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ORIGINAL ARTICLE

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Demographic responses of eastern bluebirds to climatic variability in northeastern Arkansas

Sara E. Harrod | **Virginie Rolland**

Department of Biological Sciences,
Arkansas State University, PO Box 599,
State University, Arkansas, 72467

Correspondence
Sara E. Harrod, Department of Biological Sciences, Arkansas State University, PO Box 599, State University, AR 72467.
Email: sara.harrod@smail.astate.edu

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Abstract

As climate change continues to alter temperature and precipitation patterns, numerous species have declined. However, populations of some species that show responses to climate change, such as eastern bluebirds (*Sialia sialis*), have increased or remained stable nationwide. To understand how species are adapting to climate change, we estimated demographic parameters and their responses to climatic variability, using nesting and banding-recapture data between 2003 and 2018 in a northeastern Arkansas eastern bluebird population. Increasing variability in precipitation in the nonbreeding season negatively affected hatchability. Hatching success was negatively affected by increasing variability in maximum temperatures and the number of hot days during the breeding season, but positively affected by increasing winter snow depth. Adult survival was positively affected by increasing snow depth and variability in the number of hot days during the breeding season, but negatively affected by increasing variability in nonbreeding season temperatures. Our results demonstrate that for this study population, annual breeding parameters, though canalized against interannual environmental variation, were affected by seasonal climatic variability. Although climate change may benefit bluebird survival due to increasing variability in winter temperatures and the number of hot days, climatic variability negatively affected breeding parameters and is expected to increase. Because breeding parameters are typically the drivers of population growth rate in short-lived species, these results raise concern for the future of this population of eastern bluebirds.

KEYWORDS
adult survival, climate change, hatching success, season, *Sialia sialis*

1 | INTRODUCTION

As a result of anthropogenic activities, global temperatures have risen ~ 1.0°C above preindustrial levels. At the current rate of warming, temperatures are expected to rise by 1.5°C between 2030 and 2052 (IPCC, 2018), with additional warming contingent on the quantity of greenhouse gas emissions (Hayhoe et al., 2017). Climatologists predict increasing temperatures will lead to an increase in extreme weather events (e.g., heatwaves, floods) and climatic variability, changing precipitation patterns and rising sea levels (IPCC, 2018). Species extinctions, loss of suitable habitat and decreased biodiversity are also predicted byproducts of climate change (IPCC, 2018). Multiple studies have already documented discernable impacts across multiple taxa, including mammals

(Campbell, Nouvellet, Newman, MacDonald, & Rosell, 2012; Sultaire et al., 2016; Whiteman et al., 2018), birds (Jenouvrier, 2013; Samplonius et al., 2018; Visser, Holleman, & Gienapp, 2006), plants (Hultine et al., 2016; Jump, Hunt, & Penuelas, 2006; Slodowicz, Descombes, Kikodze, Broennimann, & Müller-Schärer, 2018) and insects (Giannini et al., 2017; Nufio, McGuire, Bowers, & Guralnick, 2010; Oliver et al., 2015). These impacts include phenological mismatch, habitat loss, range contraction and decreased population growth rate. However, some species also benefit from climate change via range expansion or an increase in population growth rate (Hongoh, Berrang-Ford, Scott, & Lindsay, 2012; McClelland et al., 2018; Szlachetko et al., 2017). Determining how successful species are adapting to climate change allows biologists to predict range shifts/expansions and the effects of increased population growth rates of these successful species on other species in their communities, including threatened species (Hamilton, Okada, Korves, & Schmitt, 2015). To understand why species respond in differing ways to climate change, we need to understand how their demographic parameters are affected.

Demographic parameters respond to changes in both mean climatic conditions and climatic variability (Boyce et al., 2006; Campbell et al., 2012; Vázquez, Gianoli, Morris, & Bozinovic, 2015). The specific parameters affected by these changes depend on the season in which climatic changes occur and the species' life history (i.e., slow vs. fast). The climate-specific tub- and tap-hypotheses predict that climatic conditions cause population fluctuations via changes in demographic parameters, depending on the period of the year (i.e., breeding or nonbreeding season) (Sæther, Sutherland, & Engen, 2004). The tub-hypothesis predicts that population fluctuations are highly correlated with variations in survival affected by climate during the nonbreeding season, whereas the tap-hypothesis predicts that population fluctuations correlate with variations in reproductive success during the breeding season (Sæther et al., 2004). Additionally, the environmental canalization hypothesis predicts that the parameter that contributes the most to a population's growth rate is canalized against temporal variation (Gaillard & Yoccoz, 2003). The canalized parameter is usually fecundity for short-lived species and adult survival for long-lived species (Lebreton & Clobert, 1991; Sæther & Bakke, 2000).

To help improve our understanding of how some species are adapting to climate change, we studied the eastern bluebird (*Sialia sialis*; hereinafter “bluebird”), a short-lived species for which most populations across North America have increased or remained stable since the 1980s (Sauer et al., 2017). However, bluebird populations have exhibited high variability (Pitts, 1981), including sharp declines in the 1970s, partly due to several years with severe winter weather (Gowaty & Plissner, 2015; Sauer & Droege, 1990; Wetzel & Krupa, 2013). Additionally, bluebirds have advanced their egg-laying dates (Torti & Dunn, 2005) and shifted their range northward (Zuckerberg, Woods, & Porter, 2009). For our study, we used 15 years of nesting and banding-recapture data collected from a population in northeastern Arkansas. Our objectives were to (a) estimate the annual breeding demographic parameters (i.e., average clutch size, hatching success, hatchability, fledging success) and adult apparent survival of eastern bluebirds along a nest box trail, and (b) assess the relationships between climatic variables and these parameters. Due to the variability in climatic conditions at our site, we included measures of mean and variability for precipitation and temperature in both breeding and nonbreeding seasons to evaluate the tub- vs. tap-hypothesis. This research will provide useful information for determining why and how some species persist in spite of increasing climatic variability.

2 | METHODS

2.1 | Study site

The field site is situated within the Crowley's Ridge Ecoregion, in the northeast of Arkansas. The smallest of Arkansas's ecoregions, Crowley's Ridge is characterized by a large geological formation that rises up to 170 m above the surrounding Arkansas Delta (Stroud, 2018). Forest covers much of the ridge, with common tree species including white oak (*Quercus alba*), shortleaf pine (*Pinus echinata*) and sweetgum (*Liquidambar styraciflua*) (Clark, 1977).

