Population response to environmental productivity throughout the annual cycle in a migratory songbird

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Abstract

Environmental factors affect migratory animal populations in every phase of their annual cycle and have significant impacts on breeding success and survival. The Breeding Bird Survey provides a long-term database for examining population trends in North American birds, allowing us to examine large-scale environmental factors that influence population abundance. We examined plant productivity as measured by NDVI (Normalized Difference Vegetation Index) over a 24 -year period from 1983 – 2006 in bird conservation regions (BCRs) that overlapped Bullock's oriole (*Icterus bullockii*) breeding, moult, and wintering ranges to ask whether plant productivity in one year influences population abundance in the subsequent breeding season. Bullock's orioles have a moult-migration strategy, with a stopover moult in the Mexican monsoon region, which necessitates examining each stationary phase of the bird's annual cycle to understand the impacts of environmental factors on population abundance. Our results show increased breeding abundance in three (Great Basin, Coastal California and Shortgrass Prairies) of the six BCRs in which the species breeds following years with high NDVI values. We did not detect a response of breeding abundance to high NDVI values in the previous year in either the moulting region or in their primary over-wintering area in central Mexico. Our results demonstrate that large-scale annual variation in primary productivity on the breeding grounds can have an impact on breeding abundance in the following season, but further studies on migratory connectivity and on ecological mechanisms during the non-breeding seasons are needed to understand why we did not detect an influence of productivity during these periods.

Keywords

Abundance • BBS • Bullock's oriole • Climate • Long-term • NDVI

Introduction

Throughout the annual cycle, numerous biotic and abiotic factors interact to influence variation in the survival and breeding success of animals. For migratory birds, studying these interactions can be challenging due to the vast distances individuals travel in a year. Most studies have focused on birds on their breeding grounds, at migratory banding stations, or occasionally on their wintering grounds, but relatively little is known about how these phases of the annual cycle interact to influence individual and population level processes (Marra et al. 1998; Webster et al. 2005; Bowlin et al. 2010; Harrison et al. 2013; Senner et al. 2014). A more comprehensive, annual-cycle approach to the study of migratory birds, which integrates the phases of breeding, moult, migration, and over-wintering, is necessary to understand the interactions among them (Marra et al. 1998; Bowlin et al. 2010; Newton 2011; Harrison et al. 2013).

Variation in climatic conditions and the influence of this variation on resource availability can have important effects on individuals throughout the annual cycle. For example, spring migration of individual red-backed shrikes (*Lanius collurio*) and thrush nightingales (*Lanius luscinia*) is delayed by the need for a longer stopover during periods of drought in eastern Africa (Tøttrup et al. 2012). Resource availability can be measured in a number of different ways, including the use of remotely sensed measures of plant productivity such as NDVI (Normalized Difference Vegetation Index). In bobolinks (*Dolichonyx oryzivorus*), declines in primary productivity, as measured by NDVI, appear to lead to early departure during fall migration as well as movement from one stopover site to another (Renfrew et al. 2013). Similarly, greater plant cover is positively related to diurnal body mass gain during migration stopover for forest dwelling willow warblers (*Phylloscopus trochilus*) and Eurasian redstarts (*Phoenicurus phoenicurus*) (Ktitorov et al. 2008). Thus, plant productivity appears to be critical for migratory birds and can be measured both directly (i.e., in the field), as well as indirectly, through the use of metrics such as NDVI.

Although climatic conditions and plant productivity may influence individuals immediately and directly, these effects may also carry-over to subsequent seasons. Carry-over effects occur when conditions in one phase of the annual cycle have a significant effect on the animal in a subsequent phase; these effects are thought to be especially strong among migratory species, and may have a significant impact on their life history and evolution (Inger et al. 2010). For example, environmental conditions on over-wintering territories can carry over to impact arrival dates (Marra et al. 1998; Reudink et al. 2009) and reproductive success in the following season (Saino et al. 2004; Reudink et al. 2009). Annual variability in amount of rainfall in the wintering range of American redstarts (*Setophaga ruticilla*) is associated with changes in both the physical condition of individuals and the timing of their departure during spring migration (Studds and Marra 2005). In the case of birds that utilize stopover sites to moult during migration (i.e., moult-migrants), it is possible that these types of carry-over effects are likely to be contingent on both the over-wintering environment and the condition of the stopover moult location.

