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A reversal of the shift towards earlier spring phenology in several Mediterranean reptiles and amphibians during the 1998-2013 warming slowdown

Running head

Reversal of shift towards earlier phenology

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Warming pause or hiatus, appearance date, hibernation, activity period, North Atlantic

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Type of paper

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Abstract

Herps, especially amphibians, are particularly susceptible to climate change, since temperature tightly controls many parameters of their biological cycle – above all, their phenology. The timing of herps' activity or migration period – in particular the dates of their first appearance in spring and first breeding – and the shift to earlier dates in response to warming since the last quarter of the 20th century has often been described up to now as a nearly monotonic trend towards earlier phenological events.

In this study, we used citizen science data opportunistically collected on reptiles and amphibians in the northern Mediterranean basin over a period of 32 years to explore temporal variations in herp phenology. For 17 common species, we measured shifts in the date of the species' first spring appearance – which may be the result of current changes in climate – and regressed the first appearance date against temperatures and precipitations. Our results confirmed the expected overall trend towards earlier first spring appearances from 1983 to 1997, and show that the first appearance date of both reptiles and amphibians fits well with the temperature in late winter. However, the trend towards earlier dates was stopped or even

reversed in most species between 1998 and 2013. We interpret this reversal as a response to cooling related to the North Atlantic Oscillation (NAO) in the late winter and early spring.

During the positive NAO episodes, for certain species only (mainly amphibians), the effect of a warm weather, which tends to advance the phenology, seems to be counterbalanced by the adverse effects of the relative dryness.

Introduction

One of the most evident responses of terrestrial plants and animals to global warming in the northern hemisphere over the last decades is the shift towards earlier spring phenology (Walther, 2002; Parmesan & Yohe, 2003; Parmesan, 2007; Ovaskainen, 2013). This observed warming-related phenological shift is often described as a progressive advance over the years (generally adjusted to linear functions) in the first date of breeding or the first observation of a species in the spring. Meta-analyses have estimated that across a set of 1700 species, phenology advanced by 2.3 days decade⁻¹ (Parmesan & Yohe, 2003), and by 5.1 days decade⁻¹ when considering a subset of plant and animal species showing substantial change (>1 day decade⁻¹) (Root *et al.*, 2003). Among the amphibians, which are considered the most responsive to climate change, the mean advance of spring phenological events is estimated to be -7.6 ± 3.09 (maximum -34) days decade⁻¹ (Parmesan, 2007), or -6.9 ± 1.65 (maximum -41.9) days decade⁻¹ (While & Uller, 2014). Yet these mean values conceal large variations between species. Some species show no trend towards earlier phenology, while a few others exhibit delayed phenology (Corn, 2005; Todd *et al.*, 2011; Arnfield *et al.*, 2012; Walpole *et al.*, 2012; Klaus & Loughheed, 2013). Data on amphibians regarding these trends is relatively plentiful; however, data on reptiles is much rarer. In reptiles, the advance is estimated to be -0.36 days yr⁻¹ for *Zootoca vivipara*, and about -0.79 days yr⁻¹ for *Vipera aspis* (Ovaskainen *et*

al., 2013; Rugiero *et al.*, 2013). Yet comparative studies of amphibians vs. reptiles in the same geographical area are still lacking. Moreover, whether these phenological shifts are the result solely of temperature increase or due to other climatic variables is still under discussion (e.g. Arnfield *et al.*, 2012; Green, 2016).