Classified as humid subtropical (Cfa) by the Köppen-Geiger climate classification system, the northeast Arkansas region experiences hot, humid summers and variable, year-round precipitation (Peel, Finlayson, & Mcmahon, 2007). The region is also subject to increasingly high variability in climatic conditions, with summers becoming hotter and winters becoming colder (Partridge et al., 2018). Average temperatures reach a high of 32.6°C in July and a low of −3.5°C in January. Annually, the region receives an average of 12.4 cm of rainfall, with the highest rainfall occurring during the spring and fall months. Average annual snowfall is minimal at 13 cm (US Climate Data, 2019), but snowfall of up to 17.8 cm has occurred (The Weather Company, 2019).

2.2 | Study species

As abundant secondary-cavity nesters, bluebirds occur throughout much of eastern North America, from western Oklahoma to New England and as far north as Saskatchewan (Gowaty & Plissner, 2015). They are primarily insectivores (Pinkowski, 1974; Stanback & Mercadante, 2009); however, small fruits are an important food source in the winter (Pinkowski, 1977). Bluebirds form monogamous pairs, though extra-pair copulations by both sexes can occur (Gowaty & Bridges, 1991). The breeding season varies by latitude; at our site, it typically began in mid-March and lasted through late August. Females can produce up to three successful clutches of ≤6 eggs/clutch during a single season. Incubation lasts 11–19 days, and chicks fledge at ~18 days of age (Gowaty & Plissner, 2015). Although the northernmost populations migrate south for the winter, many populations, including our study population in northeast Arkansas, are permanent residents. During extreme winter weather, 15–20 individuals may roost in a single nest box to conserve heat (Frazier & Val Nolan, 1959; Pinkowski, 1977; Pitts, 1978), including at our study site (Fowler, 2014). The maximum recorded lifespan is 10.5 years (USGS, 2016), though the average lifespan is not reported for this species. In our study population, 67.6% of eastern bluebirds banded as chicks and resighted as second-year were not resighted as after-second-year; the other 32.4% lived at least 2–5 years. Most bluebird populations are increasing or stable (Sauer et al., 2017), including in our region with a 1% annual growth rate between 1967 and 2018 (National Audubon Society, 2010) and in our population with an observed 3.0% annual growth rate between 2003 and 2018 (Harrod & Rolland, unpublished).

2.3 | Nest monitoring and banding

We monitored 150 nest boxes ~7.5 km north of Jonesboro, Arkansas, for which nesting and banding data were collected from 2003 to 2018 (excluding 2011). Nest boxes were situated along roadsides, fences and forest edges, or within private yards and pastures, and spaced 100 m apart from the nearest box (Figure 1). Most nest boxes were mounted to metal poles 1.2–1.8 m from the ground, except for three boxes installed by property owners on trees or telephone poles. Shapes, dimensions and orientations varied, but all nest boxes had a circular entrance diameter of 3.81 cm to prevent use by European Starlings (*Sturnus vulgaris*); other species (i.e., Carolina Chickadee [*Poecile carolinensis*], Tufted Titmouse [*Baeolophus bicolor*] and Carolina Wren [*Thryothorus ludovicianus*]) occasionally used these boxes for nesting. Two thirds of boxes had predator guards in the form of axle grease (Lombardo, Bosman, Faro, Houtteman, & Kluisza, 1995) or a Kingston Stovepipe baffle (Kingston, 1990) installed on their poles. From 2003 to 2010, the boxes were monitored and maintained by other researchers. Because we began monitoring in 2012 and no record was made of when a box received a predator guard, we could not determine which boxes to exclude from our analyses. However, we tested for a difference in breeding parameters before and after 2012 and this test was mostly inconclusive (see Supporting Information). To further minimize the potential bias, we assigned each box a unique ID number and used this ID as a random variable in our models. Overall, just as natural nest cavities differ in their characteristics, so did the nest boxes in our study population. However, because all nest boxes experienced the same climatic conditions and the differences in characteristics remained similar across years, these differences likely did not bias our analysis of the effect of climatic variability on demographic parameters at the population level, over the study period.

Monitoring took place between mid-March and late August, or until the last brood fledged. Nest boxes were checked once a week unless egg-laying or nest building were observed. We considered a nest to be active when we first observed an egg in the nest. We then recorded the date the first egg was laid, and the nest was

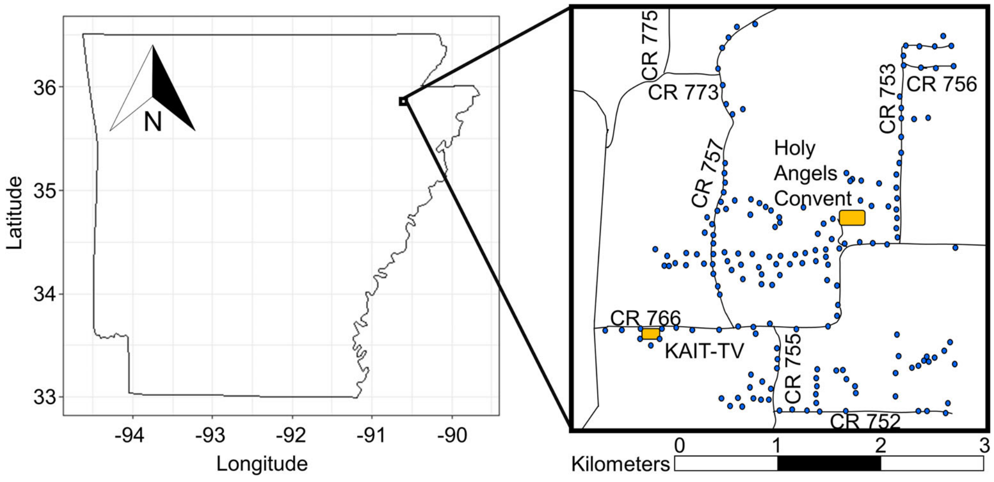

FIGURE 1 The Jonesboro bluebird trail in Craighead County, Arkansas. Each point represents one nest box [Color figure can be viewed at wileyonlinelibrary.com]

monitored every 2–5 days until nest failure or until chicks were 13 days-old (hereafter Day 13). To avoid premature fledging, we did not visit the nest again until Day 18; if chicks were still present, we checked every day thereafter until the chicks fledged or the nesting attempt failed. Once the box was vacated, we removed the nest to determine the start of a new nesting attempt. The methods used for the first clutch were used for subsequent clutches.

