Temperature can interact with landscape factors to affect songbird productivity

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Abstract

Increased temperatures and more extreme weather patterns associated with global climate change can interact with other factors that regulate animal populations, but many climate change studies do not incorporate other threats to wildlife in their analyses. We used 20 years of nest-monitoring data from study sites across a gradient of habitat fragmentation in Missouri, USA, to investigate the relative influence of weather variables (temperature and precipitation) and landscape factors (forest cover and edge density) on the number of young produced per nest attempt (i.e., productivity) for three species of songbirds. We detected a strong forest cover × temperature interaction for the Acadian Flycatcher (*Empidonax virescens*) on productivity. Greater forest cover resulted in greater productivity because of reduced brood parasitism and increased nest survival, whereas greater temperatures reduced productivity in highly forested landscapes because of increased nest predation but had no effect in less forested landscapes. The Indigo Bunting (*Passerina cyanea*) exhibited a similar pattern, albeit with a marginal forest cover × temperature interaction. By contrast, productivity of the Northern Cardinal (*Cardinalis cardinalis*) was not influenced by landscape effects or temperature. Our results highlight a potential difficulty of managing wildlife in response to global change such as habitat fragmentation and climate warming, as the habitat associated with the greatest productivity for flycatchers was also that most negatively influenced by high temperatures. The influence of high temperatures on nest predation (and therefore, nest predators) underscores the need to acknowledge the potential complexity of species' responses to climate change by incorporating a more thorough consideration of community ecology in the development of models of climate impacts on wildlife.

Keywords: fragmentation, neotropical migrants, nest predation, North American forest birds, precipitation, temperature

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Introduction

Increased temperatures and weather variability associated with global climate change can have profound effects on plants and animals. The distribution, abundance, and phenology of numerous species have been affected (Parmesan & Yohe, 2003; Root *et al.*, 2003), and extinction risks are predicted to rise through the next century in response to climate change (Maclean & Wilson, 2011). The task of mitigating the potential effects of climate change on species and their habitats is particularly daunting because addressing the fundamental challenges of climate change (i.e., regulation of greenhouse gases) largely falls outside the purview of land managers. Nevertheless, climate change does not act upon populations in isolation, but instead can exhibit synergetic interactions with other factors known to limit populations (Opdam & Wascher, 2004; Rowe,

2007; Brook *et al.*, 2008; Mantyka-Pringle *et al.*, 2012). Knowledge of how climate change interacts with threats that managers may control is a necessary prerequisite to developing conservation plans. Despite this, nearly half of published studies on climate change fail to consider other threats to long-term population stability of wildlife in their analyses (Felton *et al.*, 2009).

Habitat loss and fragmentation have had pervasive effects on wildlife (Lindenmayer & Fischer, 2006) and may exacerbate the effect of climate change on populations. Habitat fragmentation can interrupt northward range expansions that occur in response to warming temperatures (Opdam & Wascher, 2004), and may isolate habitat specialists in patches that undergo transitions to suboptimal temperature and rainfall patterns (Stefanescu *et al.*, 2011). More generally, the effects of climate change on wildlife can be spatially explicit, as variance in local conditions leads to variation in the interaction between climate and habitat features (e.g., Wolf *et al.*, 2010; Fernández-Chacón *et al.*, 2011). In many cases, however, land-use patterns influence populations far more

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substantially than climate (Rowe, 2007; Hof *et al.*, 2011), so understanding the relative influence of (and potential interaction between) habitat loss and fragmentation and climate is a critical component of developing successful conservation strategies (Willis & Bhagwat, 2009).

Breeding songbirds present an ideal study system in which to investigate potential interactions between habitat fragmentation and climatic variables. Landscape factors have been shown to affect midwestern songbirds as described by the fragmentation hypothesis (Thompson *et al.*, 2002). Many species of songbirds have lower nest survival and higher rates of brood parasitism from Brown-headed Cowbirds (*Molothrus ater*) in highly fragmented habitats (e.g., Robinson *et al.*, 1995), and in areas with increased edge densities (e.g., Peak, 2007), which may result in sink populations (Donovan *et al.*, 1995, 1997). However, songbird reproduction may also be influenced by climatic variables such as rainfall and temperature. Winter and breeding season rainfall patterns have been shown to influence clutch size and hatching rates (Rotenberry & Wiens, 1991), the number of young per nest attempt (Rodríguez & Bustamante, 2003), the number of young produced per female per breeding season (Chase *et al.*, 2005), and nest survival rates (Woolfenden & Fitzpatrick, 1984; Collister & Wilson, 2007). Similarly, warm ambient temperatures (e.g., 24–36 °C) can reduce egg viability (Cooper *et al.*, 2005; Olsen *et al.*, 2008), and small differences in mean breeding season temperatures (e.g., ~4 °C; Chase *et al.*, 2005) can influence the number of young produced per successful nest (hereafter fledging brood size). Furthermore, increased temperatures may decrease nest survival by increasing activity of frequent nest predators such as snakes (Morrison & Bolger, 2002), although this is not always the case (e.g., Dyrcz & Halupka, 2009; Wesołowski & Maziarz, 2009).