The response of a given species to climate warming has often been modelled by calculating linear regressions of the date of a given phenological event against years (e.g. Blaustein *et al.*, 2001; Todd *et al.*, 2011; Walpole *et al.*, 2012; Rugiero *et al.*, 2013; Ovaskainen, 2013). Yet the prediction of a continuous warming has been challenged by the observation of an apparent pause in the increase of average world temperatures from 1999 to 2008 (Kerr, 2009), and particularly in Eurasia from 1998 to 2013 (Li *et al.*, 2015). Several studies have shown that this pause had a significant impact on plant phenology. Remote sensing data shows, for instance, that first leaf appearance shifted to an earlier date between 1982 and 1991 in boreal Eurasia and North America, but that this trend reversed after 1994 (Delbart *et al.*, 2006). In western Central Europe, the spring phenology of 31 plant species significantly advanced during the 1982–2011 period at an average rate of $-0.45 \text{ days yr}^{-1}$, but this shift was not monotonic; cooling in late winter resulted in a slowdown, and even a reversal, of the shift between 2000 and 2011 (Fu, 2014). In the Mediterranean, a continuous advance in the first flowering date of olive trees up to the late 1990s was followed by a relatively stationary time series. This change correlated to a temperature fluctuation in the Mediterranean area that has been explained by the North Atlantic Oscillation (NAO), a large-scale atmospheric phenomenon (Orlandi *et al.*, 2012). Close relationships between variations in the NAO and the phenology of amphibians have been demonstrated in Northern Europe (Forchhammer *et al.*, 1998). Yet to date there are still few published observations on possible recent slowdowns or reversals of the general trend towards earlier animal phenology.

In our study, we examine the phenology of the most common amphibian and reptile species in the French Mediterranean region over a 32-year period. To this end, we used a database containing opportunistic observations from more than 3000 volunteer naturalists in southern France, the vast majority of which were amateurs. In published literature, the first breeding date of amphibians is often documented, since their breeding grounds are concentrated and easy to survey, but is documented more rarely for reptiles, whose reproduction sites are diffuse and difficult to find. For this reason, we focused on the date of the first spring appearance (i.e. annual onset of spring activity, which marks the end of hibernation), a parameter that allowed us to compare amphibians and reptiles on the same basis. For each species, we first tested whether or not there was a shift in the annual onset of spring activity over the 32-year interval. We then tested if a shift in the first appearance date of certain species seemed to result from temperature changes alone, or might also be explained by additional factors such as precipitation or sampling effort. The latter is believed to greatly influence the measurement of first appearance dates, especially in the case of opportunistic citizen data (Van Strien *et al.*, 2013).

Materials and methods

Data selection

The database we used for this study was first created in 1970 and has been managed since then by our laboratory (Geniez & Cheylan, 2012). It includes over 120,000 records of 59 amphibian and reptile species (native or introduced). It covers the area in the south of France between the Rhône River and the Pyrenees mountain range. Each data entry is checked and validated by the database managers before being included. No sampling design is imposed on observers as regards to the distribution of time effort. Attempts are made to ensure that the

sampling effort covers the entire study area by collaborating with naturalist societies in each French administrative department in the area. Despite this, sampling has considerably varied in space, generally decreasing in pressure from the well-sampled Mediterranean plains to the less-sampled hinterlands.

In this database, we first defined a spatial area restricted to 9 departments (Ardèche, Aude, Aveyron, western Bouches-du-Rhône, Gard, Hérault, Lozère, Pyrénées-Orientales and Tarn). We then restricted this further to elevations lower than or equal to 900 m in order to limit the data to the Mediterranean domain. Within the resulting study area, covering about 44,500 km², the climate can be considered relatively homogeneous and Mediterranean in a broad sense.

We used the data for this study area from 1983 to 2014. In this space-time window, sampling effort increased irregularly over the years, but its variations were roughly parallel in all departments except one (Ardèche).

Given this space-time window, we further constrained the data to species that had more than 1200 records in the database. From this subset of species, we excluded *Tarentola mauritanica*, a species that has rapidly expanded in the area, probably due to anthropogenic transport during the time interval of the study, frogs of the genus *Pelophylax* due to difficulty in the field identification of the three species of this genus present in the area, and *Salamandra salamandra*, an autumn breeder with minimum observations in August since its resting season is in summer rather than winter. The 17 common species we considered in our study were (by decreasing number of records) *Lacerta bilineata*, *Podarcis muralis*, *Bufo bufo*, *Hyla meridionalis*, *Malpolon monspessulanus*, *Timon lepidus*, *Bufo calamita*, *Podarcis liolepis*, *Natrix maura*, *Lissotriton helveticus*, *Pelodytes punctatus*, *Psammodromus algirus*, *Rhinechis scalaris*, *Alytes obstetricans*, *Natrix natrix*, *Hierophis viridiflavus* and *Zamenis*

