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Heat waves measured with MODIS land surface temperature data predict changes in avian community structure

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ABSTRACT

Heat waves are expected to become more frequent and severe as climate changes, with unknown consequences for biodiversity. We sought to identify ecologically-relevant broad-scale indicators of heat waves based on MODIS land surface temperature (LST) and interpolated air temperature data and assess their associations with avian community structure. Specifically, we asked which data source, time periods, and heat wave indices best predicted changes in avian abundance and species richness. Using mixed effects models, we analyzed associations between these indices and data from the North American Breeding Bird Survey in the central United States between 2000 and 2007 in four ecoregions and five migratory and nesting species groups. We then quantified avian responses to scenarios of severe, but commonly-occurring early, late, and summer-long heat waves. Indices based on MODIS LST data, rather than interpolated air temperatures, were more predictive of avian community structure. Avian communities were more related to 8-day LST exceedances (positive anomalies only); and were generally more sensitive to summer-long heat waves. Across the region, abundance, and to a lesser extent, species richness, declined following heat waves. Among the ecoregions, relationships were most consistently negative in the southern and montane ecoregions, but were positive in a more humid northern ecoregion. Among migratory groups, permanent resident species were the most sensitive, declining in abundance following a summer-long heat wave by 19% and 13% in the montane and southern ecoregions, respectively. Ground-nesting species, which declined in the south by 12% following a late summer heat wave, were more sensitive than avifauna overall. These results demonstrate the value of MODIS LST data for measuring ecologically-relevant heat waves across large regions. Ecologically, these findings highlight the importance of extreme events for avian biodiversity and the considerable variation in response to environmental change associated with different functional groups and geographic regions. The magnitude of the relationships between avian abundance and heat waves reported here raises concerns about the impacts of more frequent and severe heat waves in a warming climate.

1. Introduction

The loss of biodiversity is the least reversible form of global change, and has been observed recently in numerous taxonomic groups, including birds (Novacek & Cleland, 2001). Biodiversity decline results from numerous interacting factors, including habitat loss and fragmentation (Fahrig, 2003), invasive species (Courchamp et al., 2003), overexploitation (Hutchings, 2000), and climate change (Parmesan & Yohe, 2003). A factor attracting increased attention, climate change encompasses changes in mean temperature and precipitation throughout the year and changes in variability among years. In some regions of North America, changes in interannual variability may be the most evident manifestation of climate change (Diffenbaugh et al., 2008) and more frequent extreme events such as heat waves are predicted (IPCC, 2007; Meehl & Tebaldi, 2004). Heat waves, which typically connote two or more consecutive days of hot and higher than average temperatures for a particular time period, have been linked to increased mortality among some wildlife species (Gordon et al., 1988; Jiguet et al., 2006).

However, relatively little is known about their effects among avian communities across diverse regions. Communities represent groups of species interacting at particular locations and may be subdivided according to taxonomic and functional characteristics. Responses by avian communities to heat waves are of particular interest for several

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reasons. Birds are near-ubiquitous, mobile, and responsive at fine temporal scales. Birds are of conservation interest because of a number of population declines in the United States (North American Bird Conservation Initiative — U.S. Committee, 2009) and worldwide, where one in eight species is threatened (BirdLife International, 2008). Birds also perform a broad array of ecosystem services including pollination, pest control, and recreation (Sekercioglu, 2006). In our study region, threats to already-diminished grassland habitats and associated grassland-specialist birds are of particular concern (Herkert, 1995). Finally, birds, being generally conspicuous, are among the most well monitored taxonomic groups.

Effectively relating heat waves to avian response requires spatially- and temporally-detailed data. Remote sensing plays an important role in informing biodiversity science (Turner et al., 2003), and Moderate Resolution Imaging Spectroradiometer (MODIS) data offer retrievals of biophysical parameters such as land surface temperature (LST, Wan et al., 2003) with an attractive balance of spatial and temporal resolution. Remote measurements of LST have been widely used in energy balance and agro-meteorology studies (e.g. Anderson et al., 2007; Dakhore et al., 2008), but much less in ecological and biogeographic studies (but see Mildrexler et al., 2007). Concurrently, advances in databases and interpolation algorithms have spurred the availability of gridded weather and climate summaries based on networks of ground measurements (e.g. Daly et al., 2002; Hijmans et al., 2005). The relative strengths of satellite and ground measurements for biodiversity and ecological studies are not clear. There are several key differences between these remotely-sensed and ground-based data sources. Meteorological stations measure air temperature, T_{air}, typically at 1.5–2.0 m in height. In contrast, remote sensors measure land surface temperature, which, though correlated, can differ greatly from T_{air}. Land surface temperature is heavily influenced by latent heat flux associated with evapotranspiration and is thus related to vegetation condition (Zaitchik et al., 2006). Because birds are often dependent on vegetation, this property of LST may render it an especially useful indicator of individual-scale weather conditions. For both T_{air} and LST, it is important to consider whether there are critical periods in the year when birds are more sensitive to extremes or whether entire seasons of above normal temperatures are most relevant. Lagged demographic responses (e.g. reduced recruitment) may influence whether population and community effects are more apparent during the year of a heat wave or in subsequent years.

