COMMENTARY

Testing alternative hypotheses for the cause of population declines: The case of the Red-headed Woodpecker

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ABSTRACT

The Red-headed Woodpecker (*Melanerpes erythrocephalus*) has experienced strong population declines during the past 3 decades. Using North American Breeding Bird Survey (BBS) and Audubon Christmas Bird Count (CBC) data, we investigated 4 hypotheses that may explain this decline, including: (1) interspecific competition with native Red-bellied Woodpeckers (*Melanerpes carolinus*) and nonnative European Starlings (*Sturnus vulgaris*); (2) predation by Cooper's Hawks (*Accipiter cooperii*) and Sharp-shinned Hawks (*Accipiter striatus*); (3) climate change; and (4) changes in forested area within their range. In analyses of both the breeding and overwintering periods, our results indicated a role of increased accipiter populations in driving Red-headed Woodpecker declines through increased predation. We also found evidence for significant effects of warmer winter temperatures and increased forest cover, both directly and indirectly through their effects on enhancing accipiter populations. In contrast, our results failed to support the hypothesis that interspecific competition with either Red-bellied Woodpeckers or European Starlings has played a role in Red-headed Woodpecker declines. Despite considerable evidence for nest-site competition and aggression between Red-headed Woodpeckers and both Red-bellied Woodpeckers and European Starlings, these interactions do not appear to be limiting Red-headed Woodpecker populations.

Keywords: avian declines, climate change, European Starling, habitat change, nest-hole competition, predation, Red-bellied Woodpecker, Red-headed Woodpecker

Evaluando hipótesis alternativas sobre la causa de descensos poblacionales: el caso de *Melanerpes erythrocephalus*

RESUMEN

Melanerpes erythrocephalus ha experimentado descensos poblacionales marcados a lo largo de las tres últimas décadas. Usando datos del Muestreo de Aves Reproductivas de América del Norte (BBS por sus siglas en inglés) y del Conteo de Aves de Navidad de Audubon (CBC por sus siglas en inglés), investigamos cuatro hipótesis que podrían explicar esta disminución, incluyendo: (1) competencia interespecífica con la especie nativa *Melanerpes carolinus* y la especie no-nativa *Sturnus vulgaris*; (2) depredación por *Accipiter cooperi* y *Accipiter striatus*; (3) cambio climático; y (4) cambios en el área boscosa dentro de su rango. Nuestros análisis de los períodos de reproducción y de invernada indicaron que el incremento de las poblaciones de *Accipiter* juega un rol en el descenso de *M. erythrocephalus* a través de un aumento de la depredación sobre adultos y juveniles. También encontramos evidencia de efectos significativos de inviernos con temperaturas más calurosas y un aumento en la cobertura del bosque, ambos directa e indirectamente relacionados con un aumento de las poblaciones de *Accipiter*. En contraste, nuestros resultados no apoyaron la hipótesis de que la competencia interespecífica, ya sea con *M. carolinus* o con *S. vulgaris*, haya jugado un rol en los descensos de *M. erythrocephalus*. A pesar de la cantidad considerable de evidencia que indica competencia por los sitios de anidación y agresión entre *M. erythrocephalus* con *M. carolinus* y *S. vulgaris*, estas interacciones no parecen estar limitando las poblaciones de *M. erythrocephalus*.

Palabras clave: cambio climático, cambio de hábitat, competencia por huecos para nidos, depredación, descensos poblacionales de aves, *Melanerpes carolinus*, *Melanerpes erythrocephalus*, *Sturnus vulgaris*

INTRODUCTION

The causes of population declines can be notoriously difficult to determine, even when the species of interest is charismatic and the scope of the decline unambiguous. For example, whether the decline of the California Condor (*Gymnogyps californianus*) from being a widespread scavenger within western North America during historical

times to near extinction by the 1980s was due to habitat loss, human disturbance, food scarcity, pesticide contamination, or lead poisoning remains a controversial and critically important issue as recovery efforts continue (Walters et al. 2010, D'Elia et al. 2016). Similarly, whether the apparent decline of more than 100 species of North American migratory songbirds has been primarily driven by events occurring on their overwintering or breeding grounds is contentious (Robbins et al. 1989, Rappole and McDonald 1994, Faaborg 2002, Stutchbury 2007). Part of the difficulty is that only rarely can population declines be attributed to a single, unambiguous factor. More commonly, the cause of declines is multifactorial, as exemplified by amphibian declines in Latin America (Young et al. 2001, Collins and Storfer 2003, Whittaker et al. 2013).

The Red-headed Woodpecker (*Melanerpes erythrocephalus*) is a conspicuous, cavity-nesting species, locally common throughout much of central and eastern North America, that has experienced a survey-wide decline of -2.5% yr^{-1} in breeding populations since 1966 (Sauer et al. 2014), qualifying it for the Yellow Watch List in the 2015 State of the Birds Report (North American Bird Conservation Initiative 2014) and warranting listing as "near threatened" by the IUCN Red List authority (IUCN 2015). Although seasonally migratory, its range is largely confined to the United States, and thus data on populations during both the breeding and nonbreeding seasons spanning decades are readily available. Here, using data from the North American Breeding Bird Survey (Bystrak 1981, Sauer et al. 2014) and the Audubon Christmas Bird Count (Raynor 1975, Bock and Root 1981), we test whether the dramatic population declines that this species has experienced during the past several decades may be due, directly or indirectly, to interspecific competition, increased predation on adults and juveniles, climate change, or landscape-scale changes in forested areas within their range.

