95**

Note: Values in boldface indicate significant effects ($P < 0.05$).

APPENDIX D

Predicted changes in abundance following 100-year extreme events: Permanent resident birds.

Ecoregion	PF_STRESS	EB_STRESS	DRYCOOL
HotContiEast	2.97 ± 7.22	**14.35 ± 13.24**	–1.31 ± 5.70
HotContiMtn	–0.94 ± 8.02	**23.44 ± 13.91**	–2.70 ± 5.72
HotContiWest	–2.36 ± 4.75	**8.20 ± 6.05**	–1.21 ± 3.71
PrairieSubtrop	–4.03 ± 8.16	1.96 ± 11.68	1.68 ± 9.57
PrairieTemp	7.52 ± 7.88	**16.79 ± 8.73**	2.85 ± 5.95
SEMixedForest	–1.57 ± 5.19	–0.04 ± 6.42	1.74 ± 6.08
SWMountains	2.25 ± 10.27	**13.2 ± 11.4**	–6.22 ± 10.44
SubCoastPlain	–3.70 ± 6.53	0.19 ± 8.21	3.30 ± 7.22
TempDesert	–8.07 ± 9.48	**–8.04 ± 6.03**	**–8.13 ± 6.09**
TempSteppe	0.47 ± 5.77	**13.81 ± 5.48**	**13.00 ± 6.20**
TempStpMtns	**–6.77 ± 6.02**	**10.64 ± 6.36**	1.14 ± 5.80
TropSubDesert	**–14.21 ± 9.06**	**–27.22 ± 7.25**	–4.16 ± 10.14
TropSubSteppe	–3.87 ± 5.10	–0.98 ± 5.65	3.21 ± 6.68
WarmConti	–1.62 ± 7.37	6.83 ± 9.33	–1.72 ± 4.95
WarmContiMtn	2.49 ± 10.70	**–15.45 ± 11.76**	**6.33 ± 6.23**
WestLowlands	0.83 ± 17.70	–5.54 ± 14.23	0.02 ± 8.83
WestMtns	–7.13 ± 8.85	0.55 ± 8.71	1.56 ± 4.65

Note: Values in boldface indicate significant effects ($P < 0.05$).

APPENDIX E

Predicted changes in abundance following 100-year extreme events: Short distance migrant birds.

Ecoregion	PF_STRESS	EB_STRESS	DRYCOOL
HotContiEast	–3.1 ± 3.82	3.33 ± 6.87	**5.33 ± 3.44**
HotContiMtn	0.35 ± 4.60	**9.92 ± 7.12**	2.57 ± 3.39
HotContiWest	**–5.90 ± 2.57**	–0.85 ± 3.12	1.08 ± 2.12
PrairieSubtrop	–1.63 ± 4.82	6.52 ± 7.00	**6.51 ± 5.75**
PrairieTemp	**–5.27 ± 3.82**	**7.50 ± 4.44**	2.38 ± 3.27
SEMixedForest	–1.79 ± 2.94	–0.96 ± 3.63	**5.28 ± 3.55**
SWMountains	**–12.65 ± 4.98**	**–6.48 ± 5.31**	1.79 ± 6.39
SubCoastPlain	–0.26 ± 3.85	–0.26 ± 4.65	1.99 ± 4.05
TempDesert	–1.27 ± 5.53	**–12.32 ± 3.11**	**–5.84 ± 3.39**
TempSteppe	**–4.68 ± 2.72**	**–3.17 ± 2.33**	2.29 ± 2.83
TempStpMtns	**–8.28 ± 3.25**	**8.17 ± 3.43**	1.03 ± 3.19
TropSubDesert	**–13.68 ± 5.32**	**–32.66 ± 3.81**	–4.70 ± 5.76
TropSubSteppe	**–5.52 ± 2.89**	–1.10 ± 3.19	1.67 ± 3.75
WarmConti	–3.04 ± 4.01	2.00 ± 4.93	1.12 ± 2.79
WarmContiMtn	–5.30 ± 5.50	7.81 ± 8.39	**4.96 ± 3.40**
WestLowlands	**–14.89 ± 8.60**	5.11 ± 9.15	–0.25 ± 4.97
WestMtns	–4.38 ± 5.14	**8.13 ± 5.33**	**4.05 ± 2.68**

Note: Values in boldface indicate significant effects ($P < 0.05$).

Appendix F

Predicted changes in abundance following 100-year extreme events: Neotropical migrant birds.

Ecoregion	PF_STRESS	EB_STRESS	DRYCOOL
HotContiEast	–1.16 ± 4.35	1.51 ± 7.41	1.39 ± 3.68
HotContiMtn	–0.09 ± 5.07	2.75 ± 7.30	**3.84 ± 3.83**
HotContiWest	–0.92 ± 2.99	–1.1 0 ±3.44	–1.29 ± 2.30
PrairieSubtrop	–4.47 ± 5.10	–4.58 ± 6.94	2.72 ± 6.10
PrairieTemp	–1.73 ± 4.42	1.30 ± 4.66	0.75 ± 3.56
SEMixedForest	–2.01 ± 3.23	–2.39 ± 3.92	0.66 ± 3.79
SWMountains	0.86 ± 6.36	–5.33 ± 6.00	5.41 ± 7.38
SubCoastPlain	–1.49 ± 4.22	–3.00 ± 5.03	3.28 ± 4.57
TempDesert	**–9.02 ± 5.71**	**–11.52 ± 3.47**	–0.32 ± 3.97
TempSteppe	2.78 ± 3.27	**–15.12 ± 2.32**	**–4.66 ± 2.93**
TempStpMtns	1.63 ± 4.02	1.55 ± 3.59	–0.77 ± 3.45
TropSubDesert	–5.85 ± 6.42	–1.08 ± 6.29	**–10.95 ± 6.05**
TropSubSteppe	**–5.25 ± 3.19**	**–5.83 ± 3.42**	0.01 ± 4.09
WarmConti	–2.63 ± 4.46	–0.93 ± 5.32	1.07 ± 3.09
WarmContiMtn	–5.73 ± 6.11	3.76 ± 8.96	–0.19 ± 3.58
WestLowlands	–5.65 ± 10.65	4.94 ± 9.88	1.59 ± 5.65
WestMtns	–4.14 ± 5.78	–2.22 ± 5.26	2.92 ± 2.93

Note: Values in boldface indicate significant effects ($P < 0.05$).