In addition to the effects of climate and environmental conditions on individuals, large-scale climate patterns can have major impacts on population-level dynamics. For example, the El Nino Southern Oscillation (ENSO) influences rainfall patterns and temperature and thus food availability for black-throated blue warblers (*Dendroica caerulescens*) wintering in Jamaica, leading to lower survival rates in drier, El Nino years (Sillett et al. 2000). Climate indices for ENSO and other large-scale cyclical climatic events have also been shown to account for the majority of variability in reproductive success of 10 other migratory bird species (Nott et al. 2002). Temperature trends have affected yellow-billed cuckoos (*Coccyzus americanus*), as populations have increased in size following cooler years (Anders and Post 2006). In addition, Saino et al. (2004) and Wilson et al. (2011) demonstrated that plant productivity, as measured by NDVI, is a significant driver of population dynamics in both barn swallows (*Hirundo rustica*) and American redstarts (*Setophaga ruticilla*). In both species, years with low NDVI on the wintering grounds resulted in a significant decrease in abundance during the subsequent breeding season (Saino et al. 2004; Wilson et al. 2011).

Although a vast majority of migratory songbirds have two stationary phases during the annual cycle, some western North American songbirds, including Bullock's orioles (*Icterus bullockii*), have an interesting migratory strategy that includes a prolonged stationary moult period in the Mexican monsoon region (Rohwer et al. 2005; Pyle et al. 2009). Rather than undergoing a partial or complete post-breeding moult on the breeding grounds, birds that employ this strategy make use of a stopover location to moult while en route to their wintering grounds (Rising and Williams 1999; Newton 2011). These moult-migrants generally stop in the Southwestern United States and Northwestern Mexico during the late summer through early fall period, apparently timing moult to coincide with an increase in food abundance resulting from a dramatic increase in plant productivity during and following late summer monsoon rains in these areas (Rohwer and Manning 1990; Rohwer et al. 2005; Pyle et al. 2009). Because moult and migration are energetically costly, these stopover sites may be crucial, allowing birds to build up important fat stores, and grow high quality plumage, which is necessary for both flight and communication (Hutto 1998; Leu and Thompson 2002). To our knowledge, no research to date has investigated environmental conditions during each stationary phase of the annual cycle to explore population-level effects of environmental variability on moult-migrants.

Using publically available Breeding Bird Survey (BBS) and environmental data (i.e., NDVI), we ask whether environmental variation during the three distinct stationary phases of the annual cycle influences Bullock's oriole breeding abundance in subsequent years. Bullock's orioles breed in riparian areas of Western North America from Northern Mexico to the Southern Interior of British Columbia. Bullock's orioles undergo an entire pre-basic moult while en route to their over-wintering grounds in the fall (Rohwer and Manning 1990; Pyle 1997; Rising and Williams 1999); After Hatch Year (AHY) birds appear to complete an entire pre-basic moult, while Hatch Year (HY) birds moult contour feathers and a variable number of flight feathers (Pyle 1997; A.G. Pillar et al., unpublished data). With the exception of some individuals that are resident in southern California, orioles winter from Western Mexico to as far south as Costa Rica, with the core of the wintering range being in Central Mexico (Rising and Williams 1999), although details of migratory connectivity are currently unknown. As we expected that increased plant productivity would enhance resource abundance for orioles, we predicted that increased productivity in the monsoon region would be positively related to breeding bird abundance in the subsequent year. Similarly, we predicted positive relationships between the NDVI in oriole breeding and over-wintering regions and abundance in the next breeding season.

Material and methods

Survey data

We obtained range-wide BBS data for Bullock's orioles from 1983 to 2006 and classified data by Bird Conservation Regions (BCRs). BCRs capture a combination of geophysical and environmental conditions within a specified area (Commission for Environmental Cooperation 1997), and are a useful way to delineate regions within which individuals would be exposed to broadly similar habitat and climatic conditions (Sauer et al. 2003; Wilson et al. 2011). Bullock's orioles are present on BBS routes in 17 BCRs across western North America, but many have few detections of this species, either because the BCR has few BBS routes or because it is located on the periphery of the species' range. We therefore limited our analysis to six BCRs (5, 9, 10, 16, 18 and 32), which represent the core of the breeding range and contained 80 % (*n* = 35,020) of the Bullock's orioles detected over the 24 years of BBS data used in this analysis. Within these six BCRs (hereafter referred to as 'strata'), many BBS routes only had data for a small number of years or had very few Bullock's oriole detections. To limit the influence of these routes, we further restricted the analysis to routes that had been surveyed for 14 or more of the 24 years and where 2 or more Bullock's orioles were recorded on average across all years.