We attempted to band all adults that used the nest boxes with a USGS aluminum band and three color bands to form a unique combination. Adults banded in previous years that reused nest boxes were resighted with binoculars to identify their combinations. Upon capture at the nest box (following Robinson, Siefferman, & Risch, 2004) when chicks were between 2 and 4 days of age, unbanded adults were sexed, aged and banded. All field activities were approved by the Arkansas State University Institutional Animal Care and Use Committee (IACUC).

2.4 | Estimation of demographic parameters

We calculated annual estimates of our demographic parameters: clutch size, hatching success (i.e., probability that ≥1 egg hatches in a given nest), hatchability (i.e., the proportion of eggs that hatch in a successful nest), fledging success (i.e., probability that ≥1 chick survived to Day 13) and adult apparent survival. We defined fledging success as chick survival to Day 13 because some nests were not monitored after Day 13 in the first 8 years of the study period. Using data from 2012 to 2018, we found that survival to Day 13 was strongly correlated with fledging success at the last check day ($\rho = 0.87$, $p < .001$). Adult apparent survival was defined as an adult bluebird surviving to the following year and remaining at our study site. Birds that switched to natural cavities were not resighted. Cavity-switching (to another nest box or a natural cavity) is more likely to occur after nest failure (Gowaty & Plissner, 1997; Stanback & Rockwell, 2003).

We used generalized linear mixed models to estimate breeding parameters in program R (R Core Team, 2015) using the lme4 package (Bates, Mächler, Bolker, & Walker, 2015). Because bluebirds may successfully breed up to three times in a season and reuse nest boxes, we accounted for potential pseudoreplication by including Box ID and Female ID as random effects (Bates et al., 2015). We did not include Male ID because males show higher natal and breeding site fidelity (Gowaty & Plissner, 1997; Plissner & Gowaty, 1996), and therefore including Male ID and Box ID as random effects would be mostly redundant. Box ID also accounted for consistent differences among nest boxes, including dimensions and the presence of a predator guard.

We used an information-theoretic approach (using Akaike's Information Criterion; Burnham & Anderson, 2002) to select the model with the best random structure to consider for each parameter analysis (Bates, 2010). We compared four constant models (i.e., with no random effect, with Female ID only, with Box ID only and with both random effects) and selected the model with the lowest AIC from which to obtain parameter estimates. If multiple models were equivalent (i.e., $\Delta\text{AIC} \leq 2$), we chose the simplest model based on the principle of parsimony (Burnham & Anderson, 2002). For clutch size, models with random effects were equivalent to the null model, so we discarded both effects (Table S2a in Supporting Information). We then modeled clutch size using a generalized linear model and a Poisson error distribution for count data (Coxe, West, & Aiken, 2009). For hatchability, we used a generalized linear mixed-effect model for proportion data with Female ID as a random effect (Table S2c in Supporting Information). We estimated hatching and fledging success using the logistic-exposure method (package MASS; Ripley et al., 2010), which uses a binary response variable (i.e., 0 = failure, 1 = success) and a logistic-exposure link function (instead of the traditional logit link) to account for variability in the length of nest exposure (i.e., the number of days between nest visits; Shaffer, 2004). For both analyses, we included Female ID and Box ID as random variables (Table S2b,d in Supporting Information, respectively).

Adult annual apparent survival was estimated with Cormack-Jolly-Seber models of survival (Lebreton, Burnham, Clobert, & Anderson, 1992) using the RMark package (Laake, 2013) in program R (R Core Team, 2015). To estimate annual adult apparent survival, we used 15 years of capture-mark-recapture data from 1,411 adult bluebirds banded and recaptured or resighted between 2003 and 2018, excluding 2011. Cormack-Jolly-Seber models assume that recapture probability is the same for all individuals (no trap-dependence, no transience; Lebreton et al., 1992). To test this assumption, we conducted goodness-of-fit tests on our general model with time-dependent survival (Φ_t) and capture (p_t) probabilities, using program U-CARE (Choquet, Reboulet, Lebreton, Gimenez, & Pradel, 2009). The test for transience (Test3.SR) was not significant ($\chi^2 = 29.0$, $df = 13$, $p = .07$), but the test for trap-dependence (Test2.CT) was ($\chi^2 = 20.0$, $df = 8$, $p < .001$). The other two tests were not significant (Test3.SM: $\chi^2 = 5.23$, $df = 9$, $p = .81$; Test2.CL: $\chi^2 = 3.18$, $df = 7$, $p = .87$). [Correction added on 8 June 2020, after first online publication: the names of the tests 'Test2.Sm' and 'Test3.CR' have been corrected to 'Test3.SM' and 'Test2.CL' in the preceding sentence.]

The annual probability of capturing an individual depended on whether it was caught in the previous year. To account for this, we incorporated a trap-dependent probability of capture (td) into our general model such that the model became $\Phi_t p_{t*\mathrm{td}}$. Trapping effort varied across the study period, with less effort made in 2003–2010, no effort made in 2011 and high effort made in 2012–2018. As a result, we defined three periods for recapture probability: period 1 from 2004–2010, period 2 for 2011 and period 3 from 2012–2017. For period 2, we fixed recapture probability to 0. We used AIC-based model selection to determine which general structure (constant, time-dependent, temporal trend or period-dependent) best fit our recapture and survival data (Table S3 in Supporting Information). Finally, after estimating our demographic parameters, we calculated their coefficient of variation (CV; $\frac{\sigma}{\mu}$). For binomially distributed parameters, we also measured their relative variance ($\mathrm{RV} = \frac{\sigma 2}{\mu * (\text{maximum value} - \mu)}$) across the study period (Table S4 in Supporting Information).