We assessed the effect of climate and landscape features on breeding productivity measures for three songbird species in the midwestern United States using nest data spanning 20 years across a gradient of habitat fragmentation. We evaluated hypotheses that rainfall, temperature, landscape forest cover, and edge density had additive and/or synergetic effects on the number of young produced per nest attempt (hereafter productivity) through their influence on nest survival and fledging brood size. On the basis of our review of the literature, we predicted that an increase in temperature would be associated with reduced nest survival because of increased predator activity, and reduced fledging brood size because of increased egg or nestling mortality. We also predicted that rainfall would increase nest survival by reducing predator activity but reduce fledging brood size through nestling mortality associated with heavy rainfall. Furthermore, on the basis of reported effect sizes,

we predicted that temperature and precipitation effects on nest survival and overall productivity would be modest compared with the negative effects of reduced landscape forest cover and increased edge density, two measures that relate to the substantial effects of forest fragmentation on midwestern songbirds (Robinson *et al.*, 1995; Thompson *et al.*, 2002).

Materials and methods

Data collection

We compiled nest-monitoring data from 11 studies that occurred throughout Missouri, USA, during 1991–2011. Studies occurred in a variety of wooded habitats, including old fields within forested areas, mid- and late-successional oak-hickory forests, bottomland hardwood forests, cottonwood plantations, savannahs, oak woodlands, and riparian floodplain forests. The location and duration of each study varied (Fig. 1), but all studies were associated with the same research group and followed similar field protocols. Nests were found by systematic search or from behavioral cues (Martin & Geupel, 1993) and were typically monitored every 1–4 days until the nest fledged or failed. Nests with unknown or questionable fates (i.e., >4 days between the penultimate and final nest check and no evidence of fledglings or signs of predation noted) as well as those that failed because of researcher activities were right censored to minimize the potential for bias in our survival estimates (Manolis *et al.*, 2000).
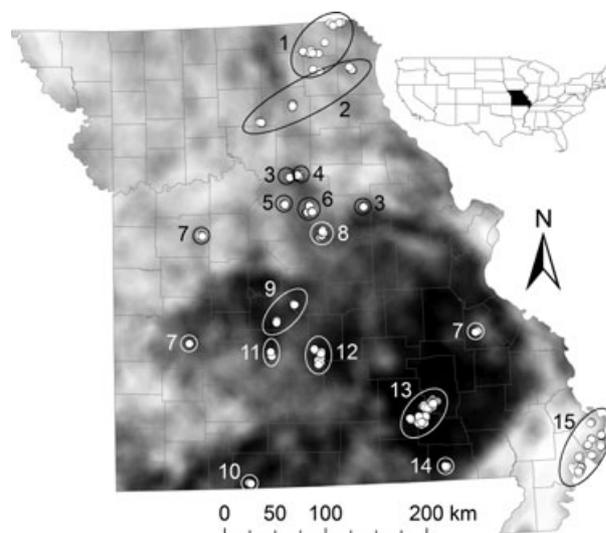
Fig. 1 Nest locations in a study of landscape and weather factors affecting nest survival, fledging brood size, and overall productivity of songbirds in Missouri, USA, 1991–2011. Background shading indicates the percent forest cover in a 10 km radius, with darker shading indicating higher forest cover (range: <1–97%). Numbers refer to years of study.

We limited our analysis to two migrant species and one resident species that were each well represented across a broad range of habitat fragmentation. The migratory Indigo Bunting (*Passerina cyanea*, hereafter bunting) builds nests in saplings and shrubs within old fields, along forest edges, and in dense understory vegetation in forests. The migratory Acadian Flycatcher (*Empidonax virescens*, hereafter flycatcher) is a forest interior species that typically nests in the subcanopy, often in small understory trees. The Northern Cardinal (*Cardinalis cardinalis*, hereafter cardinal) is a resident species and habitat generalist that nests in shrubs and trees at a variety of heights in old fields and wooded habitats. All three species are predicted to remain at relatively high densities in Missouri on the basis of several future climate/habitat scenarios (Matthews *et al.*, 2011).

Our dataset included 2003 bunting nests, 1475 flycatcher nests, and 551 cardinal nests that were active for ≥ 1 nest check interval (i.e., nests never observed with eggs or young were excluded from analysis). Geographic coordinates for nests were recorded with handheld GPS units at the time of the study ($n = 2558$) or from nest ($n = 1408$) or territory ($n = 63$) maps that were digitized in a GIS. A preliminary analysis suggested that forested land cover surrounding our nests changed <3% between the earliest (1992) and latest (2006) available land cover databases, so we used the 2001 National Land Cover Database (NLCD; http://www.mrlc.gov/) to calculate landscape forest cover and edge density for all nests to avoid compatibility issues between different NLCD releases. We generated a raster in which we reclassified pixels as forest or nonforest and used the focal statistics tool to calculate percent forest in a 10 km radius around each nest; we chose this radius because it best explains variation in nest predation for forest songbirds in the United States (Lloyd *et al.*, 2005). We then used Fragstats v3.3 (McGarigal *et al.*, 2002) with the raster to calculate edge density (defined as the interface between forest and nonforest) at a local scale (500 m radius) to reflect the hypothesis that nest predators preferentially use edges (Dijak & Thompson, 2000; Blouin-Demers & Weatherhead, 2001). We obtained daily precipitation and daily high-temperature data from 32 weather stations (mean distance from each nest to nearest temperature station: 18.1 ± 0.1 km; to nearest precipitation station: 13.2 ± 0.1 km; $n = 4029$) from the Midwestern Regional Climate Center (http://mcc.sws.uiuc.edu). For the nest survival analysis we calculated mean precipitation and mean daily high-temperature values for each nest interval (see below for explanation of nest intervals). For the fledging brood size analysis, we calculated mean daily high- and maximum daily high-temperature values across the entire nest cycle and mean and maximum precipitation values across the nestling stage for each successful nest using actual or estimated nest initiation, hatch, and fledge dates derived from nest-monitoring data (see Table 1 for justification of the selection of weather variables).

