Climate change correlates with rapid delays and advancements in reproductive timing in an amphibian community

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Climate change has had a significant impact globally on the timing of ecological events such as reproduction and migration in many species. Here, we examined the phenology of reproductive migrations in 10 amphibian species at a wetland in South Carolina, USA using a 30 year dataset. We show for the first time that two autumn-breeding amphibians are breeding increasingly later in recent years, coincident with an estimated 1.2°C increase in local overnight air temperatures during the September through February pre-breeding and breeding periods. Additionally, two winter-breeding species in the same community are breeding increasingly earlier. Four of the 10 species studied have shifted their reproductive timing an estimated 15.3 to 76.4 days in the past 30 years. This has resulted in rates of phenological change that range from 5.9 to 37.2 days per decade, providing examples of some of the greatest rates of changing phenology in ecological events reported to date. Owing to the opposing direction of the shifts in reproductive timing, our results suggest an alteration in the degree of temporal niche overlap experienced by amphibian larvae in this community. Reproductive timing can drive community dynamics in larval amphibians and our results identify an important pathway by which climate change may affect amphibian communities.

Keywords: amphibian declines; environmental change; isolated wetlands; phenology; reproductive timing

1. INTRODUCTION

There is growing evidence that the rate of global temperature increases in the past 30 years is greater than at any time in the past two millennia [1]. Climate, most notably temperature and rainfall, directly affects many species via physiological constraints associated with species' tolerances and the seasonal timing of activities such as growth and reproduction. Consequently, there is much interest in the effects of climate change on species that rely on climatic cues for seasonal activities such as migration and reproduction [2]. For example, in areas that have experienced warming, many vernal events now occur earlier than they have in the past [3–6]. By contrast, autumnal events often occur later in recent years, although reports of such phenological shifts are less widespread [2].

Widely reported shifts in life-history phenology of species in many regions have led to concern over possible changes in ecological dynamics and community interactions [2,7–9]. This concern is due in part to the potential for climate warming to affect the coincidence of organisms (*sensu* [10]), due in large part to variation among species in their sensitivity or response to climatic cues. Such variation has led to a mismatch in the timing of previously synchronous life-history events in

interacting species [11–13]. As a consequence, these changes in temporal overlap and resulting effects on predator–prey and competition dynamics may have important implications for populations or community structure [14].

Temperature and rainfall are two climatic factors critical to amphibian physiology and behaviour because of their role in gametogenesis and reproductive migrations [3,15–17]. Previous work has described earlier breeding in several amphibian species in regions that have experienced recent climate warming [3,18,19]. However, discussions continue over the breadth of this phenomenon and its implications for amphibian communities [18,20–24], a dialogue that is hampered by a scarcity of long-term data. Moreover, although the impact of precipitation on amphibian breeding phenology has been incorporated into analyses at least once [23], precipitation is frequently neglected, despite its importance to breeding migrations and pond hydrodynamics.

Here, we analyse a 30 year dataset of amphibian reproductive migrations at a wetland community that has been monitored daily since 21 September 1978. We conducted analyses to determine whether (i) species exhibited significant advancements or delays in reproductive timing across years and (ii) whether reproductive timing in these species was correlated with temperature or rainfall. Our results provide the first evidence of delayed breeding in amphibians and identify some of the fastest

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Table 1. Changes in breeding phenology estimated by linear regression of median arrival date (MAD) on year for 10 amphibian species in a wetland community in SC, USA. Rates reflect differences in estimated MADs between the first and last breeding year analysed for each species. Bold text denotes significance at the $\alpha = 0.05$ level.