2.5 | Analyses of weather and climatic effects

To analyze the effect of weather conditions and climatic variability on bluebird demographic parameters, we considered two global climatic indices and 21 local weather variables (Table 1). Our climatic indices included the Oceanic Niño index (ONI) and North Atlantic Oscillation (NAO) index (NOAA, 2017b, 2017c), which measure El Niño Southern Oscillation (ENSO) and NAO activity, respectively. These indices were obtained from the National Oceanic and Atmospheric Administration's (NOAA) Climate Prediction Center (NOAA, 2017b, 2017c). ONI values ≥0.5 are indicative of ENSO

TABLE 1 Variability and temporal trends in breeding (BS) and nonbreeding season (NBS) variables (2003–2018) for Jonesboro, Arkansas

Season	Dependent variable	Abbrev.	CV	Slope	*SE*	*p*
BS	CV days above 35°C	CVAbove	0.87	<−0.01	0.02	.87
	Average days above 35°C	AVAbove	0.47	−0.04	0.22	.86
	CV precipitation	CVPrecip_BS	0.30	0.01	0.01	.57
	Average precipitation	AVPrecip_BS	0.25	0.02	0.06	.75
	CV maximum temperature	CVMax_BS	0.15	<0.01	<0.01	.44
	CV monthly temperature	CVTemp_BS	0.13	<0.01	<0.01	.40
	CV minimum temperature	CVMin_BS	0.11	<0.01	<0.01	.45
	Average maximum temperature	AVMax_BS	0.01	0.04	0.13	.74
	Average minimum temperature	AVMin_BS	0.01	0.06	0.10	.53
	Average monthly temperature	AVTemp_BS	0.01	0.06	0.11	.58
NBS	Average snow depth	Snow	1.40	−0.03	0.02	.16
	CV precipitation	CVPrecip_NBS	0.40	0.01	0.01	.52
	Average precipitation	AVPrecip_NBS	0.30	0.02	0.06	.72
	CV days below 0°C	CVBelow	0.22	<0.01	<0.01	.50
	Average days below 0°C	AVBelow	0.19	−0.27	0.13	.06
	CV minimum temperature	CVMin_NBS	0.13	<0.01	<0.01	.89
	CV monthly temperature	CVTemp_NBS	0.12	<0.01	<0.01	.99
	CV maximum temperature	CVMax_NBS	0.11	<0.01	<0.01	.89
	Average ONI	ONI	–	−0.02	0.06	.74
	Average NAO	NAO	–	0.06	0.03	.07
	Average minimum temperature	AVMin_NBS	0.01	0.10	0.12	.42
	Average maximum temperature	AVMax_NBS	0.01	0.17	0.15	.26
	Average monthly temperature	AVTemp_NBS	0.01	0.15	0.11	.20

Note: Year was used as the only independent variable in linear regression models for each weather and climatic variable. Variable abbreviations (Abbrev.), interannual coefficient of variations (CV), slopes, standard errors (*SE*) and *p*-values are shown. Underlined variables were retained due to high CV values (≥0.10). CV values are not shown for the Oceanic Niño index (ONI) and North Atlantic Oscillation (NAO) index because these indices contain negative values.

conditions, which typically cause increased precipitation, cooler temperatures and increased storminess in the southeastern and south-central United States (Kovats, Bouma, Hajat, Worrall, & Haines, 2003). The NAO also affects winter weather in the eastern United States; during the NAO's positive phase (positive NAO index values), the southeastern United States experiences below-average snowfall, warmer temperatures and decreased storminess (Myoung, Kim, Kim, & Kafatos, 2015). Because the effects of ENSO and the NAO are felt strongest during fall and winter months (Myoung et al., 2015), we only used ONI and NAO index values for the nonbreeding season (NBS, September–February).

The 21 local weather variables included 11 average seasonal variables and, for climatic variability, 10 CV seasonal variables. Specifically, we extracted monthly averages from the Jonesboro Municipal Airport weather station via Weather Underground (The Weather Company, 2019) for four weather parameters for breeding (BS, March–August) and nonbreeding seasons: minimum, maximum, and mean temperature, and precipitation. We also extracted the number of days ≥35 and ≤0°C (The Weather Company, 2019) and average snow depth, which we retrieved from NOAA's PGLA4 station (NOAA, 2017a). The 10 CV seasonal variables were created to correspond to each of the 11 average seasonal variables, except for snow depth. These CV seasonal variables were calculated by dividing the average seasonal variable values by their associated standard deviation. Because the coefficient of variation can only be calculated for variables measured along a ratio scale (i.e., having a true and meaningful zero), we first converted our temperature variables from Celsius to Kelvin, then calculated the CV seasonal variables. Additionally, for each of the 21 weather variables, we calculated an interannual CV to identify those with the most variability. Only variables with ≥10% interannual variability across the study period were retained for subsequent analyses. Finally, we checked for temporal trends using linear models and z-transformed all final variables (Table 1).

To estimate the effects of weather and climatic variables on our breeding and survival parameters, we used a three-step approach. At each step, we considered all models within ΔAIC of ≤2, but for steps 2 and 3, we applied the principle of parsimony to select a final model (Burnham & Anderson, 2002). First, we built single-covariate models for each parameter. Second, we ran forward model selections (using AIC) on each of our three sets of variables (global [NAO and ONI], average, and CV; see Table S5a–e in Supporting Information). We tested for significant correlations among variables using a Pearson's product–moment correlation test ($\alpha = 0.05$), and only uncorrelated variables were used to build additive models. Within each set, we compared additive models to retained single-covariate models. Finally, our last step consisted of comparing, and when possible