Normalized Difference Vegetation Index

We obtained bimonthly Normalized Difference Vegetation Index (NDVI) data from the GIMMS (Global Inventory Mapping and Mapping Studies) remotely-sensed raster image dataset for a 25 year period from 1982 to 2006 (Carroll et al. 2004). The NDVI is calculated as (NIR-

Red)/(NIR+Red) with NIR (near-infrared) and Red being equal to the amount of near-infrared and red light, respectively, reflected by a surface and recorded by remote sensing (Jensen 2007; Pettorelli et al. 2011). The NDVI is positively correlated with several measures of plant productivity including photosynthetic capacity, leaf area index, canopy extent and carbon assimilation (Myneni et al. 1995; Hicke et al. 2002; Wang et al. 2005; Pettorelli et al. 2011). As a measure of plant productivity, the NDVI is often used in wildlife studies as an index of resource abundance, and variation in that abundance, over time or space (Pettoretti et al. 2005; Boone et al. 2006; Wilson et al. 2011; Tøttrup et al. 2012). We were interested in examining how annual variation in plant productivity, as measured by the NDVI, during the breeding, moult and over-wintering periods influenced BBS abundance on the breeding grounds in the following season.

Bullock's orioles exhibit strong breeding site fidelity among years (mean adult dispersal of 111 m; Rising and Williams 1999) and therefore strata-level measures of productivity during the breeding season in year t-1 were predicted to influence abundance in the following breeding season through positive effects on reproductive output. The onset of breeding for Bullock's orioles is delayed with increasing latitude and decreasing longitude (i.e., more northern and eastern populations within the range breed later; Rising and Williams 1999). To accommodate this in our measure of productivity during the pre-breeding and breeding periods, we used NDVI values averaged from April 1 – June 30 for BCRs 5, 9, 10, 16 and 18, and March 15 – June 15 in BCR 32. Using Esri's ArcGIS (Zonal Statistics) we extracted NDVI values from the raster image dataset for each BCR in which these values intersected with BCRs and the known Bullock's oriole range. In each area, we excluded NDVI values for which (i) data was missing, (ii) the values may have been influenced by snow reflectance, or (iii) the values were retrieved from spline interpolation or average seasonal profile.

Because of absolute differences in the average NDVI across western North America, we standardized it within each stratum. Breeding season primary productivity was very low during the 1999 La Niña event, particularly in the Great Basin and Coastal California strata (standardized NDVI values = -3.19 and -3.01 respectively). Large-scale climatic oscillations like the ENSO influence a variety of ecosystem processes at large spatial and temporal scales (Stenseth et al. 2003). Because of the potential for strong influence of this single year anomaly, we ran models with and without BBS abundance data from 2000 to examine how this year affected the beta coefficient and we report both in the results text for these strata. It is possible that density-dependent competition and habitat quality influence inter-annual movement among regions (Johnson and Grier 1988; Rohwer 2004; Studds et al. 2008), although the scale of this movement is not well understood for passerines. Such an effect could mean that BBS abundance is also influenced by current year productivity; however, we chose not to test this effect here because fidelity to previous breeding areas appears to be relatively strong among adult Bullock's Orioles (Rising and Williams 1999) and adults likely comprise the majority of detections on BBS routes. Without an ability to separate yearlings and adults, we were unable to properly test whether current year conditions have an effect on settlement, especially at the scale of a BCR. Movement at the scale of routes within BCRs might be more reasonable, even among adults, but we did not have route level measures of NDVI to assess this.

Identification of the optimal temporal and spatial window for the moult and winter periods is more difficult because individuals are not directly monitored and their presence in an area during these periods must be inferred through other methods. The monsoon region as described by Comrie and Glenn (1998) covers the Southwest United States (primarily eastern Arizona and New Mexico) and western Mexico, including the states of Sonora, Chihuahua, Sinaloa, Durango, Nayarit and northern Jalisco (Fig. 1). However, the moulting area for Bullock's Orioles is more concentrated in the west central portion of this region (Navarro-Sigüenza et al. 2003; Rohwer et al. 2009; Atlas of Mexican Birds, unpublished data) and primarily falls within two bird conservation regions: Sierra Madre Occidental (BCR 34) and Planicie Costera, Lomerios y Coñones de Occidente (BCR 43). We thus defined these two BCRs as the moult region and for each year, used the area weighted average NDVI values for the species' moult period (mid-July through mid-October) as described in Rising and Williams (1999).