longissimus. There is no clear evidence of a decline of the amphibians during the study period (Crochet et al., 2004), but *Timon lepidus* decreased unambiguously in a study plot (La Crau plain; Cheylan & Grillet, 2004), and the snakes show unquantified signs of decline (pers. obs.). We discarded observations of eggs, juveniles or tadpoles, but included individuals crushed on roads despite the resulting imprecision of a few days on their date of death. The resulting final dataset for the analysis was based on 54,125 total records, ranging from 6286 records for *L.bilineata* to 1352 records for *Z. longissimus*. (Fig. S1).

Spring appearance dates

We considered the first spring day of sighting of a given species by observers as a proxy of its onset of activity after the resting period. The origin of the date axis was set at 1 January (day 1 of the year), which falls in the inactivity period of both amphibians and reptiles; the minimum number of records occurred in late December.

The date of a first recorded appearance of the year is likely to depend on sampling effort (Van Strien *et al.*, 2013). As we relied on presence-only data, without repeated visits to most of the sites, we defined the appearance date of a species as the date (day of the year) on which 5% of the observations of this species were recorded, i.e. the fifth percentile of the distribution of the year's records (Arnfield *et al.*, 2012).

Environmental variables

The climate variables (temperature and rainfall) were averaged from four stations distributed over the study area (in Montpellier, Nîmes, Perpignan and Carcassonne). This data was provided by the national agency "Meteo France".

We used the average maximum daily temperature for February–March since the peak of the appearance date accumulation rate for the whole dataset was on day 63. Preliminary tests showed that the February–March daily maxima (T_{maFM}) resulted in a generally better fit for the models than the daily minima, and the February–March values provided a better fit than those of January–February (the average appearance date of 13 species was in February–March; the appearance date for the remaining four species was at the beginning of April).

We quantified the precipitation in two different ways: (i) we first use the monthly cumulative values (measured in mm); but these values alone do not give a precise idea of rainfall distribution over time in the beginning of the year. (ii) we thus calculated the date (day of the year) when the cumulative rainfall reaches a given threshold for each year; we chose a threshold of 117 mm, which corresponds to the mean value of the cumulative rainfall from day 1 to 63 each year calculated over the 1983–2014 interval.

We also considered a large-scale climate indicator, the North Atlantic Oscillation index (NAO_i), which is calculated from the normalized pressure difference between the Azores and Iceland and is an important predictor of the climate in Western Europe, especially in winter (Hurrell, 1995). The values of the NAO winter index were downloaded from the website of the National Oceanic and Atmospheric Administration, and its annual variations were compared to that of temperature and precipitation in the same season.

We used the total number of records per year (N_{obs}) of all species taken together as a proxy of the sampling effort.

Modelling

Fitting phenological time series with linear regression models to measure changes – as is often done – can be misleading because the variation may not be linear over time (Dose & Menzel, 2004). Thus, for each species, we explored the variation in first appearance dates

over the years using generalized additive models (GAM) with no constraints on smoothing terms. In these models, the linear predictor depends on unknown smooth functions – which can be nonlinear – of predictor variable(s). The shapes of predictor functions are fully determined by the data (in parametric functions the shape is defined by a small set of parameters). GAMs allow more flexible estimation of the underlying predictive pattern than parametric modeling. They reveal more complex patterns of temporal variation than strictly linear trends, and provide better fit to data, with testing procedures (*P-values*). Moreover, on limited segments of the appearance date–year graphs, we measured the responsiveness of a given species to climate change by the slope of the corresponding linear model, which is a straightforward measure of shift speed.

We then used generalized linear models (GLM) to test the impact of selected environmental variables on the appearance date per year and per species. We fitted a set of models for each species in order to identify which variable was the best predictor of appearance date. These models include, for each year, the mean February–March daily maximum temperature, the cumulative rainfall in February–March, the date when cumulative rainfall reached the 117-mm threshold, and the number of records in the study area. We tested several additive or interactive combinations of temperature with precipitation (either cumulative or date-threshold rainfall) and with the number of observations. The impact of the NAO index, which summarized the weather type of the period, was tested alone.