Analysis

Our overall statistical approach was to construct a set of *a priori* candidate models explaining nest survival and a separate set explaining fledging brood size and then combine predictions from both model sets using a bootstrapping approach to estimate effects of the climatic and fragmentation covariates on productivity. This approach allowed us to assess whether there was a differential effect of climate and habitat on two important components of productivity, and also allowed us to assess hypotheses specific to each component based on our review of the literature. We evaluated support for nest survival and fledging brood size candidate models within an information theoretic framework (Burnham & Anderson, 2002). We evaluated support for models with Akaike's Information Criteriaon (AIC), the difference between the top model and other candidate models (ΔAIC), and Akaike weights (w_i), which represent relative support for each model in the candidate set and sum to one. We model-averaged predictions, which accounts for model-selection uncertainty by weighting predictions across the entire set of candidate models. Furthermore, model averaging and interpreting predictions are more appropriate than model-averaging parameter estimates when some parameters occur as additive and interactive terms in various models (Burnham & Anderson, 2002).

We modeled nest survival by the logistic exposure method, which considers the fate of a nest for each nest-monitoring interval and uses a modified logistic link function to account for exposure, measured as the number of days in each interval (Shaffer, 2004). Repeated observation intervals on each nest do not represent pseudoreplication in survival models because the precision of parameter estimates depends on the number of mortality events rather than the number of intervals (Allison, 2010). We evaluated 7 models representing hypotheses of climatic and fragmentation effects on nest predation (Table 1), all of which included a term for nest stage (laying, incubation, nestling) because it strongly influences nest survival rates for flycatchers and buntings (Cox *et al.*, 2012a). All models included a random effect for study site (as defined by the original researchers with the exception of one study in which nine study sites were merged into two sites because of shared borders) to acknowledge potential correlated fates of nests within sites. There was no serious multicollinearity (all tolerance values >0.4; Allison, 1999) among the explanatory variables. The logistic exposure method estimates daily nest survival, which we converted into period survival (i.e., probability of survival from the first day an egg is laid until young fledge the nest) by raising daily survival to the power n where n equaled the mean number of days in a nest cycle for each species at our study sites (buntings: 25, cardinals: 25.5, flycatchers: 30), with period survival confidence intervals calculated using the delta method (Armstrong *et al.*, 2002; Powell, 2007).

For models predicting fledging brood size, we used the number of young present in a successful nest on the penultimate monitoring visit as the response variable, and only included nests for which exact counts were recorded. We fit our response variable as a function of our covariates using generalized linear models with a normal distribution, an approach that is most robust to deviations from an assumed distribution when analyzing egg or nestling count data (McDonald & White, 2010). We evaluated 9 models representing hypotheses from the literature regarding fragmentation and climatic effects on fledging brood size (Table 1). All models included a random effect for study site, a term for ordinal date to control for the fact that

Table 1 *A priori* candidate models describing fragmentation and weather effects on nest survival and fledging brood size for three species of songbirds in Missouri, USA, 1991–2011

Model	Variables	Description	Citations
Nest survival models			
Null[*]	Nest stage	Null model accounts for documented variation in predation rates by nest stage	[1]
Fragmentation	Forest cover × edge density	Landscape features influence nest survival, but edge effects are not linear across a gradient of fragmentation	[2, 3, 4]
Fragmentation + temperature	(Forest cover × edge density) + mean daily high temperature + ordinal date[†]	Landscape effects, but warm temperatures may influence some predators' behaviors	[5]
Fragmentation × temperature	(Forest cover × edge density × mean daily high temperature) + ordinal date[†]	Warm temperatures may change some predators' behaviors, but important predators differ with respect to landscape and edge	[5, 6]
Weather	Precipitation + mean daily high temperature + ordinal date[†]	Weather influences nest survival	[5, 7]
Global (additive)	(Forest cover × edge density) + mean daily high temperature + precipitation + ordinal date[†]	Global additive nest survival model	
Global (interactive)	(Forest cover × edge density × mean daily high temperature) + precipitation + ordinal date[†]	Global nest survival model with landscape/temperature interaction	
Fledging brood size models			
Null[*]	Ordinal date + parasitism status	Null model accounts for documented seasonal declines in songbird clutch size and reduced productivity because of cowbird brood parasitism	[8, 9]
Forest cover	Forest cover	Parasitism and predation (and thus partial predation) occur more frequently in less forested landscapes, but edge effects may not influence cowbird abundances or parasitism rates	[2, 4, 10, 11]
Fragmentation	Forest cover × edge density	Rates of parasitism may also be influenced by edge effects	[12, 13, 14]
Mean temperature	Mean maximum temperature during nest cycle	High mean temperatures may induce nestling mortality or reduce hatching success, isolated from brood parasitism	[15, 16, 17]
Max temperature	Max daily high temperature during nest cycle	Extreme temperature events may induce egg or nestling mortality, isolated from brood parasitism	[17, 18, 19]
Mean precipitation	Mean precipitation during nestling stage	Rainfall during the nest cycle may influence nestling survivorship, isolated from brood parasitism	[19, 20, 21]
Max precipitation	Max precipitation during nestling stage	Extreme rainfall events may induce nestling mortality, isolated from brood parasitism	[19, 22, 23]
Global (mean weather values)	Forest cover + mean daily high temperature during nest cycle + mean rainfall during nest cycle	Global model (mean temperature and precipitation)	
Global (extreme weather values)	Forest cover + max daily high during nest cycle + mean rainfall during nest cycle	Global model (extreme temperature and precipitation events)	