The Bullock's oriole wintering range is concentrated in central Mexico, including both coasts and higher elevation regions in the interior (Rising and Williams 1999). The northern and southern extents of the wintering range include a narrow strip along the north Pacific coast and the Chiapas region. Analyses relating NDVI to breeding abundance become statistically limiting as the spatial correlation of the NDVI weakens across the area of interest. To reduce this effect we focused on the core of the wintering range described by Rising and Williams (1999) with further observational support from the eBird database (Sullivan et al. 2009). Although coarse, the latter shows that Bullock's orioles are most common in winter along Pacific coastal and interior regions between approximately 15.7° and 20.5° North latitude and -96.6° and -105.7° West longitude. This region includes BCRs 45, 46, 47, 50, 51, 53 and 54, among which the NDVI shows high spatial autocorrelation: average pairwise correlation, $r_p = 0.62$. The pairwise correlations for NDVI are lower when these BCRs are compared to those in the Sinaloa region of the north Pacific coast (BCRs 43, 44), the Caribbean coastal regions in Veracruz state (BCRs 49, 52 and 55), and those in Chiapas state at the southern extent of the species' range (primarily including BCRs 49, 52 and 58-61). Because these three regions represent the outer portions of the wintering range, and because the spatial correlations of the NDVI were lower, we did not include NDVI values from these regions in our analysis. To identify an annual winter NDVI covariate (Dec through Mar), we calculated the average NDVI corrected for area for BCRs 45, 46, 47, 50, 51, 53 and 54 and used this as our estimate of winter productivity. The NDVI values for the moulting and over-wintering regions were standardized prior to analysis.

Statistical analysis

Population change for Bullock's Orioles was modeled with a hierarchical, over-dispersed Poisson regression and analyzed under a Bayesian framework with Markov Chain Monte Carlo (MCMC) methods in WinBUGS 1.4.3 (Lunn et al. 2000). Each count $C_{i,j,t}$ (for stratum i, observer-route combination j and year t) was modeled as a Poisson random variable with mean $\lambda_{i,j,t}$ defined as a log-linear relation to the predictor variables, which include process and sampling components:

$$[1] \qquad \log(\lambda_{i,j,t}) = \alpha_i + \beta_{1,i} \times \text{year} + \beta_{2,i} \times \text{breed NDVI}_{t-1} + \beta_{3,i} \times \text{moult NDVI}_{t-1} + \beta_{4,i} \times \text{winter NDVI}_t + \beta_5 \times \text{start-up}_{j,t} + \text{observer-route}_{j,t} + \varepsilon_{i,j,t}$$

The model includes strata-specific estimates for average BBS abundance (α_i), temporal trend (β_1), and the NDVI-based estimates of productivity for the breeding period in year t - 1 (β_2), moulting period in year t - 1 (β_3) and the wintering region in year t (β_4). Betas 1-4 were assigned flat, normal distributions with mean 0 and variance 10^3. Parameter estimates at the stratum-level need to incorporate sources of variation in the data associated with routes and observers (Link and Sauer 2002, 2007). Observer-route combinations (ω) were treated as normal random variables. Observers also differ in their experience at identifying species on BBS routes, with variation being particularly high between their first year and all subsequent years (Link and

Sauer 2007). We incorporated these start-up effects by assigning a 1 if that count ($C_{i,j,t}$) was the first year of service for that individual and a 0 otherwise. Beta 5 (β_5) represents this first year influence in the model and was assigned a flat, normal distribution with mean 0 and variance 10^3. The component $\varepsilon_{i,j,t}$ helps accommodate over-dispersion, which is common in count data such as that provided by the BBS. Because of our interest in the effects of an annually-varying covariate, we did not include the variance of year effects as is typically done for the analysis of temporal trends using BBS data (Sauer and Link 2011). Variance associated with observer-route combinations (σ^2_ω) and over-dispersion (σ^2_ε) were assumed to be constant across strata and were assigned vague inverse-gamma prior distributions with shape and scale parameters = 0.001.

We chose not to include density dependence in our models and instead used an approach similar to other analyses relating environmental covariates to BBS abundance of a species (LaDeau et al. 2007; Link and Sauer 2007; Wilson et al. 2011). While abundance on BBS routes in year t may be related to abundance in year t + 1, estimation of temporal autocorrelation is difficult in these models. Because of missing data, this approach requires deriving an estimate for abundance on a route when it was not surveyed in year t and then using that value as a predictor in year t + 1. A specific estimate of the density dependent coefficient can also be biased because the large sampling variation present in citizen science data makes it difficult to estimate the return to an equilibrium population size (Lillegård et al. 2008). We acknowledge that temporal autocorrelation may occur in our data, but there was no evidence of temporal autocorrelation in the NDVI for any period or region and therefore, autocorrelation in the count data should at most only influence our ability to detect a relationship between the NDVI and subsequent abundance.

We ran three Markov chains for the model, each for 50,000 iterations, and examined convergence through individual parameter history plots, Gelman-Rubin diagnostics, and the estimation of MC error/SD for each parameter (Gelman et al. 2004; Link and Barker 2010). The chains typically converged within 1,000 iterations, but we discarded the first 10,000 iterations as a burn-in before drawing samples from the posterior distribution. Graphical posterior predictive checks were used to examine the fit of the model (Gelman et al. 2004). This measure involves drawing replicate samples of data from the posterior distribution and comparing the fit of the observed data to the replicate data that conform to the assumptions of the model. We examined the temporal trend and NDVI influence in each period by examining the median estimate along with 95 % credible intervals (CI) for β_1 and $\beta_{2\text{-}4}$ respectively. Parameters were interpreted as significant when 95 % CIs excluded zero.