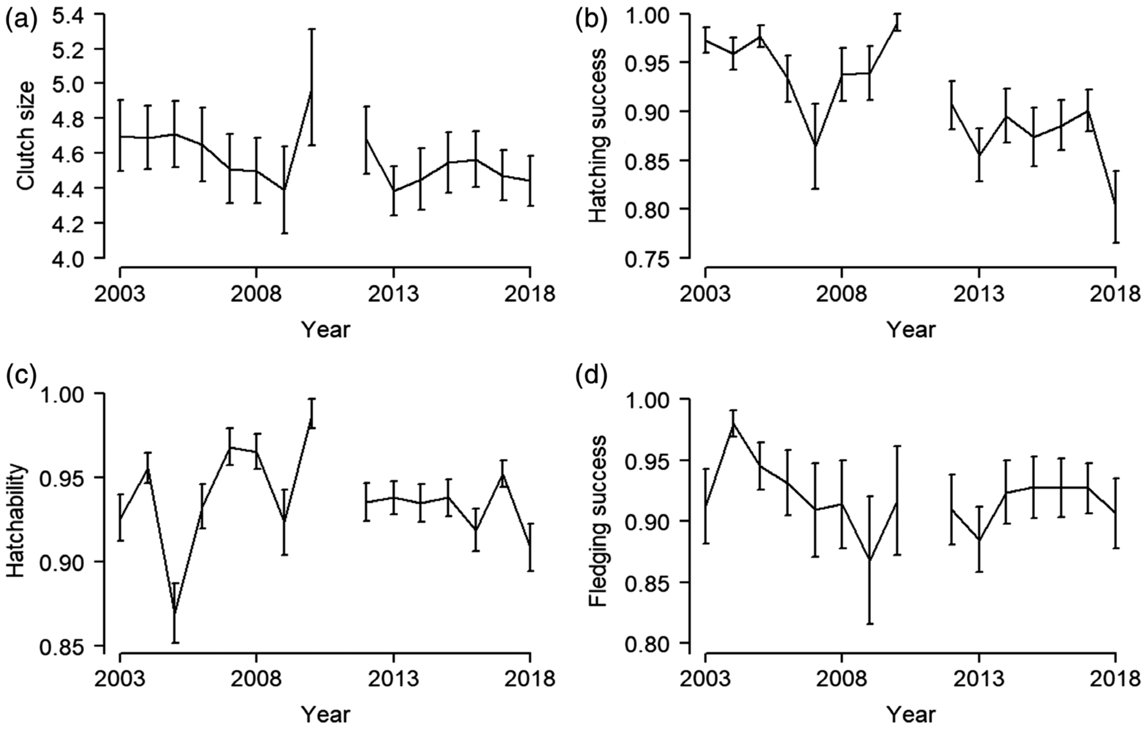

FIGURE 2 Annual estimates ± *SE* of (a) average clutch size, (b) hatching success, (c) hatchability and (d) fledging success of eastern bluebirds in northeast Arkansas, 2003–2018

FIGURE 3 Estimates ± *SE* of adult annual apparent survival of eastern bluebirds in northeast Arkansas, 2004–2018. Years represent time periods and are presented as the second year in the interval; for example, 2003–2004 is presented as 2004

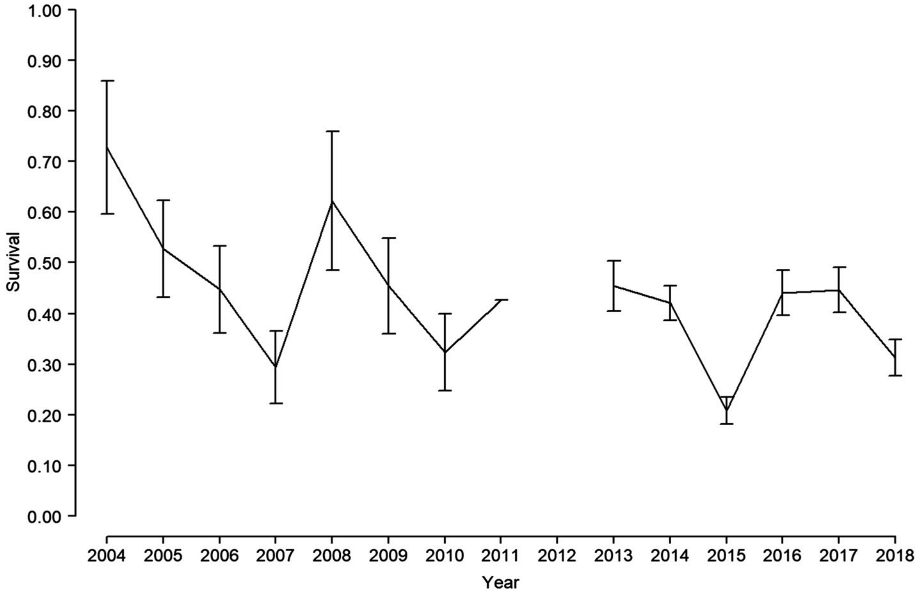

TABLE 2 Model selection for hatching success in a bluebird population monitored during 2013–2018 in Jonesboro, Arkansas

	Model	*K*	AIC	ΔAIC	*w*
CV	CVMax_BS + CVAbove	5	2,390.7	0.00	0.76
	CVMax_BS	4	2,394.1	3.45	0.14
	CVAbove	4	2,396.1	5.46	0.05
	CVTemp_BS	4	2,396.4	5.72	0.04
	Null	3	2,398.5	7.82	0.02
Combined	CVMax_BS + CVAbove + Snow	6	2,386.1	0.00	0.90
	CVMax_BS + CVAbove	5	2,390.7	4.53	0.09
	Snow	4	2,396.1	10.01	0.01
	Null	3	2,398.5	12.36	<0.01

Note: Only variables (Table 1) selected from our first-step model selection (Table S5b in Supporting Information) were considered in these models. CV and combined in the first column indicate models containing seasonal coefficient of variation variables or a combination of CV and Average variables. Models are presented with corresponding *K* (number of parameters), AIC (Akaike's Information Criterion), ΔAIC (difference in AIC between given model and lowest AIC model) and *w* (model weight) values.

combining, the best models from each set of variables (global, average and CV). All slope (i.e., beta) estimates are reported ±1 *SE* to indicate directionality and effect size of variables in our final models. We also calculated the coefficient of determination (R^2) to estimate the proportion of variation in the demographic parameters explained by weather and climatic variable(s) in our final models (Grosbois et al., 2008).

3 | RESULTS

3.1 | Demographic parameters

Between 2003 and 2018, 2,343 clutches (i.e., nests with at least one egg laid) were monitored. The earliest first egg date was 12 March (in 2004), and the latest fledging date was 18 September (in 2016). We found no significant temporal trend for average clutch size ($p = .10$) or hatchability ($p = .09$), but detected significant negative trends in hatching (−0.11 ± 0.003, $p < .001$) and fledging success (−0.02 ± 0.003, $p < .001$) across the entire study period. Similarly, we found that hatching success was significantly ($p < .001$) lower in the second period (0.88 ± 0.01) than in the first period (0.96 ± 0.01). However, we detected no significant difference between periods in fledging success ($p = .29$), clutch size ($p = .13$) and hatchability ($p = .98$) (Table S1 in Supporting Information).