The most general hypothesis for declines is climate change, which has been implicated as a causal factor in the changing distribution and abundance of a wide range of flora and fauna in the past several decades (Walther et al. 2002, Root et al. 2003, Schimel et al. 2013). Climate change, most obviously expressed by increasing mean temperatures (global warming), also has an important influence on patterns of rainfall (Wheeler and von Braun 2013), increased temperature extremes (Seneviratne et al. 2014), and even increased spatial synchrony (Koenig and Liebhold 2016), and affects nearly all other potentially important ecological factors either directly or indirectly. Thus, climate change can be a proxy for other environmental factors, including many that we otherwise do not consider here, such as changes in food supply.

The second most general hypothesis that we consider is landscape change, particularly reforestation as a conse-

quence of land-use changes during the past several decades. Red-headed Woodpeckers are a species of oak savanna and forest edges (Frei et al. 2013), and an important constraint on their nesting success and range expansion is the lack of savanna habitat with a low density of tall dead trees (Emlen et al. 1986, Hudson and Bollinger 2013, Berl et al. 2015). Thus, loss of savanna and edge habitat within the range of Red-headed Woodpeckers may be an important driver of recent population declines.

The third hypothesis that we consider is interspecific competition. Several species compete with Red-headed Woodpeckers for either food or nest cavities, but Red-bellied Woodpeckers (*Melanerpes carolinus*) and European Starlings (*Sturnus vulgaris*) have been identified repeatedly in the literature as being involved in aggressive interactions with Red-headed Woodpeckers and other cavity-nesting species. The hypothesis that the Red-bellied Woodpecker is an important interspecific competitor with the Red-headed Woodpecker is suggested by observations of aggression between the 2 species (Kilham 1958, Willson 1970, Reller 1972) and by Root's (1988, p. 134) statement, based on winter abundance from Christmas Bird Counts, that "The abundance peaks of these two species show complementarity, which provides circumstantial evidence for interspecific interactions." These congeneric woodpeckers are similar in size (56–91 g), rendering competition for nesting cavities a potentially important factor contributing to Red-headed Woodpecker population declines (Ingold 1989).

The second potential competitor that we consider is the European Starling (hereafter, starling), a nonnative species introduced to North America in the late 1800s (Cabe 1993) that is known to usurp nesting cavities of Red-headed Woodpeckers (Jackson 1976, Ingold 1989, 1994, Frei et al. 2015a). An earlier analysis found no evidence of starlings having adversely affected most native cavity-nesting species, including the Red-headed Woodpecker (Koenig 2003), but in Great Britain, where starlings are native, the starling's recent population decline has been suggested to have been instrumental in facilitating increases of Great Spotted Woodpeckers (*Dendrocopos major*; Smith 2005).

The fourth and last hypothesis that we consider is increased predation by Cooper's Hawks (*Accipiter cooperii*) and Sharp-shinned Hawks (*Accipter striatus*), both of which are geographically widespread and common bird predators (Bildstein and Meyer 2000, Curtis et al. 2006). A role for increased predation in driving declines in Red-headed Woodpeckers is suggested circumstantially by the overall increase in populations of Cooper's Hawks in North America in the past several decades (Curtis et al. 2006) combined, more directly, with work on Red-headed Woodpeckers in South Carolina, USA, which indicated that predation by accipiters, including both Cooper's and

Sharp-shinned hawks, accounted for 85% of all deaths in the population (Kilgo and Vukovich 2012).

Predictions

Our goal was to test hypotheses for the cause of observed declines in Red-headed Woodpecker populations. Consequently, the predictions of the interspecific competition and predation hypotheses were that population trends of the competitor or predator would be inversely related to population trends of Red-headed Woodpeckers; that is, trends of Red-bellied Woodpeckers, starlings, and accipiters should be positive and inversely correlated with declines in Red-headed Woodpecker populations. If climate change has driven population declines of Red-headed Woodpeckers, population abundance should be inversely correlated with range-wide environmental conditions that have increased during the past several decades, and positively correlated with any condition that has decreased. Finally, if population declines have been driven by reforestation, we predicted that the relationship between change in forest cover and Red-headed Woodpecker abundance would be negative, since these birds are primarily found in open woodlands, not closed-canopy forests (Frei et al. 2015b).

METHODS

Data

Population abundance data for Red-headed Woodpeckers, Red-bellied Woodpeckers, European Starlings, and 2 accipiter species (Cooper's and Sharp-shinned hawks combined) were obtained from the North American Breeding Bird Survey (BBS) and Audubon Christmas Bird Count (CBC). Each BBS "site" consists of the summed counts of birds detected during 3-min surveys at a series of 50 stops located 0.8 km apart along road transects conducted during the main breeding season (usually May or June; Bystrak 1981), and data were available for 1966 through 2014. Relatively few counts were performed in the first year, however, and thus we restricted our analyses to the 48 yr from 1967 to 2014. We refer to the BBS data below as representing populations during the breeding season. Each CBC survey consists of a one-day intensive census conducted by a variable number of observers within a 2-week period around Christmas within a specific 24-km-diameter circle, and thus represents population estimates during the winter. CBCs were begun at the start of the 20th century, but data from early years are generally variable in quantity and quality, and thus we restricted our analyses to the 55 yr from 1960 to 2014.