Model comparison and selection was based on the Akaike information criterion (Burnham & Anderson, 2004). All analyses were performed using R software (R Core Team, 2016). The GAMs were fitted using library(mgcv) (Wood, 2006).

Results

In the defined study area, sampling effort increased from about 900–1000 records yr⁻¹ in 1983–84 to culminate at about 10,000 records yr⁻¹ in 2013–14. The sampling effort was 1.86 records km⁻² on average, but varied by a factor of 10 depending on the department (from 3.4 records.km⁻² in Hérault to 0.3 in Aveyron) (Fig.S1).

On average, reptiles and amphibians first appeared in spring 17 days earlier in 2014 than in 1983 (Table 1). The difference between amphibians (20 days earlier) and reptiles (15 days earlier) was not significant (one-way ANOVA, $F_{1,15} = 1.013$, $P = 0.33$). Thus, the first appearance dates advanced over this period at an average rate of 0.56 days yr⁻¹. However, the overall trend was far from linear.

Six of our species (*Bufo bufo*, *B. calamita*, *Hyla meridionalis*, *Psammodromus algirus*, *Podarcis liolepis*, *Rhinechis scalaris*,) do not show any significant variation of their appearance date during the 32-year interval, because of their low responsiveness to climate variations, or of the insufficient quality of the data. In a first period (from 1983 to 1997; cf. Fig. 1 and 2, and Table 1), almost all the other species, reptiles as well as amphibians, showed a rapid shift towards earlier dates. For nine species, this rapid shift can be considered linear, from about two days yr⁻¹ earlier for *Timon lepidus* to more than four days yr⁻¹ for *Malpolon monspessulanus* and *Natrix natrix*. This shift reached the extreme value of 4.7 days yr⁻¹ for *Alytes obstetricans*, whose first appearance was 54 days earlier in 1993 than in 1983. But from 1997 onwards, the pattern differed depending on the species. Out of the 17 species studied, 11 species showed a pause or a reverse temporal shift that, in certain cases, returned the first appearance date in 2013 to a date not far from that of 1983 (see Fig.1 and Fig. 2). Although the smoothing terms of the GAMs were unconstrained, most of the models converge on quadratic patterns, with a minimum of the appearance date situated between

1993 and 2002 (average 1997). The significance of this temporal pattern is shown by the confidence intervals of the estimates of the generalized additive models linking the appearance date to the year on the figures (Table 1).

Relationship with environmental variables

If the mean annual temperature in the study area stabilized or only slightly increased from ~1997 (the year with the warmest and driest early spring) following a 15-year period of rapid warming, the average temperature in February–March significantly decreased from ~1997, such that the climatic conditions of late winter and early spring in 2010 were relatively similar to those of 1987 (Fig. 3). The reversal of the phenological shift from an earlier first appearance date to a later first appearance date that we observed from 1998 onwards in several of the studied species (Fig. 1 and Fig. 2) mirrors the decreasing late-winter/early-spring temperature since that date.

The correlation between first appearance dates and average daily maximum temperatures in February–March was significant for all species at the $P = 0.05$ level, and for 12 species at the $P = 0.01$ level (Fig. 4). A species first appeared in spring on average 6.35 days earlier for every 1 °C increase in temperature, with variation between species: from 4.5 days degree⁻¹ for *P. punctatus* to more than 9 days degree⁻¹ for *A. obstetricans* and *R. scalaris*. The responsiveness of a species to temperature change (i.e., the shift speed) appeared uncorrelated with their appearance date in the year ($r = 0.11$, $P = 0.66$).

Only five species (including three amphibians) showed a precipitation effect in the best model predicting first appearance date, but in complement to the temperature (which remains the main effect), and preferentially in the form of the date of the 117-mm rainfall threshold (Tables 1 and 2). The correlation between the first appearance date and the NAO index was significant at the $P = 0.05$ level for all reptile species except *H. viridiflavus*, and was not

significant for any amphibian species except *H. meridionalis*. In the study area, the NAO index is significantly correlated, positively with the temperature, negatively with the precipitations (Fig. 5). However, local temperatures and precipitations are more relevant than this large-scale climatic index to predict the appearance dates.