In our examination of the relationship between NDVI and BBS abundance, we performed an initial run of the model to first identify significant relationships between the NDVI in a period of the annual cycle and BBS abundance. We then ran the model again and in this second run, included a derived estimate of the expected change in BBS abundance in relation to a 1-unit change in the standardized NDVI for those strata in which the effect was significant for a period of the annual cycle. The use of a standardized NDVI value in this case was because of variation in the absolute NDVI among strata. The predicted stratum-specific abundance in relation to NDVI was specified as a derived parameter in the model following Sauer and Link (2011) as:

$$[2] \qquad N_{i,t} = \exp(\alpha_i + \beta_{1,i} \times \text{year}_{t\text{-mid}} + \beta_{2,i} \times \text{breed NDVI}_{t-1} + \beta_{3,i} \times \text{moult NDVI}_{t-1} + \beta_{4,i} \times \text{winter NDVI}_t + 0.5 \times \sigma^2_\omega + 0.5 \times \sigma^2_\varepsilon)$$

We estimated how BBS abundance varied in relation to a change in the NDVI by comparing the predictions from two models that differed in one unit of the standardized NDVI during that period of the annual cycle while holding other variables constant. We set the NDVI beta parameters for the other periods of the annual cycle equal to 0, which is equivalent to average productivity in those regions. We used the mid-point (t-mid = year 12) of the time series for each stratum to incorporate temporal trends. Variance components for observer-route effects and over-dispersion were included to improve estimates of mean abundance from the log-normal distribution (Sauer and Link 2011).

We also considered the power to detect a significant relationship at 95 % certainty between the NDVI and subsequent BBS abundance. This analysis was performed for each stratum in relation to NDVI in the breeding, moulting and wintering regions. Power was measured by taking the lower credible interval half-widths (2.5 %) of the posterior distribution for β_2 through β_4 to predict the change in abundance for a 1 unit change in the NDVI. These half-widths are the values that would be required for the credible intervals to exclude zero, assuming a positive effect of the NDVI in each period of the annual cycle; they thus provide a measure of the extent to which the NDVI would need to influence BBS abundance in order for us to declare the existence of a significant effect in the face of other sampling and process variance.

Results

Survey data

We included BBS data from 161 routes across six strata on which 24,689 individual orioles were recorded between 1983 and 2006. Bullock's oriole abundance was highest in Coastal California (BCR32), Shortgrass Prairie (BCR 18), and Great Basin (BCR9), and lower in the Northern Pacific Rainforest (BCR5), Northern Rockies (BCR10 and Southern Rockies-Colorado Plateau (BCR16, Table 1). Because the species was less abundant in the latter three strata, the proportion of BBS routes that met our minimum criteria was lower, particularly for the Northern Rockies (8.4 % of routes) and Southern Rockies-Colorado Plateau (11.5 %).

Population model results

Our model included three NDVI covariates for the breeding season, moulting region and over-wintering region (Fig. 1). There was no evidence that productivity in the moulting region or the over-wintering region influenced subsequent abundance for any of the six breeding strata (95 % credible intervals for all strata overlapped zero). In contrast, breeding season productivity resulted in significantly greater abundance in the following year with 95 % certainty for the Great Basin, Shortgrass Prairie and Coastal California (Table 2, Fig. 1). For the Great Basin, this interpretation was based on the analysis without data from 2000, which followed the 1999 La Niña event, when breeding season plant productivity was very low. The estimated coefficient for the Great Basin was 0.065 [95 % CI (0.001, 0.129)] without BBS data for the year 2000 and 0.014 with the year 2000 included [95 % CI (-0.029, 0.057)], indicating a strong single year influence on the slope of the relationship between breeding season NDVI and subsequent BBS abundance. This result indicates that Bullock's oriole abundance was higher than expected in 2000 given the low primary productivity associated with the La Niña event in 1999. There was less influence of the La Niña event on the slope for Coastal California (β_2 = 0.051 with 2000 vs 0.039 without 2000) or Shortgrass Prairie (β_2 = 0.052 with 2000 vs 0.053 without 2000) and in both cases the response from 1999 to 2000 was more similar to the pattern across all years. The predicted percentage change in BBS abundance in response to a 1 unit change in the standardized breeding season NDVI was 6.70 [95 % CI (0.00, 13.70)] in the Great Basin, 5.40 [95 % CI (0.10, 10.90)] in Shortgrass Prairie and 5.20 [95 % CI (0.40, 10.20)] in Coastal California. There were no significant relationships between breeding season NDVI and subsequent BBS abundance in the other three strata (Table 2). All three strata actually had negative coefficients, but the credible intervals were wide due to the low precision (Table 3).