As an index of relative abundance, we ln-transformed ($\ln[n + 1]$) the number of birds counted (BBS) and the number of birds per party hr (CBC). In both cases, ln-transformation helped to normalize and stabilize the variance of the data (Koenig 2003). Analyses of population trends using the BBS and CBC databases generally restrict consideration to a subset of sites where abundance values are above a minimum threshold (Thomas and Martin 1996). Here, we first limited analyses to the main distributional range of Red-headed Woodpeckers. For the winter, this was defined as states in the USA where the overall mean birds per CBC party hr was >0.20, which included surveys in 8 states (Arkansas, Illinois, Indiana, Iowa, Kansas, Kentucky, Missouri, and Oklahoma), roughly corresponding to the main wintering range as mapped by Root (1988). For the breeding season, the core distributional range was defined by U.S. states where the mean number of birds counted on BBS routes was >1. This overlapped with the 8 states within the main wintering range, but also included Minnesota, Nebraska, Ohio, and Wisconsin. Within the main distributional range, we further restricted our analyses to sites where Red-headed Woodpeckers were recorded in at least 25% of survey years (13+ yr for the CBC; 11+ yr for the BBS). This limited analyses to 655 BBS and 248 CBC sites.

Analyses of climate are invariably complicated by the wide range of weather factors that may be ecologically relevant. For all analyses, we included mean maximum and mean minimum temperatures during the breeding season (for the BBS routes) and during the winter (for the CBC surveys). For the analyses of mean annual data, we included the winter North Atlantic Oscillation (NAO) index (mean of monthly data from December through March), a large-scale pattern of natural climatic variability that has been found to significantly affect many ecological processes, in some cases more strongly than local weather conditions (Hallett et al. 2004). Restricting our analyses to this small number of environmental variables was necessary in order to keep the analyses tractable and focused on the most general and obvious environmental variables that were most likely, a priori, to reflect the effects of climate change.

Across the core range of the Red-headed Woodpecker, mean maximum summer temperatures generally declined between 1967 and 2014, whereas mean maximum winter temperatures increased (Table 1). Thus, were climate change to have driven population declines of Red-headed Woodpeckers, population trends during the breeding season were expected to be positively correlated with declines in mean maximum summer temperature, but trends during the winter were expected to be negatively correlated with increases in mean maximum winter temperatures. For each BBS route and CBC survey, temperature data for the appropriate months of each year were taken from the nearest 30-arcsecond grid point in the PRISM Climate Group dataset (http://prism.oregonstate. edu). For BBS routes in year *x*, summer temperature data were taken from May through August (roughly the

TABLE 1. Mean changes in Red-headed Woodpecker, Red-bellied Woodpecker, European Starling, and accipiter populations and in mean maximum seasonal temperatures for Red-headed Woodpecker sites between 1967 and 2014 (Breeding Bird Survey; BBS) and 1960 and 2014 (Christmas Bird Count; CBC). Values are mean slope per decade based on regressions of values (ln-transformed for bird populations) on year.

	BBS			CBC		
Species or factor	Mean $\pm$ SE change per decade	% sites increasing [a]	n sites	Mean $\pm$ SE change per decade	% sites increasing [a]	n sites
Red-headed Woodpecker	-0.225 ± 0.022***	15***	655	-0.049 ± 0.006***	21***	248
Red-bellied Woodpecker	0.179 ± 0.011***	84***	597	0.052 ± 0.006***	78***	248
European Starling	-0.020 ± 0.017***	47	653	0.128 ± 0.042***	63***	248
Accipiter spp.	0.027 ± 0.003***	81***	457	0.020 ± 0.002***	89***	247
Mean maximum seasonal temperature	-0.118 ± 0.021***	43**	655	0.474 ± 0.093***	73***	248

[a] Significance of mean change per decade based on mixed-effects models. Significance of percentage of sites increasing based on binomial tests. ** $P < 0.01$; *** $P < 0.001$; other $P > 0.05$.

breeding season) of year x. For CBC surveys, winter temperature data were taken from October to December of year $x - 1$, just prior to the survey period for year x, which starts at the end of December of year $x - 1$ and ends in early January of year x.

Mean maximum and minimum temperatures at the sites included here were highly collinear during the winter ($r = 0.89$, $n = 211$, $t = 28.9$, $P < 0.001$) and, even though the correlation was lower during the summer ($r = 0.23$, $n = 458$, $t = 5.1$, $P < 0.001$), conclusions from analyses (both summer and winter) were unchanged using either mean maximum temperature, mean minimum temperature, or both variables, and thus we only report results using mean maximum temperatures. Monthly NAO data were derived from the National Weather Service Climate Prediction Center (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/norm.nao.monthly.b5001.current.ascii).
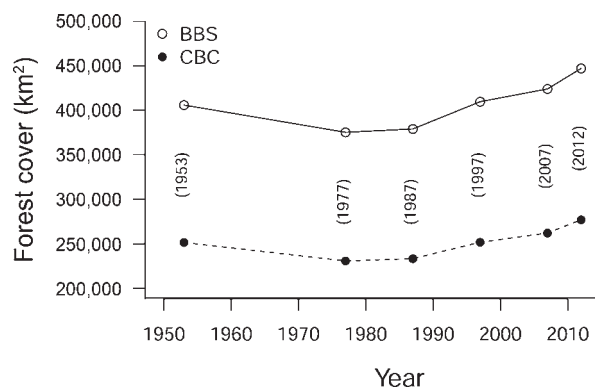

FIGURE 1. Change in overall forested area within the range of Red-headed Woodpeckers (BBS: breeding season range; CBC: overwintering range) based on statewide summaries of Forest Inventory and Analysis data (Smith et al. 2009, Oswalt et al. 2014) between 1953 and 2012. Annual values were estimated by linearly connecting the available (plotted) points.

As an index of the total amount of (un)suitable habitat for Red-headed Woodpeckers, we determined the total forested land area by state for 6 time periods (1953, 1977, 1987, 1997, 2007, and 2012) from the Forest Inventory and Analysis (FIA) National Program (Smith et al. 2009, Oswalt et al. 2014). Although crude, total forested area is reasonably assumed to be inversely related to the total amount of savanna and edge habitat preferred by Red-headed Woodpeckers (Frei et al. 2015b). In order to estimate forest cover for the years between surveys, we summed the state totals and assumed a linear relationship between each pair of time periods for which data were available (Figure 1).