Discussion

In contrast to what one might expect, the first appearance date was not affected by the large variation in sampling effort over the years, probably because we used a fifth-percentile criterion that reduced the influence of extreme values. This lack of a sampling effect is illustrated (i) by the fact that the delay in recorded appearance dates after 1997 actually coincides with an increase in the annual number of records, (ii) by the non-selection of the term related to the sampling effort in the models (Table 2). A decrease in populations of certain reptiles during the study is likely (not for amphibians: cf. Crochet *et al.*, 2004), but it was probably offset by the increase of the sampling effort. The definition of the appearance date of a species as the fifth percentile of the distribution of the year's records should minimize the potential impact of change in population sizes over years. We do not think that a progressive population size decrease, if it exists, might generate an artefactual linear relationship between appearance date and temperature. Our results confirm the possibility of using opportunistic data collected by numerous observers – including a majority of amateur volunteers – for detecting climate-induced changes in animal phenology (Breed *et al.*, 2013), despite substantial differences in species detectability, large variation in sampling effort, possible variations in numbers, and an absence of explicit sampling design.

We found that Mediterranean amphibians and reptiles respond without any time lag to variations in early spring temperatures, with shifts of their appearance dates of up to nine days

earlier for every 1 °C increase in temperature (average 6.35 days). These are within the upper range of values reported in the literature for spring phenological events (including first appearance or breeding) of reptiles or amphibians: eleven values in the literature range from 1 to 6 days degree⁻¹, with a maximum of about 9 days for the parturition date of *Vipera aspis* (calculated from Lourdaïs *et al.* in Le Galliard *et al.*, 2012). These values are also within the range reported for plant phenology in the Mediterranean (Gordo & Sanz, 2009). In our subset of species, reptiles did not differ from amphibians in temperature sensitivity, though the latter are often considered to be more sensitive to temperature change (Parmesan, 2007). Reptiles even appear to be better thermal markers than amphibians, due to their lower sensitivity to precipitation.

Despite our study area's relatively southern location, where phenological shifts are thought to be attenuated with respect to northern latitudes (While & Uller, 2014), the rates of shifts towards earlier dates that we observed in 1983–1997 (e.g. *M. monspessulanus* -4.5 days yr⁻¹ and *A. obstetricans* -4.7 days yr⁻¹) are greater than the shifts in breeding dates reported in previous literature (e.g. -7.6 ± 3 days decade⁻¹, with a maximum of -34 days decade⁻¹, for 13 amphibian species (Parmesan, 2007); -5.9 to -37.2- days decade⁻¹ for 10 amphibian species (Todd *et al.*, 2011); -6.09 days decade⁻¹ on average, with a maximum of -41.9, for 21 amphibian species (While & Uller, 2014). The rapid shifts we observed were likely due to particularly rapid warming in 1983–1997, which affected a large variety of ecosystems (Reid *et al.*, 2016; Chmielewski & Rötzer, 2002; Gordo & Sanz, 2005; Conversi *et al.*, 2010).

Less documented in previous studies is the reverse trend we observed in 1998–2013, a period during which warming slowed down or even stopped (Kerr, 2009), especially in Eurasia (Li *et al.*, 2015). One study shows that in boreal Eurasia, the date of first leaf appearance shifted earlier between 1982 and 1991, but this trend was reversed after 1994 (Delbart, 2006). In another study, (Arnfield *et al.*, 2012), in contrast to the majority of studies on amphibian

phenology, observed a shift towards later timing of breeding of *Bufo bufo* over the period 1998–2010 in the UK, correlating to a decrease of the average temperature in January–February. And in western Central Europe, a reversal in the advancement of leaf unfolding dates in 2000–2011 has been related to a cooling trend in late winter (Fu *et al.*, 2014).

