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Consistent phenological advancement of Common Toad migration in response to climate change in Flanders, Belgium

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Abstract. Many species use temperature as a cue to time certain life events. Such phenological events can be particularly sensitive to climate change. In amphibians, seasonal migration events between ponds and winter habitats are crucial to ensure reproduction. Therefore, shifts in phenological events – called phenological shifts – can significantly affect the persistence of amphibian populations, especially when induced by climate change. We used citizen science data collected during the spring migration of the Common Toad (*Bufo bufo*) from 1981 until 2020 to: (i) estimate the phenological shift, (ii) determine consistency of these changes within the studied region, and (iii) relate its temporal variation with changes in temperature. The results revealed an advancement in the peak migration of 3.1 days per decade. This shift was consistent across all populations in Flanders, indicating a regional effect that is most likely due to climate change. This reasoning is supported by the temperature-based model, which indicates that earlier migration occurs in warmer years. Nonetheless, significant local variations persist in the timing of spring migration. Our results highlight the importance of studying in detail the timing of spring migration and its variability, as it may elucidate mechanisms underlying trends in population decline at both national and international scales.

Keywords: amphibians, *Bufo bufo*, phenological shift, spring migration, temperature.

Introduction

Phenology, the timing of specific biological events, constitutes a fundamental component of fitness (Lane et al., 2012; Reed, Jenouvrier and Visser, 2013) and is regulated by both biotic and abiotic cues (Leith, 1974). Different cues may show considerable variation or consistency across temporal and spatial scales. For example, reaching critical temperatures can vary greatly across years (Arnfield et al., 2012; Dalpasso et al., 2023) and is strongly dependent on microclimate (Kemppinen et al., 2024), whereas the lunar cycle is a more predictable cue for locations concentrated within a smaller region (Grant, Chadwick and Halliday, 2009). In many organisms, timing – for instance the initiation and termination of diapause in plants and animals (Tauber and Tauber, 1986; Klupczyńska and Pawłowski, 2021), is optimized in response

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to temporal changes in their environment. Since many species rely on temperature as a primary cue for this timing event, their phenology is particularly susceptible to changes in temperature patterns related to climate change (Watts et al., 2022).

Plants and animals have advanced their spring phenology at an estimated mean rate between 2.3 and 2.8 days earlier per decade (Gibbs and Breisch, 2001; Cotton, 2003; Parmesan, 2007; Thackeray et al., 2016; Pendleton et al., 2022). For amphibians, the phenological advancement is three times stronger than those observed in trees, birds and mammals (Parmesan, 2007), with the average shift in spring phenology for temperate-zone amphibians that is approximately five days earlier per decade (Root et al., 2003). However, extremes are observed in three *Triturus* species, with an advancement of approximately one month per decade, and in the Fowler's Toad (*Anaxyrus fowleri*), where a distinct delay in breeding of 5.3 days later per decade is found (Parmesan, 2007). Not only are these shifts currently happening, they are also expected to strengthen in response to projected temperature changes due to climate change (Haest, Hüppop and Bairlein, 2018).

Raising temperatures due to climate change are the main driver of phenological shifts, as warming can shift the entire migration period or affect its duration by affecting its initiation, termination or both (Beebee, 1995; Tryjanowski, Rybacki and Sparks, 2003; Arnfield et al., 2012; Klaus and Lougheed, 2013). These climate-induced changes in phenology can potentially result in phenological mismatches with the environment (Reed, Jenouvrier and Visser, 2013; Visser and Gienapp, 2019), which can eventually result in extensive impacts on demography and population dynamics (Miller-Rushing et al., 2010) and community composition (Jara et al., 2019; Visser and Gienapp, 2019; Dalpasso et al., 2023).