species	estimated calendar date of arrival in first year of breeding data analysed	estimated calendar date of arrival in last year of breeding data analysed	estimated change in days	rate of change (days per decade)	N	F	p	R^2
E. quadridigitata	21 Sep 1978	6 Dec 2003	76.4	30.6	14	16.9	**0.0014**	0.58
A. opacum	13 Oct 1981	28 Oct 2007	15.3	5.9	27	7.3	**0.0122**	0.23
A. talpoideum	5 Jan 1979	31 Jan 2008	n.s.	n.s.	30	2.0	0.17	0.07
A. tigrinum	3 Feb 1979	8 Dec 2002	−56.4	−23.5	15	7.5	**0.0168**	0.37
P. ornata	11 Feb 1979	13 Dec 1994	−59.5	−37.2	17	10.4	**0.0056**	0.41
R. sphenocephala	14 Feb 1979	25 Feb 2004	n.s.	n.s.	9	1.3	0.30	0.15
P. crucifer	16 Feb 1979	25 Feb 2004	n.s.	n.s.	20	0.6	0.45	0.03
S. holbrookii	6 Mar 1979	11 Mar 2007	n.s.	n.s.	12	0.1	0.74	0.01
B. terrestris	22 Apr 1979	30 Apr 2008	n.s.	n.s.	25	0.2	0.68	0.01
G. carolinensis	15 Jun 1979	26 Jun 2008	n.s.	n.s.	30	0.83	0.37	0.03

rates of phenological change reported to date. Additionally, owing to the contrasting responses we observed in the study community, our work highlights a rapid increase in temporal niche overlap that may have important consequences for community structure and population persistence in future decades.

2. METHODS

The study site, Rainbow Bay, is a Carolina bay wetland [25] located in a mixed hardwood-pine forest on the US Department of Energy's 780 km² Savannah River Site (SRS) in the Coastal Plain region of South Carolina [26] in the temperate southeastern US (33°15.6′ N 81°37.9′ W; elevation 85 m). Rainbow Bay is approximately 1 ha in size with a maximum water depth of 1.40 m, and typically fills with rainwater in late autumn and dries late each spring or in summer. On 21 September 1978, we completely encircled the wetland with a terrestrial drift fence with pitfall traps and began daily monitoring of all amphibians migrating in and out of the wetland. The drift fence was constructed of aluminium flashing 50 cm high and buried 15 cm in soil with pitfall traps of 40-L buckets spaced every 10 m on each side.

To assess reproductive timing, we calculated the median arrival date (hereafter 'MAD') at the pond for each year from 1979 to 2008 for female *Ambystoma opacum*, *Ambystoma talpoideum*, *Ambystoma tigrinum*, *Bufo terrestris*, *Eurycea quadridigitata*, *Gastrophryne carolinensis*, *Pseudacris crucifer*, *Pseudacris ornata*, *Rana sphenocephala* and *Scaphiopus holbrookii* (table 1). The terrestrial adults of these amphibians migrate yearly to aquatic habitats to breed and lay eggs [26]. Reproductive adults were distinguishable by characters such as nuptial pads, dark vocal pouches, swollen cloacae and presence of eggs. Because these species undertake mass migrations to ponds and wetlands exclusively to breed, their arrival at wetlands has been used as a proxy for reproductive timing similar to the use of calling phenology (e.g. [19,22]). MADs better reflect the overall reproductive phenology of a given population than do first arrival, first calling or first spawning dates [22], all of which may be influenced by the number of animals breeding in a given year (but see [27]). Additionally, the actual timing of oviposition depends on the arrival of females, which may arrive at wetlands days to weeks later than males [28,29].

Most or all individuals of the studied species forewent breeding at Rainbow Bay in some years owing to limited availability of suitable conditions for foraging or for breeding migrations, or because the timing or depth of pond-filling was not appropriate for breeding. [26,30]. Also, a few species declined in number towards the end of the study (see [31] for discussion). We excluded any species-year in which fewer than three (for urodeles) or 10 (for anurans) individuals were captured along the drift fence to avoid analysing species-years with low sample sizes or only incidental captures of animals that were not reproductive. We used a higher cut-off for anurans than urodeles because we had more incidental captures of the former.

We converted calendar dates to breeding-season dates using 1 August as the start of each amphibian reproductive year, which generally follows pond-drying of the previous year and precedes the arrival of pond-filling rains and the beginning of a new year's cohort of larval amphibians. We used separate linear regressions to test the null hypothesis that there was no correlation between MAD and year for each species.