Citations: [1]Cox *et al.* (2012a); [2]Robinson *et al.* (1995); [3]Peak (2007); [4]Donovan *et al.* (1997); [5]Morrison & Bolger (2002); [6]Cox *et al.* (2012b); [7]Woolfenden & Fitzpatrick (1984); [8]Rowe *et al.* (1994); [9]Donovan *et al.* (1995); [10]Chapa-Vargas & Robinson (2006); [11]Ford *et al.* (2001); [12]Lloyd *et al.* (2005); [13]Hoover *et al.* (2006); [14]Morse & Robinson (1999); [15]Chase *et al.* (2005); [16]Rotenberry & Wiens (1991); [17]Low & Pärt (2009); [18]Greño *et al.* (2008); [19]Dawson & Bortolotti (2000); [20]Mattsson & Cooper (2009); [21]Siikamäki (1996); [22]Kirkpatrick *et al.* (2009); [23]Burton (2006).
*Terms in the null model are included in all models in its candidate set.
†Ordinal date is included to separate temperature and seasonal effects.

many passerines exhibit reduced clutch sizes across the breeding season (Rowe *et al.*, 1994), and a term for brood parasitism status because of its substantial negative impact on nest productivity (Burhans *et al.*, 2000; Hoover, 2003).

Productivity per nest attempt. We combined model-based predictions of nest survival and fledging brood size to calculate productivity (i.e., number of young per successful nest times the probability of successfully fledging young) as a function of fragmentation and climatic covariates using a parametric bootstrapping approach to incorporate the error associated with both sets of predictions (Efron & Tibshirani, 1993). First, we generated model-averaged predictions and unconditional standard errors for nest survival and fledging brood size across the range of observed values for the fragmentation and climatic covariates. Because nest parasitism rate covaries with landscape forest cover (Thompson *et al.*, 2000) and was a covariate in the fledging brood size model, we covaried parasitism rate with forest cover when we generated the fledging brood size predictions using parasitism rates derived from a simple logistic regression that modeled parasitism as a function of forest cover with a random effect for study site. We then randomly selected predicted values for nest survival and fledging brood size from a normal distribution of possible values defined by the predicted mean and standard errors and calculated productivity per nest attempt as nest survival × fledging brood size. We repeated the random selection 10 000 times and treated the resulting mean value of productivity per nest attempt as a point estimate of productivity and 2.5% and 97.5% percentile values as confidence intervals. This bootstrap approach incorporated uncertainty in the estimates that went into our predictions of productivity per nest attempt, which is reflected in their confidence limits. All analyses were performed using SAS v9.2 (SAS Institute, Cary, NC, USA).

Results

During 1991–2011, the mean temperature in Missouri during the songbird breeding season (i.e., May–August) was 22.7 ± 0.2 °C (range: 20.8–24.0 °C) and the mean precipitation was 45.2 ± 1.8 cm (range: 32.8–61.1 cm; Fig. 2). Of 4029 nests, 2318 (58%) failed and 812 of 3809 (21%) nests for which contents were known were parasitized by cowbirds. The global model with a fragmentation × temperature interaction was the most supported nest survival model for buntings and flycatchers, whereas the null model was the most supported nest survival model for cardinals (Table 2). Daily survival rates increased substantially for buntings with increased forest cover at low and high levels of edge density, whereas the positive association between nest survival and forest cover for flycatchers was only present at higher levels of edge density (Table 3). Precipitation was associated with an insubstantial decline in nest survival for flycatchers and buntings across most observed precipitation values, whereas cardinal nest survival was invariant with respect to precipitation (Fig. 3).
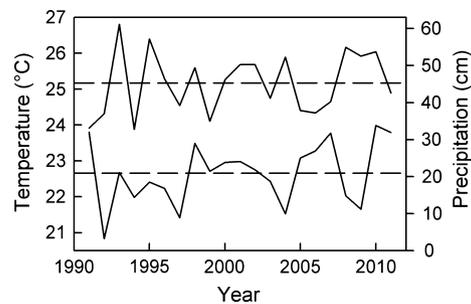

Fig. 2 Mean songbird breeding season (1 May–31 August), precipitation (top line), and temperature (bottom line) in Missouri during 1991–2011. Dashed lines indicate mean values.

Abnormally high precipitation levels were associated with substantially lower nest survival for buntings and flycatchers, which is concordant with field observations indicating that heavy rain events flooded and/or knocked down nests. However, such events were rare and the resulting confidence intervals were wide. Temperature was included in the top four models for buntings and flycatchers; most of the model weight (buntings: 53%, flycatchers: 94%) included temperature as a component of a 3-way interaction with forest cover and edge density. Increased temperature was associated with reduced nest survival for buntings and flycatchers at high levels of forest cover, but was invariant at low levels of forest cover. For example, period nest survival for buntings marginally declined from 0.41 (95% CI: 0.25–0.58) to 0.31 (95% CI: 0.21–0.42) from the lowest (14.4 °C) to the highest (38.8 °C) recorded daily high temperatures for nests in a landscape with 92% forest cover (the 95th percentile of observed forest cover for buntings) but remained essentially unchanged [0.10 (95% CI: 0.04–0.23) to 0.13 (95% CI: 0.08–0.23)] for nests in a landscape with 19% forest cover (the 5th percentile). The effect was substantially larger for flycatchers, with period nest survival declining from 0.84 (95% CI: 0.70–0.93) to 0.10 (95% CI: 0.04–0.24) across the same temperature range in a landscape with 94% forest cover and marginally declining from 0.41 (95% CI: 0.17–0.69) to 0.26 (95% CI: 0.14–0.44) for nests in a landscape with 23% forest cover.