The Common Toad (*Bufo bufo*) is a widespread species from Europe and Northern Eurasia that inhabits a variety of natural and anthropogenic habitats. The species makes up a significant part of the biomass in multiple ecosystems. The aquatic life stage is an important source of energy transfer between the pond and its surrounding habitat, while the terrestrial life stage plays a vital role in the ecosystem as mesopredator (Blaustein et al., 2011). Typically, adult toads stay within a 3 km radius from their breeding pond (Daversa, Muths and Bosch, 2012). As a predominantly pond breeding species, the migration phenology of the Common Toad is largely determined by environmental and climatic factors such as the lunar cycle and temperature, with the latter having generally the strongest impact (Arnfield et al., 2012; Lenzi et al., 2023). While habitat loss, diseases, and pollution are commonly acknowledged as main threats (Beebee and Griffiths, 2005; Grant, Miller and Muths, 2020), it is essential to recognize that climate-induced phenological changes are documented to induce a prolonged tadpole development, resulting in a lower body condition at metamorphosis and reduced female fecundity (Reading, 2007, 2010). Such changes can significantly impact the survival of Common Toad populations (Visser and Gienapp, 2019; Iler et al., 2021).

In this study, we used citizen science data on the spring migration of Common Toads in Flanders, collected by volunteers of the nature conservation organisation Natuurpunt since 1981, to estimate the extent of the phenological shift with a particular focus on determining the consistency of these changes across different populations. Additionally, we analysed its consistency at smaller spatial scales and test whether temporal variation is related to annual changes in temperature.

Materials and methods

Natuurpunt, a civil society organisation, aims to protect and restore nature in Flanders. The organization focuses on preserving open spaces, enhancing environmental quality and raising public awareness about conservation across the region (Natuurpunt, 2024). They organize toad patrol actions in the region of Flanders where they use three kind of actions to assist toads in crossing roads: fence actions, survey actions or a combination of both. For fence actions, the procedure is in general as follows. Fences with a height of 50 cm are placed along the roads to prevent roadkills. On both sides, the drift fences lead to dug-in buckets that are emptied by volunteers daily. Toads and other amphibians that are collected in such way, are released in the breeding pond or on the other side of the road, from where onward they can continue their migration towards their breeding pond. For the survey actions, toads are picked up from the roads directly, as no fences are placed along the road, often due to the presence of driveways, which would necessitate too many interruptions in the fence. Sometimes, a mixed set-up of both is used. We assume one location corresponds to one population. For each population, daily counts were collected during the spring migrations per year.

Citizen science is very useful to collect data on the demography of -often iconic and well-known or common-species (Schmeller et al., 2009; Bonardi et al., 2011). However, the diverse approaches used by volunteer groups can provide a heterogenous range of observations, which might introduce detection variability (Bonardi et al., 2011; van Strien, van Swaay and Termaat, 2013). By filtering this valuable dataset, it is possible to create a high-quality dataset. Therefore, we utilized the package janitor (Firke, 2023) to clean the dataset by standardizing names and ensuring each location had a unique name. Afterwards, we selected only *Bufo bufo* counts and excluded dates that could not be part of the spring migration period, which typically spans from December to April. Additionally, we disaggregated counts for breeding pairs to account for both male and female individuals. This resulted in consistent data spanning more than five years for 234 locations spread across Flanders, Belgium (fig. 1). Data has been collected from 1981 to 2022, with varying durations (6-30 years) across different sites.

The number of dead toads (traffic-killed while migrating towards the pond) and live toads migrating towards the pond were combined to determine the total number of migrants per night. Three estimates for breeding activities in ordinal dates were derived. The onset of migration was determined by using the date when the 5th percentile of the toads migrated to the breeding pond, assessed on a per-location, per-year basis. Similarly, the peak and end migration dates where established using the 50th percentile and the 95th percentile respectively (Arnfield et al., 2012; Dalpasso et al., 2023). Using percentiles ensures that outliers of the migration are eliminated from the data. The duration of the migration period is estimated as the difference between the end and onset of the migration. The peak migration also correlated with the “big night”, the night when the largest amount of toads is moving (non-parametric Kendall correlation $\tau = 0.47$, $p < 0.001$).