The main reason for this late winter cooling and subsequent phenological reversal is the large-scale atmospheric phenomenon of the North Atlantic Oscillation (NAO), whose effects reach the Mediterranean basin (Orlandi *et al.*, 2012). The rapid warming experienced in 1983–1997 correlates to an exceptionally strong positive NAO phase (Hurrell, 1995), and the following late winter cooling correlates to a negative NAO phase. Although the responses to temperature variations of both amphibians and reptiles (both terrestrial and aquatic) in southern France have remarkably similar patterns, and thus appear to be largely unrelated to life history traits or phylogenetic relationships (cf. While & Uller, 2014), we detected differences in their responses to large-scale climatic fluctuations: the warm, dry weather associated with positive NAO episodes in the western Mediterranean (Fig. 5) results in an earlier appearance date in most reptiles, but not in most amphibians. The effect of precipitation (taking into account its distribution over time) on phenology is limited to five species, of which three amphibians, probably because of their dependence on water for reproduction. This confirms the limited effect of cumulative precipitation on the phenology of most species reported by other studies (Arnfield *et al.*, 2012; Ovaskainen *et al.*, 2013; While & Uller, 2014).

The ambiguous response of amphibians to positive NAO episodes in our study area differs from findings in northern Europe, where these episodes correlate to mild, wet weather, favouring early first appearance dates for all amphibian species (Forchhammer *et al.*, 1998). The effect of the warm weather associated with a positive NAO index in the northern Mediterranean, which tends to advance both animal and plant phenology (Gordo & Sanz,

2010), seems to be counterbalanced by the adverse effects of the relative dryness in these periods. A partial offset of the effects of a temperature increase by the effects of a drought increase has also been described for the vegetation (Lempereur *et al.*, 2016). This hypothesis is supported by the opposite sign of temperature and precipitation variables, even if not significant, in the models that concern these species. In any case, our results confirm that local climatic variables are better predictors of first appearance dates than are large-scale climate indices (Forchhammer *et al.*, 2004).

Rapid and reversible shifts in appearance dates, which range within species' phenotypic plasticity, may allow temperature variations to be tracked, but they are not necessarily adaptive (Charmantier *et al.*, 2008; Benard, 2014; Urban *et al.*, 2014; Duputié *et al.*, 2015). Warming itself could have negative consequences on survival or on fecundity through time lags in trophic cycles, increased exposure to spring cold spells, drought or disease (Parmesan, 2007; Reading, 2007; Neveu, 2009; Blaustein *et al.*, 2010). We confirm that series longer than 30 years are necessary to clearly separate the effects of long-term anthropogenic warming from decadal fluctuations (Corn, 2005; Green, 2016). The 1998-2013 warming slowdown, with a cooling of late winter, is a relatively rare climate event, but it does not call into question the secular warming trend (Easterling & Wehner, 2009; Li *et al.*, 2015; Yao *et al.*, 2015). The nonlinearity of warming over time, the asynchrony of seasonal changes, the fact that the negative correlation between temperature and precipitation observed in the western Mediterranean during the climate fluctuations since the mid-20th century may not persist in the longer term (Camuffo *et al.*, 2010), together with the multiplicity of the biological consequences of warming: all these factors impair sound predictions of the consequences of future climate change on Mediterranean amphibians and reptiles.

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Figure legends

Fig. 1. Variations of the first appearance dates (given as the day of the year) of nine species of reptiles from 1983 to 2014. The values are fitted to generalized additive models. Predicted values (continuous lines) are shown with their 95% confidence interval (dotted lines).

Fig. 2. Variations of the first appearance dates (given as the day of the year) of six species of amphibians from 1983 to 2014 (see legend of Fig. 1).

Fig. 3. Temporal trend in late winter temperature over the study area (mean daily maximum temperature for February–March).

Fig. 4. Examples of the relationships between first appearance dates (day of the year; ordinates), mean daily maximum temperature in February–March (left column) and the NAO index (right column) for three species of reptiles, with their linear adjustments (see Table 1).