Our examination of precision considered what percent change in abundance would be needed in response to a 1 unit change in the NDVI for the 95 % intervals of the coefficients to exclude zero at the lower end (i.e., a positive response to NDVI). For the effect of prior breeding season productivity, the percent change in abundance required for the Great Basin, Coastal California and Shortgrass Prairies ranged from 4.19 to 4.97 %, whereas it was higher for the other three strata, in which abundance was lower (ranging from 7.58 to 8.59, Table 3). The pattern among strata was similar for the non-breeding periods, but precision was slightly lower compared to the prior breeding season effect (Table 3).

Variance associated with the observer-route effect was 0.900 (posterior SD = 0.038) and with the over-dispersion parameter was 0.331 (posterior SD = 0.012). The first-year effect was negative [β_6 = -0.140, 95 % CI -0.241, -0.042)], indicating that BBS observers tend to underestimate the abundance of Bullock's orioles in their first year of service. Trends were significantly negative with 95 % certainty in the two coastal strata (Coastal California, Northern Pacific Rainforest) and were not significant in the four interior strata (Table 1). The trends reported here are based only on those BBS routes used in this analysis and may differ from those in each stratum as a whole, although most are generally consistent with the broader Breeding Bird Survey analysis (Sauer and Link 2011).

Discussion

Understanding how animal populations respond to large scale changes in climate has proven difficult, especially for migratory species that inhabit areas separated by hundreds, if not thousands, of kilometres during different times of the year and that are thus subject to different climatic events. The North American BBS is an important long-term dataset that allows us to investigate trends in breeding bird populations. By linking BBS information with data from remotely-sensed estimates of primary productivity, we can begin to understand how the effects of climate and subsequent green up, which occur at different locations during temporally distinct periods, can influence breeding bird population trends. Our analysis suggests that over the past 25 years, population fluctuations in several regions across the Bullock's oriole breeding range are closely linked to changes in plant productivity during the preceding breeding season and to our knowledge this is the first example showing this large scale effect of productivity on an avian species in western North America. Contrary to our predictions, we did not observe any effects of variation in productivity in the moulting area (a portion of the monsoon region) or on the wintering grounds on subsequent breeding abundance

Our results indicate that breeding abundance of Bullock's orioles in some regions is positively influenced by an increase in plant productivity in the previous breeding season. Specifically, we detected a significant increase in abundance in response to an increase in primary productivity in the previous year for Coastal California, Shortgrass Prairie, and Great Basin BCRs. Increased productivity may help with the energy demands associated with breeding, feeding nestlings, and subsequent migration. There are two non-exclusive hypotheses that may explain the pattern we observed. First, nestling productivity may be low during years of low productivity, due to reduced food availability during breeding, resulting in lower recruitment in the following season (Holmes et al. 1992). Species richness and abundance of insects (Haddad et al. 2001), grassland arthropod abundance (Siemann 1998), and beetle abundance (Lassau and Hochuli 2008) are all positively linked to plant productivity. Increased arthropod abundance

(Lepidoptera larvae) during the breeding season has been demonstrated to lead to increased reproductive success in the same season for other avian species (Holmes et al. 1986). In a study of stonechats (*Saxicola dacotiae)* endemic to a semi-arid island in the Canary Islands, reproductive investment and clutch size were linked to increased arthropod abundance, which was in turn related to earlier rainfall (Illera and Díaz 2008). Similarly, forest productivity was positively related to insect abundance, which in turn was strongly and positively related to fledgling success in ovenbirds (*Seiurus aurocapilla*) (Seagle and Sturtevant 2005). A second hypothesis is that reduced plant productivity may lead to lowered physical condition of hatchlings and/or adults, reducing the likelihood of surviving fall migration. For example, declining productivity during the breeding season appears to have a negative influence on fitness and reproductive success in European pied flycatcher (*Ficedula hypoleuca*) populations around the Mediterranean (Sanz et al. 2003).

Our study found significant effects of breeding season productivity on subsequent abundance of Bullock's orioles in only three of the six strata. The three strata where no significant effects were observed all have lower breeding abundance in general, and one possibility is that we had limited potential to detect an effect. While our analysis of precision showed that this was true to some extent, the coefficients for these three strata were all negative, although only strongly so for the Northern Pacific Rainforest. It is possible that other factors, such as predation, habitat availability or the strength of density-dependence, have a greater influence on reproductive output and we were thus unable to detect a signal from environmental productivity in the previous year. Reproductive output may be further affected by baseline differences in productivity among ecosystems. For example, annual variation in productivity may have a proportionately greater influence on avian demography in a drier ecosystem such as the Great Basin compared to a wetter ecosystem like the Northern Pacific Rainforest. It is also possible that because the Northern Pacific Rainforest is a very wet ecosystem at the periphery of the Bullock's oriole range, years with higher NDVI values might represent less favorable conditions. Further study of the links among annual climate, plant productivity and avian reproductive output in ecosystems of western North America are needed to better understand why only some regions of the breeding range show this link between BBS abundance and the NDVI in the previous breeding season.