We obtained the gridded (5 km × 5 km) temperature data of Belgium from the Royal Meteorological Institute of Belgium covering the period from 1981 to 2023 (KMI, 2022). For each location, we identified the corresponding grid cell in which the location was situated (fig. 1). The temperature data for each grid cell was then used to investigate the relationship between migration phenology and temperature. Previous studies, showed precipitation not to affect the phenology of the species (Gittins, 1983; Reading, 1998; Tryjanowski, Rybacki and Sparks, 2003; Arnfield et al., 2012), which is why we chose not to use precipitation. For all migration dates (onset, peak and end) we calculated the average temperature of the week and month right before the actual migration dates. Additionally, for each year, we calculated the average temperature during the meteorological winter, defined as the period from December 1st to February 28th or 29th. Average temperatures correlated well with both minima ($\tau = 0.82$, $p < 0.001$) and maxima ($\tau = 0.81$, $p < 0.001$) and was preferred for our analyses because it offers a more intuitive representation of overall temporal variation in weather conditions. We aimed to examine different temporal scales, allowing us to compare the relative influence of short-term and long-term temperature variations on migration timing.

All the analyses were conducted in R (v4.3.2) (R Core Team, 2023). The exploration of the data and the construction of the graphs were done using the tidyverse package (Wickham et al., 2019). For each migratory activity date, we constructed a linear mixed model using the lme4 package (Bates et al., 2015) and the lmerTest (Kuznetsova, Brockhoff and Christensen, 2017), to assess the potential shift in migration phenology over the years, while allowing different intercepts for each population. An analogous model was made to make the link with climatic variables. The assumptions linearity, heteroscedasticity and normality were checked with a residual plot, residual-fitted plot and a histogram respectively.

In these models, the migration date was the dependent variable, while the year or average temperature variable (week or month before migration onset, or meteorological winter) was the fixed effect with the population as random intercept. A similar model was used to define changes in migration duration, whereby the length of the migration is the dependent variable. In the latter linear mixed model, only the meteorological winter temperature is used as an independent variable, since it provides a consistent average temperature for each year across all locations. This approach allows us to isolate the influence of temperature on duration by filtering out variations due to date.

To test whether the trend of the migration duration remained stable or was variable over time, we used a selection procedure. In this procedure, we compared a Generalized Additive Mixed Model (GAMM) with a smoother (full model) with a purely linear (nested) model (Linear mixed model, LMM) using the lmtest package (Zeileis and Hothorn, 2002). The model with a smoother (full model), includes the duration as dependent variable, year as fixed effect and population as random intercept, but allowing for flexibility by including a smoother for the year. The purely linear (nested) model had the same variables but without

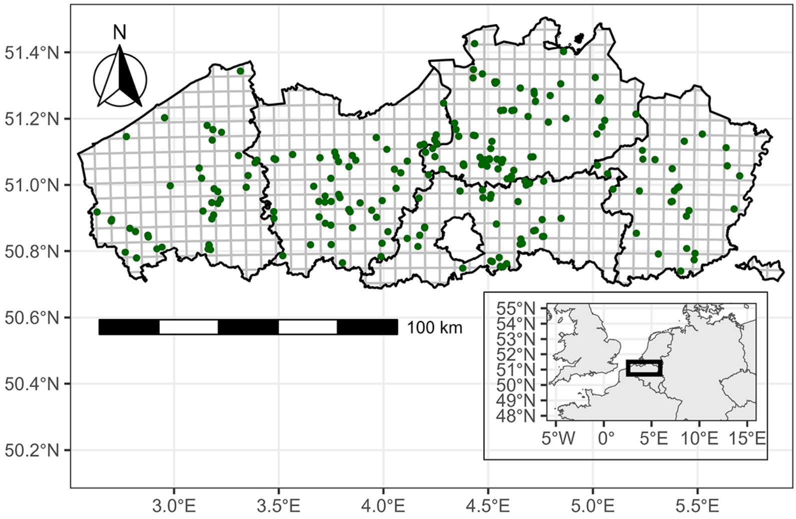

Figure 1. The 234 locations of the toad patrols with sufficiently long time series spread in Flanders, overlaid with the grid of the temperature data. The inset map provides the location of Flanders within northwestern Europe.

the smoother making it a subset of the full model. Comparing both models was done using a likelihood ratio test (LRT), which is a model selection procedure aiming to find a balance between parsimony and goodness of fit (Ruppert, Wand and Carroll, 2003). A significant outcome for this test would reject the null hypothesis, which states that the linear (nested) model should be used because both the full and nested model fit the data equally well. Thus, a significant outcome would indicate that migration duration shows significant fluctuation over the time (fig. 2). The same selection procedure was used to test the population-time interaction (consistency) in the migration date models. This interaction examines whether all populations are shifting their migration timing at the same rate or not. In this case, the full model (LMM) does not include any smoothers but consists of the migration date as the dependent variable, the year as a fixed effect and a random intercept and random slope for year within each population (1 + year|population), allowing each population to have its own intercept and rate of change over time. In contrast, the nested model does not include the random slope. Thus, a significant outcome would indicate that some populations are shifting their migration date at different rates compared to others.