We defined breeding period durations individually for each species as the total number of days it took for females in the 5th through 95th percentile to enter the wetland each year. We then calculated the average number of days it took for this proportion to enter the wetland across all years. We next derived the average MAD for each species across all years; average length of breeding period for each species was then centred on its average MAD. Finally, we calculated average overnight low temperatures (thermal minima) and cumulative rainfall totals during the species-specific breeding periods and the 90 days preceding each breeding period (i.e. 'pre-breeding period'). These periods were fixed across all years, not depending each year on arrival timing in that year, but were unique to each species. We did not use maximum temperatures because these species are nocturnal [17,32,33], and because minimum temperatures are suggested to be more important to their physiology and more predictive of their movements [17,34]. We collected temperature at the wetland using a shaded max-min thermometer and we measured daily rainfall using a rain gauge at the wetland.

To determine the climatic correlates of breeding phenology, we calculated Pearson correlations between the MAD
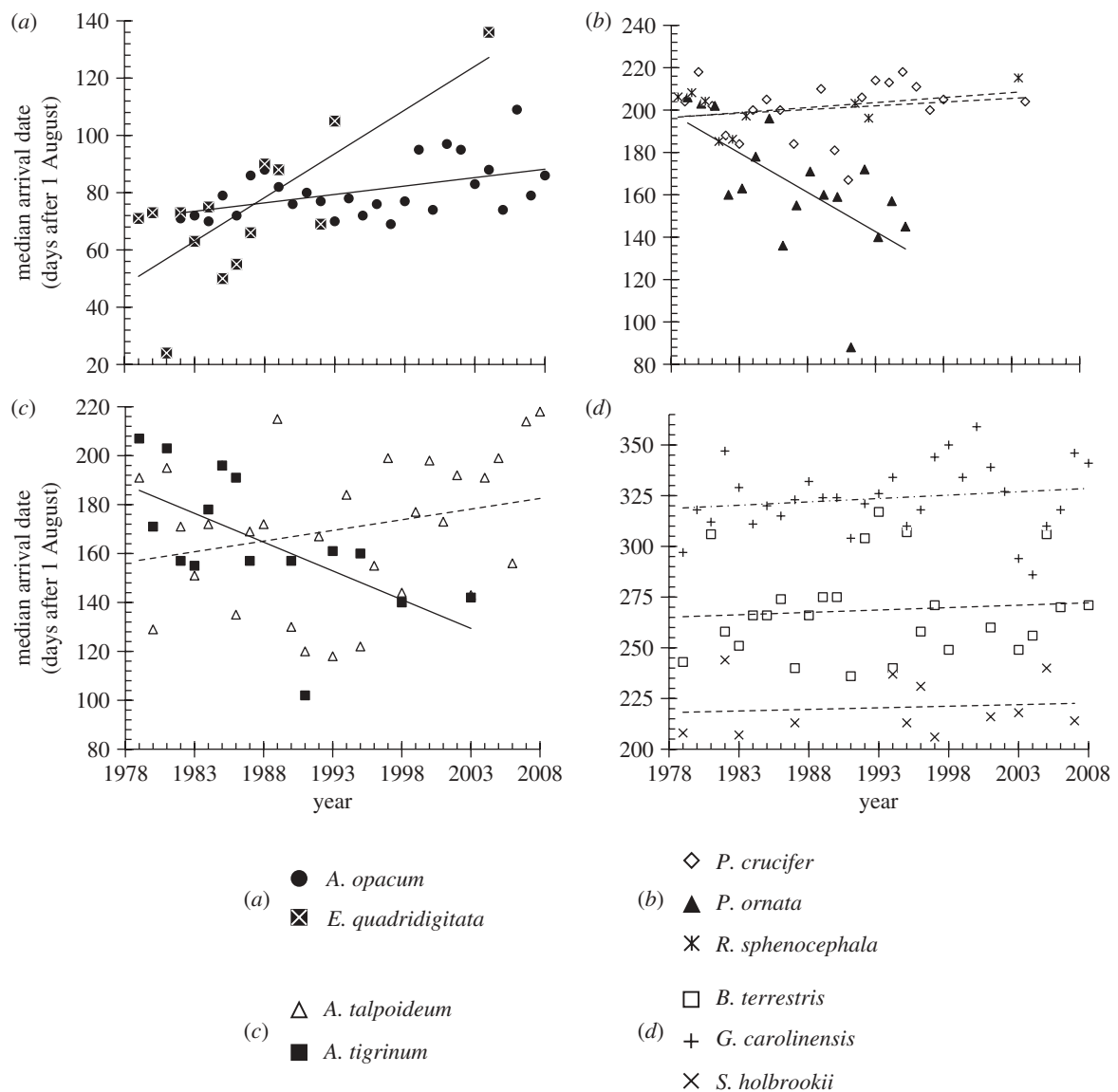
Figure 1. Median arrival dates of (*a*) autumn-breeding urodeles, (*b*) winter-breeding anurans, (*c*) winter-breeding urodeles and (*d*) spring-breeding anurans. Closed symbols with solid trend lines indicate significant shifts in breeding phenology at $\alpha = 0.05$ level. Note that data points were offset in panel (*b*) for clarity.