Heat waves can elicit direct and indirect responses from birds and other animal taxa. Direct responses may include changes in behavior (Guthery et al., 2005), reduced recruitment (Guthery et al., 2001), or death (Finlayson, 1932). The same responses may occur indirectly, through effects of heat on resources (e.g. cover, forage, prey) that animals use (Becker et al., 1997). Responses to severe weather can also include dispersal to less-affected areas (Mooij et al., 2002). Responses are likely to depend on functional traits of species and groups of species For instance, because air temperatures can differ drastically from surface temperatures, the vertical stratum (i.e. ground- vs. canopy-level) that birds occupy likely influences their sensitivity to heat waves. Migratory habit can affect both the amount of time spent in a locale and the way habitat is selected. Geographic location may also influence the severity of heat waves as well as the degree to which animals are adapted to thermal stressors (Yarbrough, 1971).

Our goal was to identify relationships between heat waves and changes in the structure of avian communities. Our primary hypothesis was that both abundance and species richness decline due to heat waves, but that abundance would be more affected because the abundance of individual species has to decline to zero before producing a decline in species richness. We asked two sets of supporting questions. The first set aimed to identify the most relevant types of heat waves and indicators for avifauna. Specifically, we asked whether avian communities 1a) are more related to remotely-sensed measurements of LST or T_{air} from interpolated ground measurements, with the expectation that they would be more related to LST than to T_{air} because of the influence of vegetation condition on the former; 1b) are more related to temperature anomalies (departures from means) or exceedances (above normal temperatures only), anticipating that that exceedances, by quantifying only above normal temperatures, would be better indicators; and 1c) respond differently to heat waves occurring during different same-season and previous-season time periods, hypothesizing that avian communities would respond more strongly to previous-season heat waves because of nest failure and that dispersal would be more common responses than outright adult mortality.

The second set of questions focused on identifying how avian response to heat waves varied with functional trait and geographic region. Specifically, we asked 2a) whether nest stratum and 2b) migratory habit influence avian response to heat waves with the expectation that birds nesting in the more thermally stressful ground level would respond most negatively and that responses would diminish with migratory distance as migration-related mortality would dominate the demography of migratory birds; and 2c) how responses vary among four ecoregions with different climatic regime, hypothesizing that responses would be greatest in warmer ecoregions where thermal stress would be greater.

2. Methods

2.1. Study region

Our study area is a large and diverse region, encompassing 15 states of the central United States (3.7 million km^2; Fig. 1), and including both eastern and western US bird species. Largely temperate, the region is centered on the Great Plains, a gently sloping prairie landscape dominated by agriculture and rangelands. In the West are the Rocky Mountains and in the East are the Southern Mixed Forest, Ozark Highlands, and Eastern Broadleaf Forest. Excluding mountainous areas, there is a gradient of declining precipitation from east (80–140 cm yr^{-1}) to west (25–35 cm yr^{-1}). The mountainous west experiences more precipitation (e.g. 95 cm yr^{-1}), much of it in the form of snow. Mean maximum temperature in July generally exceeds 35 °C in the south, but declines to less than 25 °C in the north and often less than 15 °C in alpine areas.

2.2. Avian data

We obtained 2000–2007 data from the North American Breeding Bird Survey (BBS; (USGS, 2008). Our study area includes 1233 BBS routes, each 39.4 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 data from first-year observers and those having inclement weather at the time of the survey (Link & Sauer, 1997; Sauer et al., 2004). For each suitable year within each route ("route-year"), we summed counts of individual birds for a) North American landbirds ("ALL"; (Rich et al., 2004), b) three different migratory groups ("RESIDENT", "SHORTDIST", and "NEOTROP"; (Rappole, 1995), and c) two guilds related to nest location ("GROUND" and "CANOPY"; (Pidgeon et al., 2007), for a total of 6 avian groups; (Table 1, complete membership lists in Table S1). 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). In addition to abundance, we tabulated richness, i.e. the number of species identified in each group.