Our finding that habitat quality in the previous breeding season influences subsequent abundance raises the possibility of density-dependent compensation. Conditions experienced during one stage of the annual cycle may carry-over to affect fitness and abundance during subsequent stages (Runge and Marra 2005; Harrison et al. 2011) and this may in turn lead to a sequential density-dependent response at the population level (Ratikainen et al. 2008). Bullock's Orioles, for instance, may have lower non-breeding season survival in years following higher habitat quality on the breeding grounds when there is greater production of young. As such, we may underestimate the effect of primary productivity on reproductive output, although subsequent abundance would still reflect the combination of higher reproductive output followed by density-dependent compensation. Higher breeding abundance in one year may also influence abundance the following year, perhaps through settlement decisions (Ratikainen et al. 2008), although we suspect that this is more likely to be observed at finer scales, such as among BBS routes rather than among BCRs. With missing counts in the BBS dataset it was not possible to use prior route-level abundance as a predictor for current abundance on routes. Moreover, others have expressed concern about estimating density dependent responses in large scale datasets where survey error affects our ability to properly measure the return to an equilibrium abundance

(Lillegård et al. 2008). Nevertheless, we acknowledge the likely importance of density-dependent compensation when considering how environmental quality at different stages of the annual cycle affects populations.

We found no evidence that productivity in the over-wintering area in central Mexico affected subsequent breeding abundance of Bullock's orioles. This result is similar to Wilson et al. (2011) who found that BBS abundance of American redstarts in western North America was not influenced by the NDVI in Mexico, where they are known to over-winter. This was in contrast to the strong, positive relationship between American redstart abundance in eastern North America and the annual NDVI in the Greater Antilles, where eastern birds primarily over-winter. In this case, long-term studies of American redstarts in Jamaica (Marra et al. 1998; Marra and Holmes 2001; Studds and Marra 2005, 2007) combined with knowledge of migratory connectivity (Norris et al. 2006) helped identify the mechanism by which productivity affects individuals and could translate into population level responses on the breeding grounds (Wilson et al. 2011). High NDVI on the African over-wintering grounds also had a positive influence on the reproductive success of European barn swallows (*Hirundo rustica*) showing how winter productivity can also have carry over effects on the subsequent breeding season (Saino et al. 2004). In the case of Bullock's orioles, we lack a clear understanding of migratory connectivity between breeding and wintering populations and have only limited knowledge of winter ecology, making it difficult to draw conclusions from these findings. Further study of migratory connectivity, winter habitat use and ecosystem response to rainfall would aid our knowledge of how Neotropical migrants of western North America are influenced by annual variation in productivity on the wintering grounds.

Contrary to our predictions, we did not detect an influence of monsoon region plant productivity on breeding abundance in the following year. As with the wintering grounds, we do not have a full picture of where the birds from a specific breeding population moult, which hinders our ability to detect the impact of conditions in the moult region on breeding populations. Data from recently recovered light-level geolocators (A. G. Pillar et al., unpublished data) indicate that birds from the same breeding population may moult in different locations within the Mexican monsoon region, which makes it difficult to link breeding birds to their moult locations. However, Comrie and Glenn (1998) demonstrated strong autocorrelation in temperature and rainfall across the entire Mexican monsoon region, which may suggest that birds moulting throughout the area experience similar environmental conditions. Moult-migrants using the Mexican monsoon region are thought to take advantage of resources that are not available on the breeding grounds, which experience drying out over the course of the summer (Pyle et al. 2009). In contrast, the consistent productivity in the monsoon region makes it more likely that the region provides sufficient resources to support a successful moult before the relatively short migration from the moulting region to the over-wintering region. Thus, we may not have detected any influence of conditions in the moulting grounds on breeding abundance simply because environmental conditions consistently provide abundant, high quality resources, which is likely a necessary condition for the evolution of this migratory strategy (Rohwer and Manning 1990; Rohwer et al. 2005; Pyle et al. 2009).