The coefficients of variation and relative variance in our breeding parameters were low across our study period. Average clutch size (CV = 0.04) varied from 4.39 ± 0.14 in 2013 to 4.98 ± 0.33 in 2010 (Figure 2a).

TABLE 3 Model selection for hatchability in a bluebird population monitored during 2013–2018 in Jonesboro, Arkansas

	Model	*K*	AIC	ΔAIC	*w*
CV	CVPrecip_NBS + CVMin_BS	4	2,850.0	0.00	0.33
	CVPrecip_NBS + CVTemp_BS	4	2,850.5	0.58	0.24
	CVPrecip_NBS	3	2,851.5	1.53	0.15
	CVPrecip_NBS + CVMax_BS	4	2,851.6	1.62	0.15
	CVBelow	3	2,851.9	1.90	0.13
	CVMin_BS	3	2,866.3	16.33	<0.01
	CVTemp_BS	3	2,868.2	18.19	<0.01
	CVMax_BS	3	2,870.3	20.28	<0.01
	Null	2	2,872.7	22.74	<0.01

Note: Only variables (Table 1) selected from our first-step model selection (Table S5c in Supporting Information) were considered in these models. CV indicates models containing seasonal coefficient of variation variables. Models are presented with corresponding *K* (number of parameters), AIC (Akaike's Information Criterion), ΔAIC (difference in AIC between given model and lowest AIC model) and *w* (model weight) values.

TABLE 4 Model selection for survival in a bluebird population monitored during 2013–2018 in Jonesboro, Arkansas

	Model	*K*	AIC	ΔAIC	*w*
CV	CVTemp_NBS + CVAbove	6	2,415.2	0.00	0.65
	CVTemp_NBS	5	2,418.2	3.09	0.14
	CVTemp_NBS + CVBelow	6	2,418.8	3.63	0.11
	CVAbove	5	2,419.3	4.16	0.08
	CVMax_NBS	5	2,421.9	6.77	0.02
	CVBelow	5	2,430.1	14.9	<0.01
	CVMin_BS	5	2,430.5	15.3	<0.01
	CVMin_NBS	5	2,431.1	15.9	<0.01
	CVTemp_BS	5	2,432.6	17.4	<0.01
	Null	4	2,434.9	19.8	<0.01
Average	Snow + AVPrecip_NBS	6	2,416.6	0.00	0.99
	AVPrecip_NBS	5	2,428.5	11.98	<0.01
	Snow	5	2,428.7	12.1	<0.01
	Null	4	2,434.9	18.4	<0.01
Combined	CVAbove + CVTemp_NBS + Snow + AVPrecip_NBS[a]	8	2,403.5	0.00	0.91
	ONI + CVTemp_NBS + CVAbove	7	2,408.2	4.76	0.08
	ONI + Snow+AVPrecip_NBS	7	2,413.3	9.78	0.01
	CVTemp_NBS + CVAbove	6	2,415.2	11.7	<0.01
	Snow + AVPrecip_NBS	6	2,416.6	13.1	<0.01
	ONI	5	2,426.3	22.8	<0.01
	Null	4	2,434.9	31.5	<0.01

Note: Only variables (Table 1) selected from our first-step model selection (Table S5e in Supporting Information) were considered in these models. CV, Average, and combined in the first column indicate models containing seasonal coefficient of variation variables, seasonal average variables, or a mixture of CV, Average, and global climatic indices variables. Models are presented with corresponding *K* (number of parameters), AIC (Akaike's Information Criterion), ΔAIC (difference in AIC between given model and lowest AIC model) and *w* (model weight) values.

[a] AVPrecip_NBS was not significant (95% CI: −0.14; 0.23) and excluded from discussion.

Hatching success (CV = 0.06, RV = 0.03; Figure 2c) varied from 0.99 ± 0.01 in 2010 to 0.80 ± 0.04 in 2018. Hatchability (CV = 0.03, RV = 0.01) remained high across the study period, with the lowest proportion of eggs hatched (0.87 ± 0.02) in 2005 (Figure 2b). Fledging success (CV = 0.03, RV = 0.01; Figure 2d) was highest in 2004 (0.98 ± 0.01) and lowest in 2009 (0.87 ± 0.05). The best general structure model for survival and recapture probabilities was $\Phi_{\text{time}}\ p_{\text{Period + td}}$ ($w = 0.69$; Table S3 in Supporting Information). Recapture probability showed a significantly increasing trend across the study period (0.06 ± 0.01, $p = .001$), with 2008 having the lowest recapture probability (0.15 ± 0.07) and 2015 having the highest (0.78 ± 0.09). Adult annual apparent survival varied the most (CV = 0.29, RV = 0.07), with a high of 0.73 ± 0.13 in 2004 and a low of 0.21 ± 0.03 in 2015 (Figure 3).

3.2 | Weather and climatic effects

Of the original 23 weather and climatic variables, we retained 17, most being CV seasonal variables (Table 1). The covariates average snow depth and variability in the number of days ≥35°C showed the strongest variability over the study period (1.40 and 0.87, respectively). For both seasons, average temperatures, minimum temperatures and maximum temperatures exhibited low variability (Table 1). None of the variables showed a temporal trend.

3.2.1 | Clutch size

The best model was the null model, indicating that no weather or climatic variable influenced clutch size during our study period (Table S5a in Supporting Information).

3.2.2 | Hatching success

None of our global variables had an important effect on hatching success (Table S5b in Supporting Information). The final model included average snow depth, maximum temperature variability during the breeding season, and variability in the number of days ≥35°C ($R^2 = .28$; Table 2). Snow had a positive effect on hatching success (0.25 ± 0.10), whereas maximum temperature variability (−0.26 ± 0.08) and variability in the number of days (−0.16 ± 0.08) showed negative effects.

3.2.3 | Hatchability

None of our global or average variables affected hatchability (Table S5c in Supporting Information). Our top five models were equivalent in AIC (Table 3). According to the most parsimonious model with the highest weight, hatchability decreased with increasing variability in precipitation in the nonbreeding season (−0.22 ± 0.05; $R^2 = .36$).