Fig. 5. Relationships between the mean daily maximum temperature for February–March in the study area (a), or the cumulated precipitation for the same period and the same area (b), with the NAO index (linear relationships: (a) $T_{\max FM} = 1.38 * NAO + 13.47$; $r = 0.68$; P -value < 0.001 ; (b) $precipitation_{FM} = -16.22 * NAO + 52.58$; $r = 0.52$; P -value < 0.01).

SPECIES	ALYOBS	BUFBUF	BUFCAL	HYLMER	LISHEL	PELPUN	HIEVIR	LACBIL	MALMON	NATMAU	NATNAT	PODLIO	PODMUR	PSAALG	RHISCA	TIMLEP	ZAMLON
Number of records	1596	5416	3150	5044	2578	2436	1394	6286	4463	2944	1429	3051	5964	2096	1712	3214	1352
mean appearance date	56	54	64	60	42	41	102	89	88	103	96	70	58	81	75	86	106
gam~year (<i>P</i> -value)	<0.001	0.256	0.388	0.877	0.045	0.006	0.118	<0.001	<0.001	0.011	0.052	0.495	0.024	0.616	0.136	0.028	0.089
gam~year (% variance)	63.7	20.6	4.0	0.1	22.3	39.1	34.8	53.2	70.7	38.5	32.2	7.1	33.2	0.8	41.6	26.6	31.7
shift.1983-2014 [days]	-43.07	-20.37	-9.74	-1.39	-27.63	-19.59	-21.87	-19.85	-32.37	-18.85	-10.82	-1.63	-13.42	-4.65	-11.21	-17.06	-10.46
shift.max [days]	-54.46	-21.77	-9.83	-1.44	-27.88	-37.35	-26.08	-31.34	-52.14	-31.31	-34.19	-9.94	-37.07	-4.81	-40.17	-20.04	-27.07
shift.max [days yr ⁻¹]	-5.45	-0.70	-0.32	-0.05	-0.90	-2.20	-0.84	-2.41	-3.48	-2.24	-2.63	-0.71	-2.65	-0.16	-5.02	-1.05	-1.93
slope.1983-97 [days yr ⁻¹]																	
coeff.	-4.69	-1.63	-1.82	-1.02	-2.28	-3.46	-3.67	-2.82	-4.52	-2.57	-4.32	-2.13	-3.04	-1.54	-3.85	-1.93	-2.88
<i>P</i>	<0.005	>0.1	>0.1	>0.1	<0.1	<0.005	<0.05	<0.001	<0.001	<0.05	<0.001	>0.1	<0.1	>0.1	<0.1	<0.05	<0.01
TmaFM [days degrees ⁻¹]																	
coeff.	-9.17	-5.52	-6.01	-6.27	-5.44	-4.53	-5.3	-6.04	-6.41	-6.41	-7.11	-5.48	-8.92	-4.96	-9.67	-6.24	-4.47
intercept	197.36	132.47	145.87	148.7	126.02	109.08	181.86	172.16	184.22	184.22	196.25	144.11	178.87	150.7	228.06	177.71	174.08
<i>P</i>	<0.001	<0.01	<0.01	<0.001	<0.05	<0.05	<0.05	<0.001	<0.001	<0.001	<0.005	<0.05	<0.001	<0.01	<0.005	<0.001	<0.05
naoFM [days index ⁻¹]																	
coeff.	-9.15	-4.36	-5.70	-7.61	-1.33	-1.44	-4.64	-9.10	-10.9	-8.43	-9.15	-12.52	-15.67	-8.14	-18.27	-7.00	-7.59
intercept	72.49	56.88	63.87	63.81	50.35	46.24	109.4	91.06	86.47	97.78	100.22	72.2	59.95	84.36	99.7	93.07	114.47
<i>P</i>	<0.1	>0.1	>0.1	<0.05	>0.1	>0.1	>0.1	<0.001	<0.01	<0.05	<0.1	<0.01	<0.01	<0.05	<0.005	<0.05	<0.05

Table 1: Shifts in the first spring appearance date of amphibian and reptile species and their relationship with temperature and climate. Negative values correspond to shifts towards earlier dates.

Mean appearance date in the 1983-2014 interval (days of the year).

GAM~year (*P*-value): significance of the smooth term of the generalized additive model linking the appearance date to the year.