Because the environment in which moult takes place is important for the acquisition of high quality plumage, which is necessary for both flight and mate attraction, rainfall and productivity during moult may still have important consequences for the reproductive success of individuals. Bullock's orioles appear to moult over a fairly broad area; they have been observed moulting in Arizona, Sonora, and Sinaloa (Pyle et al. 2009), suggesting that microsite variation may be important. The quality of carotenoid-based ornamental plumage in Bullock's orioles is dependent on pigments obtained through the diet and therefore is likely linked to the quality of habitat and the availability of food in the area in which moult takes place. Future work examining whether the productivity of the moulting grounds or the timing of arrival in the area, influences the feather colour of individual orioles would provide further insight into how these environmental factors influence reproductive success at both an individual and population level. A logical future step for this study would be to run a similar analysis on other moult-migrant songbirds from Western North America, examining differences and similarities among western moult-migrants. By using an inclusive approach, which takes into account breeding, stopover, and over-wintering regions, we can gain a more complete understanding of how climatic factors influence migratory bird populations, and thus be better equipped to deal with the potential conservation challenges associated with climate change.

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Table 1 Sample size, abundance per route and temporal trend (1983-2006) for Bullock's orioles in the six strata used in this analysis. Columns under "Stratum" are the total number of routes and the average number of Bullock's orioles detected per route for all routes in the Stratum. Columns under "Analysis" are those values for the routes that met our minimum criteria and used in this analysis (surveys in ≥14 of 24 years and mean of > 2 Bullock's oriole detections per year). Trends were determined from the model and are based only on the routes used in this analysis.

BCR	Stratum Name	Stratum		Analysis		Trend
		Number of routes	BUOR/route	Number of routes	BUOR/route	
5	Northern Pacific Rainforest	82	2.1	18	5.7	-1.61 (-3.16, -0.09)
9	Great Basin	204	3.4	45	6.8	- 0.11 (-0.99, 0.80)
10	Northern Rockies	143	1.6	12	7.3	0.40 (-1.42, 2.28)
16	Southern Rockies - Colorado Plateau	130	1.7	15	4.2	-0.59 (-2.22, 1.00)
18	Shortgrass Prairie	112	4.0	31	6.3	-0.08 (-1.22, 1.12)
32	Coastal California	104	9.8	40	11.5	-1.92 (-2.80, -1.02)

Table 2 Beta coefficients and 95 % credible intervals for the effects of NDVI in the breeding, moulting and over-wintering regions on the abundance of Bullock's orioles on Breeding Bird Survey routes in the following year. [1]The "Breed $NDVI_{t-1}$" coefficient for the Great Basin is from a model without data from 2000, since the 1999 La Niña event resulted in an outlier NDVI value that had considerable influence on the slope (see text). Bolded results refer to significant responses with 95 % certainty.

Strata	Breed $NDVI_{t-1}$	Moult $NDVI_{t-1}$	Winter $NDVI_t$
Northern Pacific Rainforest	-0.054 (-0.136, 0.029)	-0.036 (-0.119, 0.047)	0.008 (-0.077, 0.092)
Great Basin[1]	**0.065 (0.001, 0.129)**	0.033 (-0.016, 0.083)	-0.001(-0.054, 0.052)
Northern Rockies	-0.024 (-0.127, 0.079)	-0.007 (-0.109, 0.096)	0.006 (-0.097, 0.107)
Southern Rockies / Colorado Plateau	-0.014 (-0.093, 0.066)	-0.068 (-0.162, 0.027)	-0.011 (-0.108. 0.084)
Shortgrass Prairie	**0.052 (0.001, 0.103)**	0.041 (-0.020, 0.102)	0.005 (-0.058, 0.067)
Coastal California	**0.050 (0.004, 0.097)**	-0.015 (-0.064, 0.033)	-0.005 (-0.060, 0.050)

Table 3 Percent change in BBS abundance needed to declare a significant response to a 1 unit change in the standardized NDVI for each period of the annual cycle in each strata (based on the model with all years included). The percent change in the table is calculated using the lower 2.5 % credible interval half-width and is thus an indication of the power to detect a positive response with 95 % certainty.

Strata	Breed $NDVI_{t-1}$	Moult $NDVI_{t-1}$	Winter $NDVI_t$
Northern Pacific Rainforest	7.88	7.91	8.11
Great Basin	4.19	4.88	5.16
Northern Rockies	8.59	9.72	9.73
Southern Rockies / Colorado Plateau	7.58	8.99	9.18
Shortgrass Prairie	4.97	5.92	6.10
Coastal California	4.55	4.80	5.36

Figure Legends

Fig 1 Bullock's oriole breeding abundance in response to NDVI in the same Bird Conservation Region (BCR). Black indicates a significant response at ≥ 95 % certainty and light grey indicates no significant response. The Mexican monsoon region is shown in diagonal stripes. The Bullock's oriole wintering region is outlined in black, with the core wintering area shown in light grey.