We ran several *post hoc* analyses to clarify the interpretation of our nest survival results. First, to provide statistical support for the apparent dissimilarity in the three species' responses to temperature and landscape effects, we grouped the data for all three species and reran the global model, once with species as an additive effect and once as an interaction with the original interaction term (i.e., species × forest cover × edge density × mean daily high temperature). There was strong support for the species interaction (AIC = 13 661.0) compared with the additive model (AIC = 13 696.4; ΔAIC = 35.4); indicating the effects of forest cover × edge density × mean

Table 2 Model-selection results from *a priori* candidate models describing fragmentation and weather effects on nest survival and the number of young fledged per successful nest for three species of songbirds in Missouri, 1991–2011

	K^*	Acadian Flycatcher			Indigo Bunting			Northern Cardinal		
		$AIC^†$	$\Delta AIC^‡$	$w_i^§$	AIC	ΔAIC	w_i	AIC	ΔAIC	w_i
Nest survival models		$n = 22\ 964^¶$			$n = 19\ 688$			$n = 5935$		
Global (interactive)	13	5134.26	0.00	0.63	6704.93	0.00	0.42	1823.86	8.34	0.01
Fragmentation × temperature	12	5135.71	1.45	0.31	6707.64	2.71	0.11	1821.87	6.35	0.02
Weather	7	5139.71	5.45	0.04	6736.81	31.88	0.00	1820.55	5.03	0.04
Global (additive)	10	5141.72	7.46	0.01	6706.83	1.90	0.16	1821.01	5.49	0.03
Fragmentation + temperature	9	5143.13	8.87	0.01	6708.97	4.04	0.05	1819.03	3.51	0.09
Fragmentation	7	5165.85	31.59	0.00	6705.88	0.95	0.26	1816.47	0.95	0.31
Null	4	5162.68	28.42	0.00	6734.27	29.34	0.00	1815.52	0.00	0.50
Fledging brood size models		$n = 416$ nests			$n = 664$ nests			$n = 168$ nests		
Forest cover	6	817.17	0.00	0.36	1626.76	0.00	0.57	443.78	0.00	0.33
Fragmentation	8	818.54	1.37	0.19	1629.89	3.13	0.12	446.47	2.69	0.09
Null	5	819.10	1.93	0.14	1630.91	4.15	0.07	444.53	0.75	0.22
Max daily high temperature	6	820.44	3.27	0.07	1631.63	4.87	0.05	446.53	2.75	0.08
Mean precipitation	6	820.70	3.53	0.06	1632.02	5.26	0.04	446.48	2.70	0.09
Mean daily high	6	821.05	3.88	0.05	1631.48	4.72	0.05	446.36	2.58	0.09
Max precipitation	6	821.08	3.91	0.05	1632.29	5.53	0.04	446.51	2.73	0.08
Global (max values)	10	821.68	4.51	0.04	1632.61	5.85	0.03	450.46	6.68	0.01
Global (mean values)	10	821.73	4.56	0.04	1632.61	5.85	0.03	450.45	6.67	0.01

*The number of parameters. Models with interaction terms include all constitutive elements as per Brambor *et al.* (2006). Nest survival and productivity models include 1 and 2 parameters for the random effect of study site, respectively.
†Akaike's Information Criterion.
‡The difference between the AIC score of the current and top-ranked model.
§Weight of evidence supporting the model.
¶Effective sample size calculated as described by Rotella *et al.* (2004).

daily high temperature varied by species. Second, to determine whether the observed interaction between temperature and landscape was driven primarily by warm years rather than warm days as we modeled it, we reran the global model for flycatchers and buntings with a fixed effect for mean summer temperature (May 1–August 31). There was little support for the addition of mean summer temperature for flycatchers ($\Delta AIC = 1.74$) and buntings ($\Delta AIC = 2.00$) as a ΔAIC value of 2 indicates no increase in the model likelihood with the addition of a single parameter. Therefore, we concluded that the temperature effect was not a result of a few warm years and predominately reflected seasonal variation in temperature. Finally, to determine whether the precipitation and forest cover × edge density × temperature effects were driven by patterns of nest predation rather than nest survival (which also includes nest mortality from other factors such as adult mortality, storms, and nest abandonment), we ran the original set of models with a subset of the data for flycatchers and buntings that excluded nests which failed from causes other than predation. We did not perform this analysis for cardinals because all but one nest in the original dataset failed from nest predation. The two models that included

temperature as a component of a 3-way interaction with forest cover and edge density were still top-ranked for flycatchers (96% of overall model weight) and held substantially more support for buntings than in the original analysis (90% of overall model weight; Table S1). In contrast with our original results, the global model (with a term for precipitation) for both species was less supported than the same model without a precipitation term (Table S1) and the effect size of precipitation was muted (Fig. S1), which suggests that precipitation was directly responsible for nest mortality rather than indirectly reducing nest survival through its influence on predation rates.