of each species and mean overnight low temperature and cumulative rainfall during the pre-breeding and breeding periods. We used partial correlations to determine whether changes in breeding phenology across years remained significant after accounting for the effects of both pre-breeding and breeding season rainfall. Finally, we used linear regression to determine whether mean overnight temperatures for the months of September through February changed over time at Rainbow Bay. The September through February period encompasses the pre-breeding and breeding seasons of the four species that showed significant changes in breeding phenology over time. We corroborated field-collected temperatures from Rainbow Bay using local temperature data from a Savannah River National Laboratory weather station 2 km from Rainbow Bay. Mean monthly minimum temperatures at the two sites were highly correlated ($R^2 = 0.98$, $p < 0.0001$). We inspected all data and residuals for assumptions of normality and homogeneity of variances for all analyses. All analyses were conducted using the SAS statistical package (SAS Institute Inc., Cary, NC, USA).

3. RESULTS

Four of the 10 study species (three urodeles and one anuran) had significant changes in MAD since 1979 (figure 1 and table 1). Both autumn-breeding species, *E. quadridigitata* and *A. opacum*, arrived at the wetland significantly later in more recent years whereas two winter-breeding species, *A. tigrinum* and *P. ornata*, arrived significantly earlier in later years. Estimates of the total change in breeding phenology between the first arrival year and the last arrival year for each species varied from as little as 15.3 days for *A. opacum*, to as long as 76.4 days in *E. quadridigitata* (table 1). The corresponding rates of advancement or delay varied from 5.9 to 37.2 days per decade for those species that had significant shifts in MAD (table 1). There were no significant changes in breeding phenology of six species, including *A. talpoideum*, *B. terrestris*, *G. carolinensis*, *P. crucifer*, *R. sphenocephala*, and *S. holbrookii* (figure 1 and table 1).

Minimum overnight temperatures and cumulative rainfall during each species' pre-breeding and breeding

Table 2. Results of Pearson correlations between environmental factors and MADs for 10 amphibian species in a wetland community in SC, USA. Results are also provided for partial correlations between MAD and year after accounting for pre-breeding and breeding season rainfall. Bold text denotes significance at the $\alpha = 0.05$ level.

species	pre-breeding season		breeding season		
	Tmin	rainfall	Tmin	rainfall	year (accounting for rainfall)
E. quadridigitata	0.22	0.48	−0.11	−0.31	**0.73****
A. opacum	**0.42***	−0.20	−0.16	−0.15	**0.45***
A. talpoideum	−0.20	−**0.67****	−0.11	−0.27	0.20
A. tigrinum	−0.01	−**0.57***	−**0.66****	−**0.52***	−0.35
P. ornata	−0.28	−**0.63****	−**0.66****	−0.42	−**0.59***
R. sphenocephala	0.01	−0.65	−0.36	−0.03	0.44
P. crucifer	−0.08	0.01	−0.42	−0.07	0.21
S. holbrookii	−0.50	−0.03	0.04	−0.12	0.12
B. terrestris	−0.03	−0.19	−**0.48***	−0.09	0.10
G. carolinensis	−0.13	−0.19	−0.08	−**0.40***	0.21

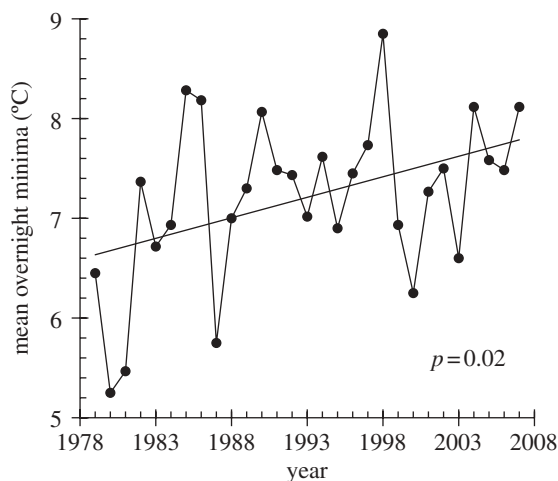* $p \leq 0.05$.
** $p \leq 0.01$.