3.2.4 | Fledging success

None of our global indices or local weather covariates influenced fledging success (Table S5d in Supporting Information).

3.2.5 | Survival

Our final model combining uncorrelated average and CV variables included average snow depth, average precipitation in the nonbreeding season, variability in temperature in the nonbreeding season, and variability in the number of days ≥35°C ($R^2 = .58$; Table 4). Because average precipitation in the nonbreeding season was nonsignificant (95% CI: −0.14; 0.23), we excluded it from further discussion. Increasing snow depth and variability in the number of days ≥35°C had positive effects (0.25 ± 0.07 and 0.19 ± 0.07, respectively) on adult annual apparent survival, whereas increasing variability in nonbreeding season temperatures had a negative effect (−0.16 ± 0.06) on survival.

4 | DISCUSSION

Climate change has had (and will likely continue to have) significant impacts on wildlife across the globe, with many species suffering detrimental effects (IPCC, 2018). Though species that are negatively affected deserve close studying and long-term monitoring, species which have experienced population increases or remained stable also warrant attention, as these studies can tell us how and why some populations are adapting to climate change. Here, we estimated breeding parameters and survival for a population of eastern bluebirds in northeastern Arkansas. We also reported the effects of climatic variability on these parameters. Other climatic variables that did not exhibit high variability and were not tested in this study could also have affected our demographic parameters. For example, hatching success could have been impacted by increasing average temperatures or droughts could have reduced hatchability (Carleton, Graham, Lee, Taylor, & Carleton, 2019), but the analysis of these effects was out of the scope of this paper.

The breeding parameters of bluebirds at our site showed low variability over the study period (Figure 2). Estimates of hatching success, hatchability and fledging success remained relatively high (~90–95%), with even the least successful years being ~80% for all three parameters. This combination of high estimates and low variability suggest that bluebird breeding parameters might be canalized against environmental variation (Gaillard & Yoccoz, 2003). By contrast, adult annual apparent survival showed higher variability (Figure 3), with annual estimates ranging from 0.21 ± 0.03 to 0.73 ± 0.13. These estimates are consistent with other comprehensive studies of bluebird survival (Lang, 2013; Plissner & Gowaty, 1996), which also showed strong interannual fluctuations in adult survival. Our estimates are also accordant with the idea that for short-lived species, the parameter that experiences the most fluctuation is survival (Lebreton & Clobert, 1991; Sæther & Bakke, 2000).

Our retained 17 climatic and weather variables showed high interannual variability (i.e., $\mathrm{CV} > 0.10$) and consisted of variables from all three sets (global index, average and CV) and both seasons (Table 1). Average snow depth showed the strongest interannual variability over the study period ($\mathrm{CV} = 1.40$), followed by variability in the number of days ≥35°C ($\mathrm{CV} = 0.87$). These findings are consistent with those from the Fourth National Climate Assessment, which predicts a decrease in the number of freezing events and an increase in the number of days ≥35°C (Reidmiller et al., 2018). Average monthly temperatures during the breeding and nonbreeding seasons showed little interannual variability ($\mathrm{CV} = 0.03$ and 0.04, respectively). These findings correlate with recent analyses of past climatic conditions in the southeastern United States, which found less overall warming in this region (Partridge et al., 2018; Vose, Easterling, Kunkel, & Wehner, 2017). Although it is important to examine the effects of mean conditions on wildlife populations, climate change occurs in terms of mean state and variability (Vázquez et al., 2015), and both can affect demographic parameters differently (Altwegg & Anderson, 2009; Jenouvrier, 2013). Correspondingly, in our study, nine of the 10 CV variables influenced one or more demographic parameters in our bluebird population.

Interestingly, our results show that both hatching and fledging success decreased over the study period. Such a decrease in hatching and fledging success is alarming for a short-lived species given that such species rely on reproduction rather than survival for population growth (Lebreton & Clobert, 1991; Sæther & Bakke, 2000). Neither clutch size nor fledging success were affected by the weather variables we considered, supporting the idea of environmental canalization (Gaillard & Yoccoz, 2003). Fledging success could have been affected by variables we did not test or nonweather variables, such as changes in predator population densities or activity (Cox, Thompson, & Faaborg, 2012; Cox, Thompson, & Reidy, 2013), improved search image and long-term memory of predators (Bailey & Bonter, 2017), variations in parental feeding behavior (Martin, Scott, & Menge, 2000) or female brooding (DuRant, 2011; DuRant, Hepp, Moore, Hopkins, & Hopkins, 2010), or density of bluebirds and competitor species (Alatalo & Lundberg, 1984; Woodworth, Wheelwright, Newman, & Norris, 2017). Additionally, fledging success could have been affected by weather variables in a nonlinear fashion (Chen, Wang, Wan, & Liu, 2015; Stenseth & Mysterud, 2002), which we did not test.

By contrast, hatching success was affected by variability in maximum temperatures during the breeding season, variability in the number of days ≥35°C, and average snow depth (Table 2), with increased variability in snow depth having a positive effect on hatching success, but increasing variability in maximum breeding season temperatures and the number of days ≥35°C having a negative effect. Variability in snow depth may benefit bluebirds by negatively impacting nest predators in one of two ways: first, increased variability may be directly detrimental to some predator populations via unpredictable prey availability, leading to lower survival and abundance. Second, this variability could positively affect other prey sources, such as mast (Wildung & Sargent, 1989) and rodents (Korslund & Steen, 2006), and result in predators switching prey (Schmidt & Ostfeld, 2008). Our other two variables, variability in maximum breeding season temperatures and the number of days ≥35°C, may also affect hatching success in multiple ways. This increased variability could halt the embryonic development of all eggs in a clutch (Cooper, Hochachka, Phillips, & Dhondt, 2006). The optimal range for embryonic developed is 36–40.5°C (Cooper et al., 2006). However, internal nest box temperatures can be significantly higher than ambient temperatures (Maziarz, Broughton, & Wesołowski, 2017), and embryos may no longer be viable at extended temperatures of ≥41°C (Cooper et al., 2006; Webb, 1987). Increased variability may also be unfavorable to the prey species of nest predators, leading to prey-switching and preferential selection for eggs.