Parasitism status had a pronounced influence on fledging brood size; flycatchers, buntings, and cardinals fledged 36% (1.57 vs. 2.46 young, $n = 421$ nests), 33% (1.87 vs. 2.80 young, $n = 803$ nests), and 20% (2.00 vs. 2.51 young, $n = 193$ nests) fewer young, respectively, in parasitized vs. unparasitized nests, regardless of whether the cowbird egg(s) hatched and successfully fledged. Parasitism rates were higher in landscapes with lower forest cover regardless of edge density (Table 3). The forest cover model was the top-ranked fledging brood size model for all three species (Table 2), which

Table 3 Model-based predictions of brood parasitism rates (CL) and fledging brood size (SE) at low and high levels of landscape forest cover and period nest survival (CL) at 5% and 95% percentile levels of edge density at low and high levels of forest cover for three species of songbird in Missouri, 1991–2011

| Species	Forest cover (%/10 km)	Edge density (m ha^{-1})	Parasitism rate	Fledging brood size	Period nest survival
Acadian Flycatcher	10	0	0.32 (0.16–0.54)	2.03 (0.17)	0.40 (0.26–0.56)
		74	0.39 (0.24–0.57)	2.06 (0.12)	0.28 (0.18–0.39)
	90	0	0.01 (0.00–0.03)	2.52 (0.08)	0.41 (0.33–0.50)
		74	0.03 (0.01-0.12)	2.51 (0.10)	0.41 (0.27–0.59)
Indigo Bunting	10	0	0.57 (0.41–0.71)	2.21 (0.12)	0.15 (0.09–0.24)
		100	0.69 (0.56–0.80)	2.07 (0.12)	0.09 (0.04–0.14)
	90	0	0.21 (0.12–0.33)	2.71 (0.07)	0.37 (0.30–0.44)
		100	0.10 (0.04–0.20)	2.83 (0.08)	0.25 (0.17–0.37)
Northern Cardinal	10	13	0.31 (0.13–0.56)	2.24 (0.14)	0.22 (0.11–0.37)
		105	0.35 (0.14–0.62)	2.19 (0.15)	0.30 (0.17–0.49)
	90	13	0.02 (0.00–0.10)	2.49 (0.16)	0.30 (0.17–0.48)
		105	0.10 (0.01–0.53)	2.55 (0.25)	0.12 (0.01–0.62)
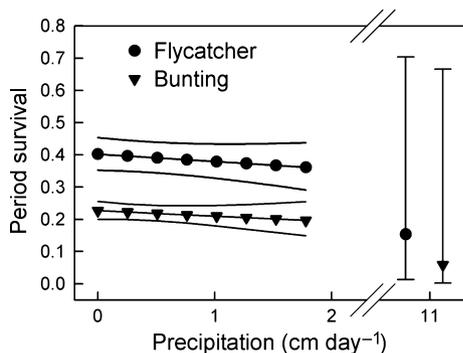
Fig. 3 Model-averaged predictions of period nest survival (±95% CI) for Acadian Flycatchers and Indigo Buntings as a function of precipitation with all other variables held constant at their mean value in Missouri, USA, 1991–2011. Estimates to the left of the axis break are for the 0–95th percentiles of precipitation values, and those to the right of the axis break are for observed extreme rain events.

indicated that fledging brood size was also lower in less forested landscapes independent of parasitism. All species fledged substantially more young in highly forested landscapes, regardless of edge density, largely because of low parasitism rates (Table 3). Neither mean nor maximum daily high temperature across the nest cycle or mean or maximum precipitation across the nestling stage was associated with a change in fledging brood size (≤1.5% change in estimated productivity between the lowest and highest 5% observed values for each variable).

Overall productivity per nest attempt was substantially influenced by forest cover and to a lesser extent edge density for flycatchers and buntings, although the edge effect was only apparent in the least forested landscapes for flycatchers (Fig. 4). Because of the lack of

climatic effects on fledging brood size (Table 2), productivity per nest attempt closely followed the patterns of nest survival, with flycatchers exhibiting substantially reduced productivity in highly forested landscapes as temperature increased and marginally reduced productivity in the least forested landscapes (Fig. 4). Buntings exhibited a similar pattern, but the effect of forest cover was modest (Fig. 4). The patterns for both species were driven by nest predation (Fig. S2).