GAM~year (% variance): percentage of variance of the appearance date explained by the gam above (in %).

shift.1983–2014: shift in first appearance dates between 1983 and 2014 (number of days).

shift.max: maximum shift in first appearance dates between 1983 and the year with the earliest date.

The two values above are calculated from the smoothed mean values provided by the gam above.

slope.1983–97: linear shift in first appearance dates with years during the 1983–1997 period of rapid warming.

TmaFM: coefficients of the model predicting first appearance dates from the mean daily maximum temperature in February–March.

naoFM: coefficients of the model predicting first appearance dates from the mean North Atlantic Oscillation index in February–March.

Abbreviation of species names (17 species): ALYOBS *Alytes obstetricans*; BUFBUF *Bufo bufo*; BUFCAL *Bufo calamita*; HIEVIR *Hierophis viridiflavus*; HYLNER *Hyla meridionalis*; LACBIL *Lacerta bilineata*; LISHEL *Lissotriton helveticus*; MALMON *Malpolon monspessulanus*; NATMAU *Natrix maura*; NATNAT *Natrix natrix*; PELPUN *Pelodytes punctatus*; PODLIO *Podarcis liolepis*; PODMUR *Podarcis muralis*; PSAALG *Psammodromus algirus*; RHISCA *Rhinechis scalaris*; TIMLEP *Timon lepidus*; ZAMLON *Zamenis longissimus*

	ALYOBS	BUFBUF	BUFCAL	HIEVIR	HYLMER	LACBIL	LISHEL	MALMON	NATMAU	NATNAT	PELPUN	PODLIO	PODMUR	PSAALG	RHISCA	TIMLEP	ZAMLON
nul model	291.53	268.69	282.53	284.24	268.36	253.87	288.37	277.64	268.05	286.08	284.63	288.45	291.25	270.32	307.13	260.61	273.43
yr	271.09	267.17	283.65	280.45	270.33	236.41	283.95	245.11	258.41	280.03	273.83	289.45	283.80	272.04	304.26	254.76	268.63
yr+Nobs	273.97	268.60	283.59	281.73	272.04	238.06	285.54	246.12	259.97	281.66	274.87	291.11	285.38	273.97	308.96	256.46	269.82
TmaFM	276.46	259.00	275.94	280.14	254.07	227.95	284.76	253.94	252.62	276.92	282.36	284.78	277.18	263.76	298.53	240.28	269.37
TmaFM+Nobs	276.77	259.33	277.92	278.82	256.06	229.95	285.19	255.94	254.60	278.23	284.34	286.47	278.04	265.60	300.37	241.00	271.34
TmaFM+PcumF	278.46	260.96	277.84	281.82	255.30	229.41	286.43	255.18	254.08	278.91	284.34	286.78	275.97	265.72	298.96	242.22	270.84
TmaFM*PcumF	278.01	262.54	277.99	282.53	254.22	231.17	288.26	256.50	255.87	278.78	285.25	288.72	276.62	266.82	300.96	244.18	271.62
TmaFM+Pthr	278.05	254.22	267.96	281.31	255.93	229.94	286.32	254.86	254.27	278.45	277.87	286.77	278.12	265.66	300.01	241.83	271.37
TmaFM*Pthr	279.98	256.22	269.96	269.44	256.84	231.74	285.59	255.52	255.00	280.25	277.53	288.77	280.11	267.65	301.63	243.80	273.14
naoFM	290.05	269.12	282.79	285.16	265.28	243.03	290.29	271.39	263.62	283.92	286.60	282.81	281.62	266.81	309.13	257.10	271.17

Table 2. AIC of different models predicting the first spring appearance dates of amphibian and reptile species (see abbreviations on Table 1), based on the year or on the climatic variables. The lowest AIC are in bold. Nobs: number of records ; TmaFM: mean daily maximum temperature in February–March ; PcumFM: cumulated precipitation of February-March ; Pthr: day of the year when the cumulative rainfall reaches the 117 mm threshold ; naoFM: mean North Atlantic Oscillation index in February–March.