Consistent with other studies (Koenig & Walters, 2018; Musselman, 1935; White & Woolfenden, 1973), a post hoc analysis revealed that within each breeding season, hatchability declined from start to end of the season (0.92 ± 0.004 to 0.89 ± 0.013, $p < .001$). Our best hatchability model contained variability in precipitation in the nonbreeding season (Table 3), with this variable having an inverse relationship with hatchability. The exact mechanisms driving this observation are unknown, but we hypothesize that precipitation variability in the nonbreeding season may indirectly affect hatchability by operating on the male's body condition. Increased variability in winter precipitation can make food sources (such as berries) inaccessible via freezing and alter plant communities, which in turn has an immediate impact on the bluebird's winter food source (small fruits) and a delayed impact on invertebrates in the spring and summer (Jamieson, Trowbridge, Raffa, & Lindroth, 2012). Zhu et al. (2014) showed that variability in precipitation decreased insect species richness and abundance. A decrease in prey abundance would result in lower foraging success, and males entering the breeding season in poor condition may suffer from low sperm quality and/or count and be unable to fertilize eggs. Additionally, the seasonal decline in hatchability estimates could be the result of the cumulative stress of the breeding season on the male. Cumulative stress can result in lower sperm production (Hemmings, West, & Birkhead, 2012), leading to a higher proportion of sterile eggs and lower hatchability.

Interannual variation in adult apparent survival was best explained by average snow depth, variability in the number of days ≥35°C, and variability in nonbreeding season temperatures (Table 4). This partially supports the tub-hypothesis (Sæther et al., 2004), which predicts that variations in survival are affected by climate during the nonbreeding season, although survival was also affected by a breeding season variable. Although it seems counterintuitive that survival increased with increasing snow depth, it should be noted that average annual snowfall at the study site is only 13 cm (US Climate Data, 2019), and snow typically melts within 1–2 days. Therefore, even a relatively high snow depth may not be enough to conceal prey (i.e., arthropods and fruits) and prevent bluebirds from foraging (Pitts, 1981), and may prevent some predators from reaching roost sites until snowmelts (Folk Jr., Coady, & Folk, 1968; Glueck, Clark, & Andrews, 1988; Goszczyński, Krauze, & Gryz, 2009). However, small amounts of snow increase soil temperatures and provide insulation for insects and plant roots (Lawrence & Slater, 2010), and increased snow depth could increase primary productivity and insect populations.

Increased variability in the number of extremely warm days could benefit bluebird survival indirectly via benefits to their prey (i.e., insects). The population growth rates and development rates of some insect species increase under greater thermal variability (Colinet, Sinclair, Vernon, & Renault, 2015; Estay, Lima, & Bozinovic, 2014). Variability in the number of days ≥35°C means insects will experience days above and below this threshold. Although summer temperatures below 35°C do not negatively affect insects, temperatures above 35°C seemingly could. However, for most species living in temperate climates, the temperature at which developmental rates peak is ~35°C (Capinera, 2010). Developmental and population increases continue until the critical thermal maxima is reached, at which point heat stupor begins (Colinet et al., 2015). Critical thermal maxima is species-specific; for example, some species of lepidopterans and coleopterans, common bluebird prey species (Gowaty & Plissner, 2015), have critical thermal maxima of ≥40°C (Cohen & Pinto, 1977; Nice & Fordyce, 2006). The highest temperature recorded at our site was 41.6°C, near the critical thermal maxima but within the supraoptimal zone of development for insects (Evans, 1984).

Conversely, survival decreased with increasing variability in nonbreeding season temperatures. We hypothesize that this variability places additional stressors on adults. Increased variability in fall and winter temperatures subjects individuals to greater temperature extremes (i.e., warm and very cold; Higgins, Leetmaa, & Kousky, 2002; Moreno & Møller, 2011). During these temperature extremes, the acclimatory capacity of individuals is exceeded, and responses to these extremes persist after the temperature variability begins to decrease (Gutschick & BassiriRad, 2003). These changes in physiological responses to wide temperature fluctuations place additional stress on bluebirds, who are already coping with fewer resources (Wingfield et al., 2017). This phenomenon of decreased survival during years with variable or extreme weather has been documented in multiple avian species (Altwegg, Roulin, Kestenholz, & Jenni, 2006; Moreno & Møller, 2011).

Overall, our findings show that even over our relatively short 16-year study period, there was noticeable variability in our climate and weather variables. Furthermore, these variables influenced three out of five of our measured demographic parameters. Unlike what was predicted with the tub-hypothesis (Sæther et al., 2004), climatic variability during both seasons influenced adult survival. Our breeding parameters showed little variation across the study period (as predicted by the environmental canalization hypothesis; Gaillard & Yoccoz, 2003), yet climatic variables from both seasons (unlike what was predicted by the tap-hypothesis) had an important effect on two of our breeding parameters. These climatic effects could have important implications for this population. Though increasing variability in winter temperatures and in the number of days ≥35°C appear to benefit bluebird survival at our site, climatic variability negatively affected breeding parameters, which are typically the drivers of population growth in short-lived species. With increased variability (Verboom et al., 2010), the benefit of seemingly better-adapted survival may not outweigh the cost of decreased fecundity, which may lower the bluebird population growth rate. The currently increasing bluebird populations in the region (1% annual growth; National Audubon Society, 2010) could stabilize or slightly decline, depending on the relative increase in survival versus reduction in fecundity. Simulations with a population model could help determine the relative importance of survival and fecundity to the population growth rate, and whether bluebird populations will remain stable or increase under projected scenarios of increased variability, despite the associated reduction in fecundity.

Because our study was exploratory in nature, with the use of 17 weather and climatic variables, our results should be interpreted with caution. We recommend future studies to further investigate these patterns and their underlying biological mechanisms. Additionally, future studies should focus on conducting not only population viability analyses to determine how continuing climate change may alter the population growth rate, but also similar demographic analyses at other populations of the bluebird's range, since the effects of these covariates on vital rates may differ across populations.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interests.

ORCID

Sara E. Harrod https://orcid.org/0000-0002-1137-883X
Virginie Rolland https://orcid.org/0000-0002-5856-8112

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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