Figure 2. Change in mean overnight temperature minima during the September through February pre-breeding and breeding periods for which reproductive timing of four species changed significantly.

periods were often correlated with MAD, although the direction, strength and significance of the correlations varied (table 2). Notably, later arrival of both autumn-breeding species was positively correlated with warmer overnight temperatures during the pre-breeding season, although the correlation was only statistically significant for *A. opacum* (table 2). For the two winter-breeding species that had significant shifts in phenology, earlier arrivals were correlated with warmer overnight temperatures during the breeding season and increased rainfall during the pre-breeding and breeding seasons (table 2). Warmer overnight temperature during the breeding season was also correlated with earlier arrival in *B. terrestris*, greater rainfall during the breeding season was correlated with earlier arrival in *G. carolinensis*, and greater rainfall during the pre-breeding season was correlated with earlier arrival in *A. talpoideum* (table 2).

Partial correlations accounting for effects of rainfall on arrival dates showed that three of the four species (*E. quadridigitata*, *A. opacum*, and *P. ornata*) had arrival dates that remained significantly correlated with year,

indicating that rainfall alone could not account for the observed changes in phenology of those species (table 2). A regression analysis of mean overnight temperatures for 1 September to 28 February, the pre-breeding and breeding period during which four species showed significant changes in phenology, revealed that overnight minima for that period increased significantly by an estimated 1.2°C from 1979 to 2008 ($p = 0.02$; figure 2).

4. DISCUSSION

Here, we show that reproductive timing of four amphibian species at a wetland in the southeastern US has shifted significantly over the past 30 years. These results are noteworthy for several reasons. First, we provide the first evidence of delays in reproductive timing of amphibians (cf. [27], table 1). Several studies have demonstrated the advancement of reproductive timing in vernal-breeding amphibians in areas ranging from mainland Europe (e.g. [22]) and the UK (e.g. [3,18]) to North America [19] and Japan [27]. However, ours is the first to demonstrate that some autumn-breeding species have delayed breeding as local climate has warmed. The delay that we observed in the arrival of two autumn-breeding amphibians is consistent with studies of other ecological phenomena that occur in the autumn. For example, although less commonly reported, studies have identified that events such as leaf colouring and autumnal leaf drop takes place later in recent warmer years than in previous cooler years [6,35], resulting in lengthened growing seasons (reviewed by [36]).

In addition to reporting previously unseen delays in amphibian breeding, our results underscore the ecological sensitivities of amphibians to their environment. Specifically, the estimated rates of phenological change of 5.9 to 37.2 days per decade represent some of the greatest rates of change in ecological phenomena reported to date, surpassing those of other taxa and even those reported previously for amphibians (cf. [2,37]). The rapid tracking of environmental conditions by amphibians is probably a result of the importance of temperature and moisture to these species [15], a factor possibly reflected

in the correlations between arrival dates and climatic factors in several species. In a meta-analysis of 203 phenology studies, Parmesan [37] identified that amphibians exhibited the greatest phenological responses of all taxa. Consequently, amphibians are likely to be increasingly valuable in understanding or monitoring the impacts of climate change on ecological communities.

Our results provide important additional insights into the study of the effects of climate change on amphibians. For example, despite the broad latitudinal gradient of previous studies that found significant advancements in amphibian reproduction (ranging from 35°37′ N to 53°12′ N; [27] and [22], respectively), we identified shifts in amphibian reproductive timing at the lowest latitude yet (33°15.6′ N). Evidence of such rapid phenological change in lower temperate latitudes is surprising given that the effects of climate change are expected to be most pronounced at high latitudes where the growing season is shorter and where many species are at the colder limits of their geographical ranges [3,38,39]. Nonetheless, the rates of change in reproductive timing seen here in *E. quadridigitata* and *P. ornata* surpass those of several species studied in colder northern climates (e.g. [20]: 42°N–46°N; [19]: 42°N). It will be important to continue to study the effects of climate change on species even in lower latitude regions.