Analyses

Both interspecific competition and predation are potential proximate drivers of the changes observed in Red-headed Woodpecker populations. Changes in either or both of these factors are in turn potentially driven in part by landscape changes in habitat (increased forest cover), and even more ultimately by climate change. Our analyses attempted to deal with the hierarchical nature of these factors by means of structural equation modeling, a multivariate technique designed to test causal relationships among variables (Shipley 2009).

We first calculated mean changes in each of the independent variables of interest and presented results in terms of the change per decade and the percentage of sites in which populations or the variable increased over the course of the study period. Tests of trends were made using mixed-effects models (procedure lme in package nlme in R; Pinheiro et al. 2016, R Core Team 2016). For each model, the value or relative abundance (ln-transformed for each survey $\times$ year combination in the case of the bird populations) was the dependent variable and year was the independent variable. The BBS route or CBC survey was included as a random factor, and year was modeled as a

continuous autoregressive time series to account for temporal autocorrelation (Crawley 2007). The percentage of sites increasing was tested using binomial tests. Analyses were conducted in R 3.3.1 (R Core Team 2016); unless otherwise stated, values presented are means ± standard errors.

Structural equation modeling was conducted using package lavaan in R (Rosseel 2012). Two sets of confirmatory analyses were performed. The first set was conducted using individual survey routes. Structural equation models (SEMs) focusing on the BBS and CBC data were run separately, but both had an identical structure in which climate (mean maximum seasonal temperature) potentially influenced all variables, densities of accipiters (as a proxy of predation) potentially affected populations of the other 3 bird species, and both Red-bellied Woodpeckers and starlings (the 2 interspecific competitors) potentially influenced Red-headed Woodpecker populations. Variables included in the models were the trends in the variables through time measured at each BBS or CBC site. Thus, for each BBS route and CBC survey, we calculated the correlations between year and the relevant variables and used the correlation coefficients in the SEMs. Also included within each subsection of the SEMs, but not shown in the figure illustrating the results, was an inverse distance-weighted autocovariance term that was included to control for spatial autocorrelation and to minimize prediction error (Wintle and Bardos 2006, Koenig et al. 2010). Changes in forest cover were not included in this analysis because such data were not available at the temporal and spatial scale of the analysis.

In order to test the role of changes in forested area, we performed a second set of structural equations using mean data for each year rather than trends through time. Mean (ln-transformed) densities of Red-headed Woodpeckers, Red-bellied Woodpeckers, starlings, and accipiters were calculated for each year across the main distributional (summer or winter, depending on the analysis) range of Red-headed Woodpeckers, as defined above. For environmental variables, we included the winter NAO index and the mean maximum seasonal temperature (summer for BBS, winter for CBC) for each year calculated as the mean across all sites included in the analysis.

The structure of the SEMs was as described above for the analysis of trends, but with the addition of forest cover (estimated from the FIA data summed across the breeding or winter range and interpolated between sampling periods for each year) and winter NAO as factors potentially influencing populations of all 4 bird species. Preliminary analyses, however, indicated that neither mean maximum summer temperature nor the NAO index had a significant effect on any other variable in the model in the BBS analysis. For the CBC analysis, mean maximum winter temperatures had no significant effect on any other variable, whereas the winter NAO index significantly affected the abundance of accipiters (standardized effect size [SES] = 0.14 ± 0.05, $z = 2.64$, $P = 0.008$), but had no significant effect on any of the other species, including Red-headed Woodpeckers (SES = −0.06 ± 0.10, $z = -0.57$, $P = 0.57$). Thus, for clarity, we eliminated both environmental variables (mean maximum seasonal temperature and the winter NAO index) from the figures, although values reported are from analyses that included all variables.

RESULTS

As expected, populations of Red-headed Woodpeckers generally declined during the study period, with ~85% of sites exhibiting overall decreases during the breeding season and ~79% exhibiting overall decreases during the winter (Table 1). In contrast, populations of Red-bellied Woodpeckers and accipiters increased during both seasons, while starling populations increased significantly in winter but decreased significantly during the breeding season.

Visual inspection indicated that, at least in some cases, population trends were nonlinear (Figure 2). In particular, Red-headed Woodpecker populations were stable or increased slightly during both the breeding season and in winter until the early 1980s, declined through 2000, and subsequently have remained consistently low (summer populations; Figure 2A) or appear to have increased somewhat in the past several years (winter populations; Figure 2B). In contrast, Red-bellied Woodpecker populations consistently increased during the study period (Figures 2C and 2D). European Starling populations were variable (Figures 2E and 2F), but increased slightly during the winter, possibly reflecting increased overwintering within the region by this species. Finally, accipiters generally increased during both seasons, at least after the early 1970s (Figures 2G and 2H), consistent with trends elsewhere in North America (Curtis et al. 2006).