Discussion

Our analysis of data from 11 studies over 20 years suggests that climatic variables can have species- and landscape-specific impacts on avian productivity. Nest survival was positively associated with increased forest cover and negatively associated with edge density for flycatchers and buntings and fledging brood size increased with increased forest cover for both species. As such, overall productivity was greater in highly forested landscapes for both species, substantially so for buntings, which is consistent with the fragmentation hypothesis for breeding songbirds in eastern North America (Robinson *et al.*, 1995; Thompson *et al.*, 2002). However, increasing temperatures substantially reduced overall productivity in highly forested landscapes for flycatchers (through a reduction in nest survival; climatic variables did not influence fledging brood size) to the extent that at the highest observed temperatures, predicted productivity was similar to productivity in the least forested landscapes. By contrast, lower bunting productivity was only marginally associated with higher temperatures in highly forested landscapes, and cardinal productivity was not substantially influenced by any of the fragmentation or weather factors we considered.
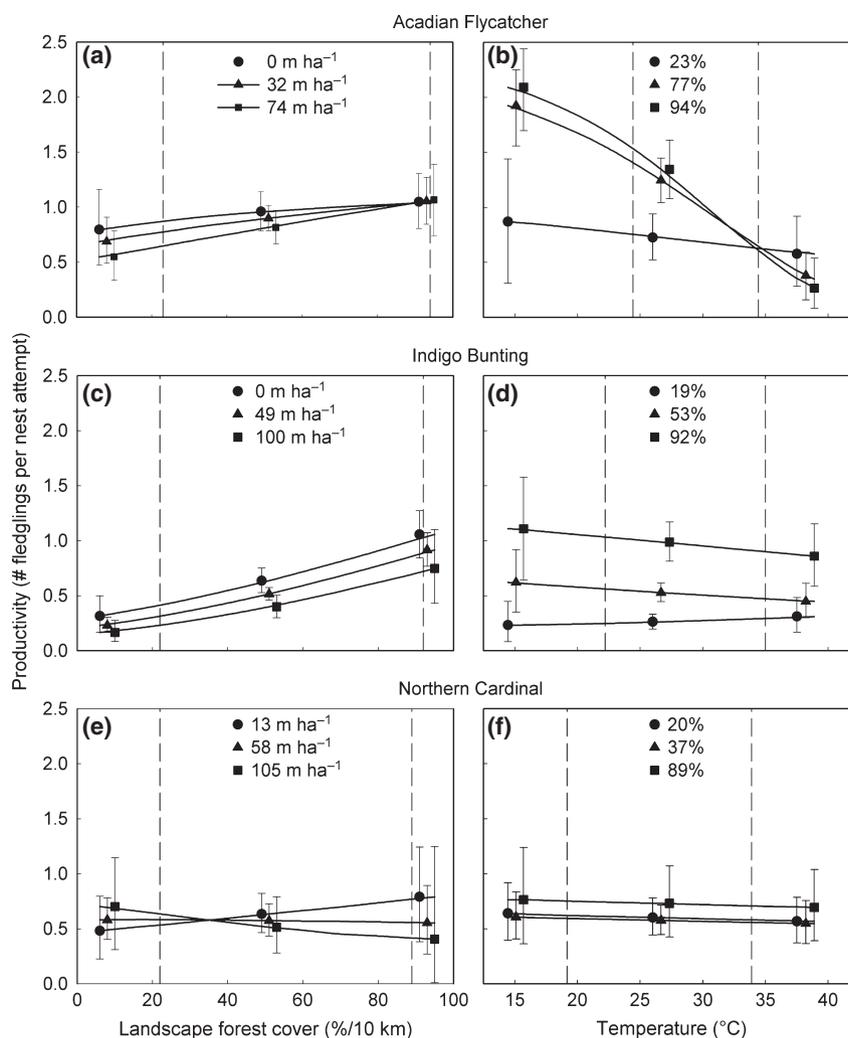
Fig. 4 Model-based productivity per nest attempt (95% CI) as a function of landscape forest cover at 5th, median, and 95th percentile values of edge density (left column), and temperature at 5th, median, and 95th percentile values of forest cover (right column) for three songbird species in Missouri, USA, 1991–2011. Brood parasitism rates are held at their estimated rate for each level of landscape forest cover (both columns), and mean edge density is held at observed values within ±5% of each level of forest cover (right column). All other variables were held constant at their means for model predictions. Vertical dashed lines represent 5th and 95th percentiles of observed values of forest cover and temperature.

As with most passerine birds (Martin, 1992), predation was the primary source of nest failure in our system (0.8% of nest failures were directly attributed to weather; W.A. Cox & F.R. Thompson, unpublished results), and our *post hoc* analysis suggests that the reduction in flycatcher nest survival associated with higher temperatures is likely driven by nest predation. Given the diverse suite of nest predators present in our system (Thompson & Burhans, 2003; Cox *et al.*, 2012a), it is possible that increased temperatures reduced nest survival by altering the activity patterns of a number of predator species or groups. Snakes are frequent predators in our system (Cox *et al.*, 2012a), they generally increase movement in response to

warmer ambient temperatures (Peterson *et al.*, 1993), and their movement patterns have been correlated with songbird nest survival in other systems (Sperry *et al.*, 2008). As such, snake activity patterns may contribute to decreased nest survival as temperatures increase. In addition, endotherms exhibit increased metabolic rates (and thus, daily energy intake requirements) when temperatures rise above thermoneutral maxima (e.g., Hayworth & Weathers, 1984; Weathers *et al.*, 2001). This could contribute to increased predation on songbird nests directly by increasing predator activity or indirectly by increasing songbird nest visitation rates (via increased food demands for adults and nestlings), which can increase the risk of predation

(Martin *et al.*, 2000). However, although maximum neutral temperatures for some avian predator species are well below the highest temperatures we observed (e.g., Hayworth & Weathers, 1984; Weathers *et al.*, 2001), many species have thermoneutral zones fully within the range of temperatures we observed, making it unclear how substantial an influence temperature could be on endothermic nest predators. It is perhaps more likely that temperature exhibits an indirect effect on nest predators, many of which [e.g., black rat snake (*Elaphe obsoleta*), Broad-winged Hawk (*Buteo platypterus*), Barred Owl (*Strix varia*)] are generalists that consume small mammals, amphibians, reptiles, and other prey in addition to songbird eggs and young. High temperatures may influence the abundance or behavior of alternate prey, leaving songbird nests at greater risk of predation.

Regardless of the mechanism driving the patterns we observed, it remains unclear why the three species exhibited differing responses. It may relate to the differing breeding habitat of the three species (flycatchers are forest interior species, whereas buntings and cardinals occur in old fields, along forest edges, and occasionally in the forest interior), but given that buntings and flycatchers suffer nest losses largely from the same suite of predators (Cox *et al.*, 2012a), it is not clear why higher temperatures would result in markedly more substantial declines in nest survival for flycatchers vs. buntings or cardinals. Given that cardinals exhibit greater flexibility in nest-site selection than flycatchers in response to nest failure and to ambient predation risk (Kearns & Rodewald, 2012), it may be that some of the differences between species we observed are a consequence of variation in each species' ability to adapt to changes in predator activity.