Results

Timing

We observed a statistically significant negative shift for the onset, peak and end of the migration, indicating that the migration of the species is occurring earlier throughout the years (table 1, fig. 3). The migration shifted on average ± SE, 10.2 ± 1.06 days over a 30-year period, or 3.4 ± 0.35 days per decade. Consequently, an onset migration which occurred on March 5th in 1990, shifted to February 22nd in 2020. These estimates remained consistent across all models (onset, peak, end), which suggests robustness of the trends, although model assumptions were only fulfilled for some models (table 1).

Taking into account the temperature as independent variable, we observed a significant negative shift for almost all the average temperatures (week or month before onset, and winter) in each migratory date (onset, peak and end). This indicates that the migration of the species is occurring earlier with current climate change (fig. 4). With every 1°C increase in the monthly average ± SE the migration peak shifts by 3.06 ± 0.12 days (table 1). Further, we did not find any statistical evidence that there is a population-time interaction for any of the migratory dates (onset: $\chi^2(2) = 3.54$, $p = 0.17$; peak: $\chi^2(2) = 5.33$, $p = 0.07$; end: $\chi^2(2) = 3.54$, $p = 0.17$). Both the full and nested model fit equally well, meaning that all migration timings (onset, peak, end) are advancing at the same rate in all locations. However,

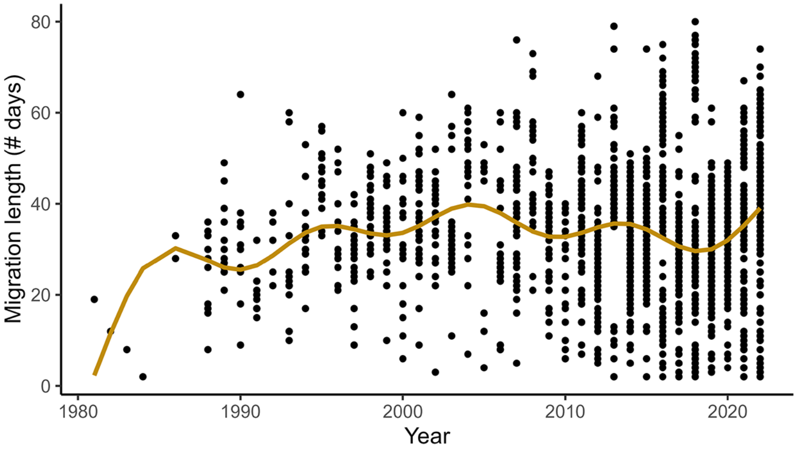

Figure 2. Estimated change in migration duration of the Common Toad (*Bufo bufo*) in Flanders. Points represent the duration at the different locations in the different years. The line shows the additive model illustrating the fluctuation over time.

Table 1. Coefficients estimated with the linear mixed model for the all the models for all migration activities (onset, peak, end, duration), in bold the models with fulfilled assumptions. This illustrates the migratory phenology of the Common Toad in Flanders between 1981 and 2022. The table shows the independent variable (time or temperature based), intercept for the reference year of 2020 with the slope, standard error (SE), degrees of freedom (df), t-value and p-value. Only the model with duration as dependent variable and year as independent variable is statistically non-significant. All the other models have statistically significant results.