Results of the first set of SEMs analyzing trends within individual BBS and CBC sites are summarized in Figure 3. Using the BBS data, 2 variables significantly affected Red-headed Woodpecker trends: trends in accipiter populations (SES = −0.13 ± 0.05, $z = -2.76$, $P = 0.006$) and trends in starling populations (SES = 0.18 ± 0.05, $z = 3.67$, $P < 0.001$). Only the former, however, was in the direction consistent with being a potential driving factor of Red-headed Woodpecker declines. Using the CBC data, all 4 factors significantly affected Red-headed Woodpecker trends, but only 2—the highly significant effects of increasing mean maximum winter temperatures and accipiter population trends—were in the direction pre-
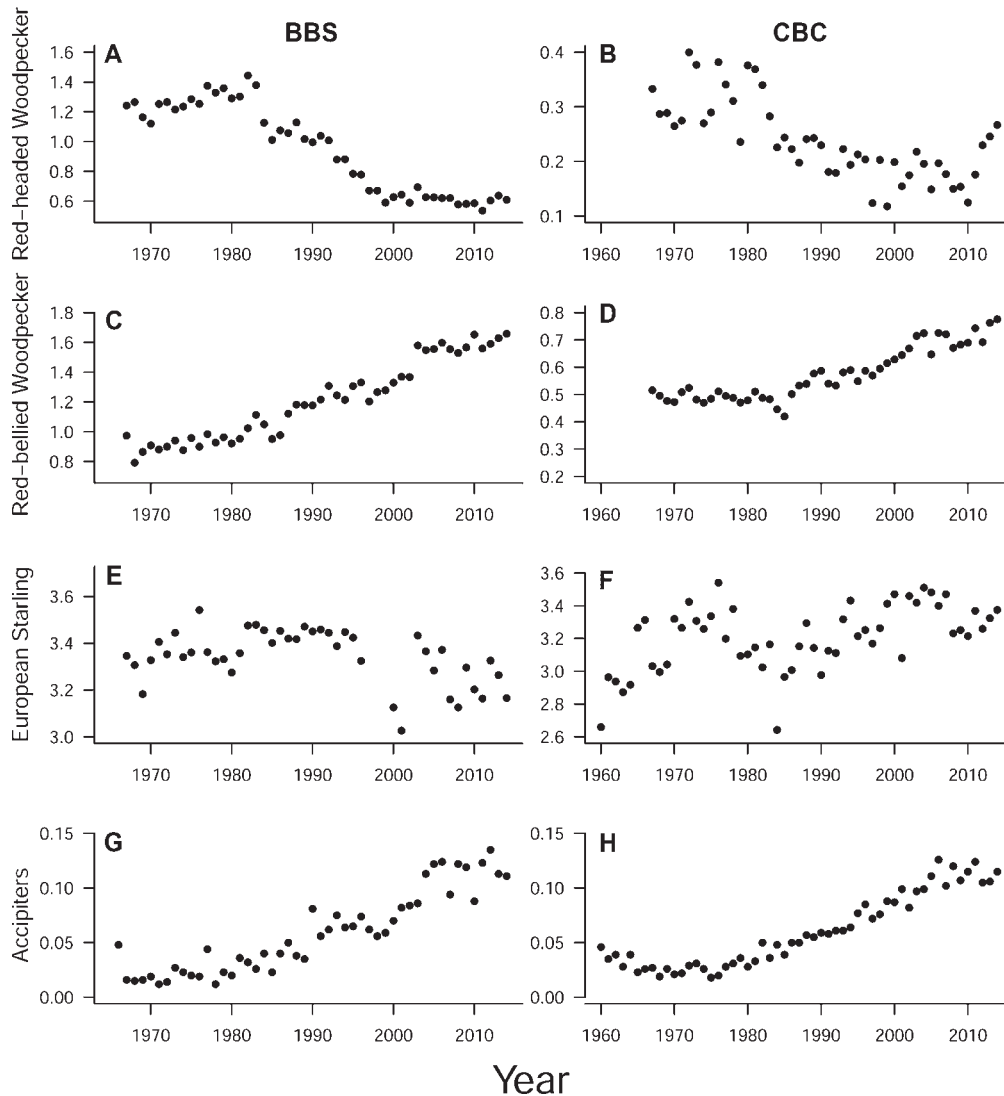
FIGURE 2. Mean abundance of (**A**, **B**) Red-headed Woodpeckers, (**C**, **D**) Red-bellied Woodpeckers, (**E**, **F**) European Starlings, and (**G**, **H**) *Accipiter* spp. over the length of the study within the core distributional range of Red-headed Woodpeckers, based on Breeding Bird Surveys (left column) and Christmas Bird Counts (right column).

dicted by the hypothesis that they played a role in Red-headed Woodpecker declines (SES: mean maximum temperature = -0.22 ± 0.06, $z = -3.52$, $P < 0.001$; accipiter population trends = -0.26 ± 0.07, $z = -3.73$, $P < 0.001$). Otherwise, increased populations of accipiters paralleled increases in populations of Red-bellied Woodpeckers in the CBC analysis and starlings in the BBS analysis.

Results of the second set of SEMs analyzing temporal trends are summarized in Figure 4. For the summer (BBS) analysis, only forest cover significantly influenced Red-headed Woodpecker densities (SES = -0.96 ± 0.14, $z = -6.68$, $P < 0.001$), whereas for the winter (CBC) analysis, only accipiter densities had a significant effect (SES = -0.85

± 0.27, $z = -3.19$, $P = 0.001$). Both effects were in the direction predicted for having a potential role in Red-headed Woodpecker declines. Also notable in both analyses was the strong positive effect of increased forest cover on densities of accipiters.