Other studies have found that not all amphibian species change reproductive timing, consistent with our findings for six species here [19,20]. Altogether, these results demonstrate that populations, and even species in the same community, will vary in their responses. This variation may be due in part to differences among species in physiology or ecology (e.g. [17]), such as the time of year during which they breed, as well as the type and degree of climate change experienced regionally. In our current study, more than half of the species studied showed no significant change in arrival dates in the 30 year period. Five of the species that did not change reproductive timing were normally the last to arrive at the wetland each year and were among those least likely to have arrival dates that correlated with environmental factors (tables 1 and 2). Thus, increases in temperature may have a greater effect on the timing of early breeders, whereas later breeders may rely more on other cues such as photoperiod, may be less sensitive to environmental variables overall, or may be less constrained by temperature because temperatures are more moderate when they breed. Nevertheless, species that did not shift reproductive timing may still encounter indirect effects from altered reproductive timing in other species in their community.

Reproductive timing in amphibians affects population trends and long-term persistence via larval interactions and effects on juvenile recruitment [40]. In previous studies, changes in the order or timing of species introduction of as little as two weeks altered the outcome of competitive interactions and predator–prey dynamics [41–44]. The changes in breeding phenology of 15.3–76.4 days documented here suggest a shift in the temporal niche overlap of larvae in the wetland, driven by delayed arrival of autumn-breeding species and earlier arrival of two species that breed afterward. Such a shift may be sufficient to alter interactive outcomes of amphibian larvae based on earlier work, including studies on some of

these species from this same locale [42]. Moreover, even species that exhibit no shift in reproductive timing must contend with shifts by other members of the larval community that may affect resource availability or competition and predation rates [40,45].

It is difficult to separate the effects of altered reproductive timing on amphibian populations at Rainbow Bay from those of changes in other factors such as pond hydroperiods, algal or zooplankton densities, or vegetation in the area [26,30,31]. An analysis of population trends up to 2004 reported declines in the number of female *A. tigrinum*, *A. talpoideum*, *P. ornata* and *R. sphenocephala*, and an increase in the number of female *A. opacum* breeding at Rainbow Bay [31]. Additionally, in the current study, only six female *E. quadridigitata* were captured at Rainbow Bay from 1994 to 2003, and the last time the population numbered above 100 females was in 1988 [46]. It would be premature to assume that alterations in reproductive timing have contributed to changes in amphibian population sizes at our study site. Broader monitoring of reproductive timing and population trends in amphibian communities at Rainbow Bay and additional nearby sites over the coming decades could provide valuable insights into the relationships between phenological change and community structure and population persistence.

Temperature and rainfall are important determinants of amphibian breeding, and the changes in reproductive timing that we observed have several environmental correlates. There has been a significant increase in minimum overnight temperatures during the September–February pre-breeding and breeding periods at Rainbow Bay. And, the shift in breeding phenology for three species remained significant after accounting for rainfall, suggesting that changing temperature or other unquantified factors better correlate with these changes through time. However, movements of many amphibians are correlated with rainfall (e.g. [15,17]), and in one species (*A. tigrinum*), the trend of earlier arrival in recent years did not remain significant after rainfall was accounted for, suggesting the covariance of rainfall with year alone was sufficient to explain changes in breeding phenology. Though the importance of precipitation in amphibian breeding phenology has been identified before [15,23], we feel that this mechanism is largely ignored. Typically, concern over the importance of rainfall to amphibian communities is relegated to its effects on hydroperiod and juvenile recruitment (e.g. [31,47]). Because changes in precipitation patterns may accompany changing temperatures [48], more attention should be given to possible effects of altered precipitation on phenology of amphibians and other taxa.

by the DOE's Set Aside Programme and status of the SRS as a National Environmental Research Park (NERP). B.D.T. and D.E.S. conceived the topic and designed the analyses with J.H.K.P. D.E.S. performed statistical analyses and, along with J.H.K.P., collected and managed data during most of the study. J.W.G. was involved in initiation of the project in 1978. All authors collected field data during parts of the study and all contributed to the manuscript.

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