It is also unclear why temperature substantially influenced nest survival in the most forested landscapes for flycatchers but had little impact in less forested landscapes, as the most frequent nest predators in our system [raptors, snakes, nonraptorial birds (Cox *et al.*, 2012a)] are frequent predators at most levels of forest cover (Cox *et al.*, 2012b). The black rat snake is the primary snake predator in our system and has been shown to prefer edges and forest clearings for the thermoregulatory opportunities such habitat provides (Blouin-Demers & Weatherhead, 2001). It may be that snakes in highly forested landscapes where edge densities are typically lowest (Faaborg *et al.*, 1995) cannot rely on forest openings to thermoregulate, which would more tightly couple an increase in activity with higher mean temperatures. In addition, cowbirds, which are frequent nest predators only in fragmented landscapes (Cox *et al.*, 2012b), have relatively high thermoneutral maxima (35–40 °C; Lustick, 1970) and often do not actually consume nest

contents (W.A. Cox, unpublished results). As such, we would not expect cowbird predation to increase as a consequence of increased energetic requirements associated with increased temperatures. It is also possible that productivity was already so low in the least forested landscapes that it was not responsive to further negative effects.

Regardless, this study and others (e.g., Wolf *et al.*, 2010; Fernández-Chacón *et al.*, 2011) exemplify the potential for spatially explicit effects of climate change and reinforce the need to consider climate change within the context of other factors that influence wildlife. Managers mitigate the effects of habitat fragmentation by attempting to provide patches that are large enough to support most or all of the regional pool of area-sensitive species, with populations in smaller, less productive patches supported by immigration from large patches that can produce excess young (Pulliam, 1988; Tittler *et al.*, 2006). Our results suggest that managers should consider how warming temperatures and other factors associated with climate change interact with landscape features to influence demography in source and sink populations. For example, at our longest running study site in the highly forested Missouri Ozarks (Fig. 1, site 13), 30% of observations in our flycatcher nest survival analysis (spanning from 22 May to 10 August) had temperatures >32 °C. In 2012, 64% of the days across the same span had temperatures >32 °C. As summers such as that in 2012 become more common, the value of the Ozarks as source habitat for flycatchers may diminish.

It remains unclear whether the associations we observed between climatic variables and songbird productivity will continue as the climate changes. Nest predator species are likely to respond differently to climate change, and future temperatures and precipitation values that fall consistently outside our observed values will almost assuredly influence forest ecosystems in novel and unpredictable ways. For example, precipitation had a relatively small effect on nest survival across the range of rainfall values we typically observed, but our data and other studies (e.g., Skagen & Yackel Adams, 2012) suggest that precipitation may become a more important source of nest failure as extreme rain and wind events become more common, as is predicted for the midwestern United States (Karl *et al.*, 2009). It is also unclear how other important demographic parameters (e.g., juvenile survival, frequency of renesting, and double brooding) are influenced by climatic variables; such information is needed if we are to accurately model demographic responses to climate change. Finally, a better understanding of the effects of temperature on behavioral and/or numerical responses of frequent nest predators is required if we are to move

toward a mechanistic explanation of species-specific links (or lack thereof) between temperature and productivity. Regardless of the mechanisms responsible for the patterns we observed, it is clear that the direct effects of weather on nestling production were minor in comparison with the effect of high temperatures on the interactions between flycatchers and their nest predators. We believe this underscores a weakness of current approaches to assessing the response of wildlife to future climate change; many do not incorporate important biotic interactions even though doing so can be an essential component of fitting predictive models (Van Der Putten *et al.*, 2010; Zarnetske *et al.*, 2012). Moving beyond a consideration of the direct effects of climate warming typically considered in bioclimatic envelope modeling and acknowledging species' interactions with a more thorough consideration of community ecology will be important in the development of future models of climate impacts on wildlife.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Model selection results from *a priori* candidate models describing fragmentation (forest cover and edge density) and weather (temperature and precipitation) effects on a subset of nests which excludes those that failed for any reason other than predation (e.g., storms, abandonment, adult mortality). Northern Cardinals were not included in this analysis because only one nest failed from causes other than predation, so the results would be essentially identical to those presented in Table 2.

Figure S1. Model-averaged predictions of period nest survival (±95% CI) for Acadian Flycatchers and Indigo Buntings as a function of precipitation for a subset of nests which excludes those that failed for reasons other than predation (e.g., storms, abandonment, adult mortality). All other variables were held constant at their mean value. Estimates to the left of the axis break are for the 0–95th percentiles of precipitation values, and those to the right of the axis break are for observed extreme rain events.

Figure S2. Model-based productivity per nest attempt (95% CI) as a function of temperature at 5th, median, and 95th values of forest cover for (a) Acadian Flycatchers and (b) Indigo Buntings for a subset of nests which excludes those that failed for reasons other than predation (e.g., storms, abandonment, adult mortality). Brood parasitism rates are held at their estimated rate for each level of landscape forest cover and mean edge density is held at observed values within ±5% of each level of forest cover. All other variables were held constant at their means for model predictions. Vertical dashed lines represent 5th and 95th percentiles of observed values of temperature.