DISCUSSION

Our analyses suggest that 3 of the 4 hypotheses that we considered were potential drivers of Red-headed Woodpecker declines during the past several decades. Arguably the strongest evidence was for a role of predation by accipiter hawks; the relationship of accipiter abundance with Red-headed Woodpecker abundance was significantly
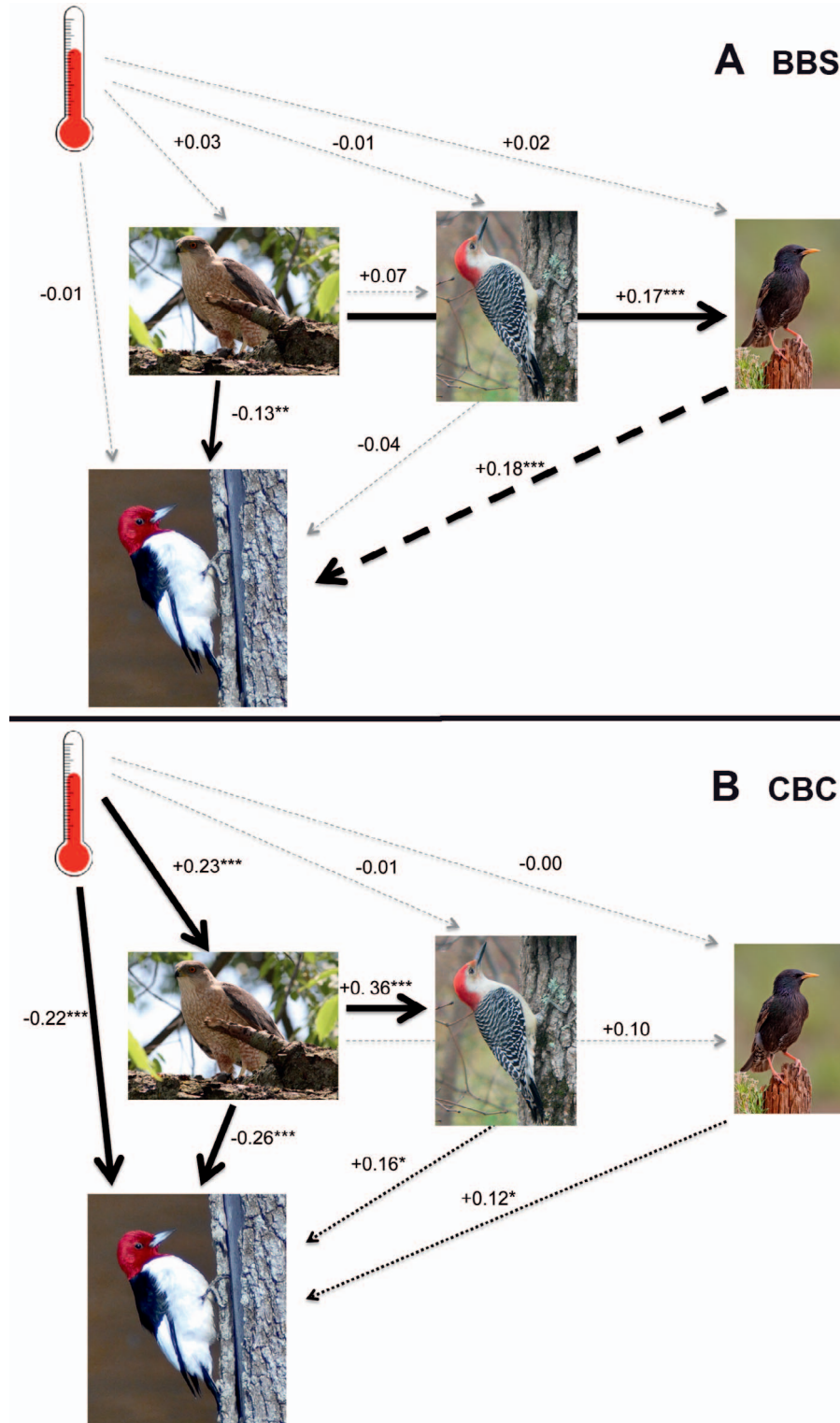
FIGURE 3. Results of structured equation models of trends in Red-headed Woodpecker populations based on (**A**) BBS routes ($n =$ 344) and (**B**) CBC surveys ($n =$ 213); analyses are based on relationships within individual survey routes. Nonsignificant relationships are indicated by gray, dashed lines; significant relationships are shown with black lines, the width of which is proportional to their statistical significance. The black dashed lines are significant relationships in opposition to the pattern expected had the factor been instrumental in Red-headed Woodpecker declines. Not shown, but included in analyses, are autocovariance terms accounting for spatial autocorrelation. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Photos courtesy of Jessica Runner/GBBC (Red-headed Woodpecker); Sagamore66 (Cooper's Hawk); Ken Thomas (Red-bellied Woodpecker); and naturespicsonline.com (European Starling).
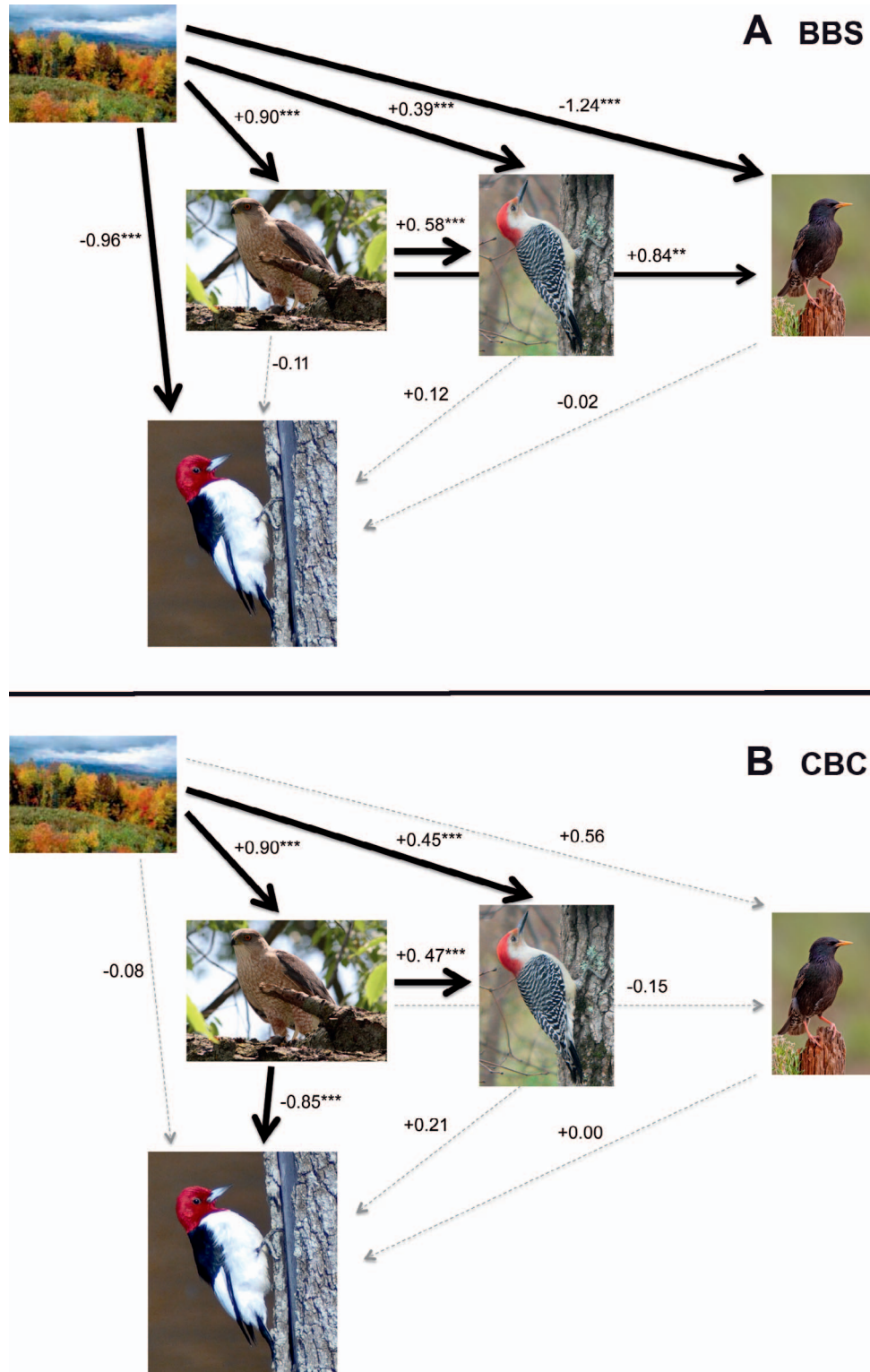
FIGURE 4. Results of structured equation models of Red-headed Woodpecker densities by year based on (**A**) BBS routes ($n = 47$ yr) and (**B**) CBC surveys ($n = 53$ yr) using annual estimates of forest cover and relative bird abundance. Nonsignificant relationships are indicated by gray, dashed lines; significant relationships are shown with black lines, the width of which is proportional to their statistical significance. Not shown, but included in analyses, are the effects of mean maximum temperature and the winter North Atlantic Oscillation (NAO) index on the bird populations. ** $P < 0.01$; *** $P < 0.001$. For photo credits, see Figure 3.

negative, as predicted, in 3 of our 4 analyses. In turn, increases in accipiter numbers were affected by some combination of increased winter temperatures (Figure 3B) and increased forest cover (Figures 4A and 4B). We found evidence that both increased temperatures and increased forest cover played a more direct role in driving Red-headed Woodpecker declines in the highly significant negative correlation between increasing mean maximum winter temperature and Red-headed Woodpecker trends revealed in Figure 3B and the strong negative correlation between forest cover and Red-headed Woodpecker densities shown in Figure 4A. Thus, the only hypothesis for which we found no supporting evidence for playing a role in Red-headed Woodpecker declines was interspecific competition with Red-bellied Woodpeckers or European Starlings.

The conclusion that interspecific competition has been unimportant in driving Red-headed Woodpecker declines is in contrast to expectations based on the aggression observed between these avian species and their potential to be competitors for nest cavities. Competition with European Starlings was previously investigated by Koenig (2003), who found little or no relationship between starlings and populations of either Red-headed Woodpeckers or most other species of native cavity-nesting birds in North America at a continental scale. Our results here provide additional support for this conclusion, with populations of starlings being, if anything, positively, rather than negatively, associated with those of Red-headed Woodpeckers during both the breeding and nonbreeding seasons at the geographic scale that we examined (Figure 2). This result is perhaps not surprising, given that starlings and Red-headed Woodpeckers often occupy similar habitats.

Although it has been well established that Red-bellied Woodpeckers have been increasing their range since at least 1910 (Kirchman and Schneider 2014), previous behavioral and demographic evidence supporting the hypothesis that this species has adversely affected Red-headed Woodpeckers is mixed. On the side of there being no negative effect of Red-bellied Woodpeckers on Red-headed Woodpecker populations, Reller (1972) found that interspecific aggression between these 2 species in the nonbreeding season had little or no detrimental effect on overall population levels of either species. Similarly, at least 2 behavioral studies during the breeding season failed to find evidence that Red-bellied Woodpeckers caused population-level declines of Red-headed Woodpeckers (Selander and Giller 1959, Ingold 1990). On the side of Red-bellied Woodpeckers having strong adverse effects on their competitors, Walters and James (2010) found that Red-bellied Woodpeckers were formidable competitors and adversely affected populations of the much smaller Red-cockaded Woodpecker (*Picoides borealis*) by compet-

ing for roost and nest holes at all times of the year. Likewise, in a community of 3 species, Kappes and Davis (2008) found that the experimental removal of southern flying squirrels (*Glaucomys volans*) failed to benefit Red-cockaded Woodpeckers, apparently because the procedure resulted in competitive release of Red-bellied Woodpeckers instead. Thus, although it is possible that interspecific competition with Red-bellied Woodpeckers is expressed in some sites and under some circumstances, our results suggest that this species has not driven Red-headed Woodpecker population declines range-wide.

In contrast, our results support the hypothesis that predation on adults and immature birds, as indicated by increases in accipiter populations, may be an important factor driving Red-headed Woodpecker declines, a conclusion supported by the observation that Cooper's and Sharp-shinned hawks accounted for a large proportion of the deaths of this species in a study conducted in South Carolina (Kilgo and Vukovich 2012). In turn, increases in accipiter populations have been facilitated by warmer winter temperatures (Figure 3B) and increased forest cover throughout the Red-headed Woodpecker's range (Figure 4). The relatively strong apparent effect of accipiters is, however, surprising, given that predation on adult and juvenile birds is rarely thought to be as demographically important as nest predation for most terrestrial bird species (Martin 1995, Ibáñez-Álamo et al. 2015).

On the other hand, a role of warmer temperatures in causing recent population declines of Red-headed Woodpeckers is not surprising given the dramatic effects of recent climate change on the geographical ecology of a wide range of animal species (Root et al. 2003, Schimel et al. 2013). The significance of habitat changes is also expected given that changes in forestation and forest structure due to forest diseases and changing land use patterns are clearly capable of influencing the long-term dynamics of avian populations and are known to affect populations of Red-headed Woodpeckers. Robbins and Easterla (1992), for example, suggested that Red-headed Woodpeckers were one of the species to benefit from increased availability of foraging and breeding habitat through the clearing of forests following European colonization. More recently, Red-headed Woodpecker populations are likely to have benefited considerably from the demise of the American chestnut (*Castanea dentata*) due to chestnut blight in the first half of the 20th century, and later from the devastation of American elms (*Ulmus americana*) by Dutch elm disease (*Ceratocystis ulmi*; Frei et al. 2015b). A role of the latter in population fluctuations of Red-headed Woodpeckers has received further support from regional reports (Kendeigh 1982, Osborne 1982, Dinsmore et al. 1984).

There are, however, many factors not considered here that could be playing an important role in driving Red-

headed Woodpecker population trends. Interspecific competition with species other than the 2 considered here—for example, flying squirrels (*Glaucomys* spp.; Kappes and Davis 2008)—is one. At least 2 other ecological factors are also known to have strong effects on Red-headed Woodpecker populations. First, Red-headed Woodpeckers are strongly dependent on the acorn crop (Smith 1986, Smith and Scarlett 1987), which varies dramatically from year to year, often over large geographic scales (Koenig et al. 1999, Koenig and Knops 2013). Consequently, populations can be expected to decrease following poor acorn years. However, annual acorn crops tend to be irregularly cyclic (Sork et al. 1993, Koenig et al. 1994, Koenig and Knops 2002), and there is no evidence to suggest that acorn production within the core Midwestern range of Red-headed Woodpeckers has systematically declined in the past 40 yr. Thus, despite the strong influence that acorn crop size may have on numbers of Red-headed Woodpeckers from one year to the next, it does not provide a satisfactory explanation for the long-term population declines observed in this species.

A second ecological factor known to be important to Red-headed Woodpeckers is insect outbreaks. This includes emergences of periodical cicadas (*Magicidada* spp.), which coincide with significantly reduced numbers of Red-headed Woodpeckers (Koenig and Liebhold 2005) but are highly synchronous and cyclic, appearing above ground once every 13 or 17 yr depending on the locality. Even more important historically were outbreaks of the Rocky Mountain locust (*Melanoplus spretus*), a swarming locust that irregularly occurred in huge numbers throughout the Great Plains and was apparently heavily exploited by Red-headed Woodpeckers (Frei et al. 2015b) until the locusts were driven to extinction at the beginning of the 20th century (Lockwood and DeBrey 1990, Lockwood 2001). Outbreaks of gypsy moths (*Lymantria dispar*) have also been shown to coincide with breeding season increases in Red-headed Woodpeckers (Koenig et al. 2011). The extinction of the Rocky Mountain locust and the patterns of periodical cicada emergences and gypsy moth outbreaks suggest that none of these species were likely drivers of the recent declines observed in Red-headed Woodpeckers.

Documenting relationships between Red-headed Woodpecker populations and factors potentially important in their declines does not imply that any of those factors are causal (James and McCulloch 1995, Dhondt 2012). Furthermore, there are always additional potentially important factors that have not been considered. Some effects are likely direct, but others may be indirect and even more difficult to detect, as has been found, for example, between Red-bellied Woodpeckers and Red-cockaded Woodpeckers (Walters and James 2010). Based on our analyses, we propose that the ultimate factors driving the observed changes are primarily climate change and changing land-use patterns acting in concert, resulting in significant reforestation and increased predator populations (Cooper's and Sharp-shinned hawks) within the Red-headed Woodpecker's range. However, our analyses are only a first step toward understanding the factors that may be important for affecting population declines of Red-headed Woodpeckers. Additional analyses, taking into account more detailed habitat information and the possibility that distributional changes may track annual environmental differences, will be needed in order to fully understand population fluctuations in this species.

What is the prognosis for Red-headed Woodpeckers? As Frei et al. (2015b) discuss, by opportunistically taking advantage of favorable ecological conditions, this species has undergone large-scale population fluctuations in the past. It is therefore likely that the decline observed in recent decades is not unusual and may eventually reverse. If nothing else, the fact that Red-headed Woodpeckers are able to successfully breed in highly modified habitats, such as golf courses, attests to the ability of this species to adapt and persist in the modern world (Rodewald et al. 2005). Such an outcome should not, however, be taken for granted, and until such time as populations stabilize or begin to increase, the Red-headed Woodpecker continues to warrant close monitoring.

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