Migration activity	Independent variable		Coefficient	SE	df	t-value	p-value
onset	**year**	**intercept**	**53.07**	**0.48**	**338.48**	**110.55**	**<0.001**
		slope	**−0.34**	**0.035**	**1938.79**	**−9.62**	**<0.001**
onset	**weekly avg**	**intercept**	**63.91**	**0.82**	**1423.34**	**77.82**	**<0.001**
		slope	**−1.38**	**0.11**	**2184.58**	**−12.76**	**<0.001**
onset	**monthly avg**	**intercept**	**65.23**	**0.69**	**965.36**	**94.87**	**<0.001**
		slope	**−2.29**	**0.12**	**2145.08**	**−19.51**	**<0.001**
onset	**winter avg**	**intercept**	**71.88**	**0.87**	**1807.25**	**82.92**	**<0.001**
		slope	**−3.5**	**0.16**	**2179.67**	**−22.03**	**<0.001**
peak	year	intercept	70.74	0.35	360.62	203.24	<0.001
		slope	−0.31	0.031	1278.04	−10.04	<0.001
peak	weekly avg	intercept	87.28	0.88	2164.26	99.68	<0.001
		slope	−2.05	0.12	2262.72	−17.80	<0.001
peak	**monthly avg**	**intercept**	**89.62**	**0.74**	**1884.57**	**120.81**	**<0.001**
		slope	**−3.06**	**0.12**	**2195.84**	**−25.72**	**<0.001**
peak	winter avg	intercept	86.02	0.79	2131.35	108.30	<0.001
		slope	−2.82	0.16	2262.11	−17.93	<0.001
end	**year**	**intercept**	**85.15**	**0.35**	**340.96**	**244.70**	**<0.001**
		slope	**−0.27**	**0.030**	**1334.76**	**−9.067**	**<0.001**
end	weekly avg	intercept	75.67	1.05	2283.53	72.62	<0.001
		slope	1.23	0.11	2283.51	10.82	<0.001
end	**monthly avg**	**intercept**	**94.65**	**1.15**	**2263.44**	**82.49**	**<0.001**
		slope	**−1.12**	**0.16**	**2268.17**	**−7.15**	**<0.001**
end	winter avg	intercept	97.63	0.79	2096.76	124.03	<0.001
		slope	−2.28	0.15	2241.27	−14.77	<0.001
duration	**year**	**intercept**	**32.88**	**0.56**	**320**	**58.22**	**<0.001**
		slope	**0.060**	**0.040**	**1999**	**1.47**	**0.14**
duration	**winter avg**	**intercept**	**26.59**	**1.05**	**1810.02**	**25.36**	**<0.001**
		slope	**1.25**	**0.19**	**2176.60**	**6.442**	**<0.001**

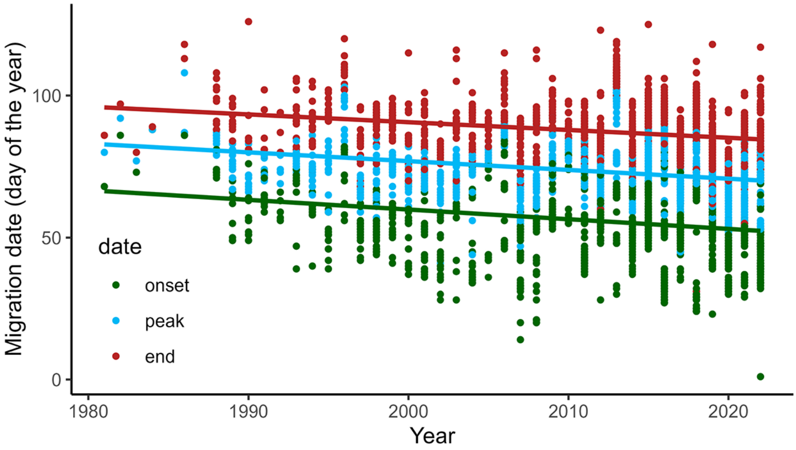

Figure 3. Estimated shift in phenological migration of the Common Toad (*Bufo bufo*) in Flanders for the different migration dates. Points represent the dates at the different locations. The lines represent the mean estimate of the linear mixed model for each migration date. Green = the onset of the migration, date where five percentile of the migrating toads to the pond of a location per year have migrated; Blue = the peak of migration, date measured as the median of the toads migrating to the pond of a location per year; Red = the end of migration, date measured as the 95th percentile of the toads migrating to the pond of a location per year.

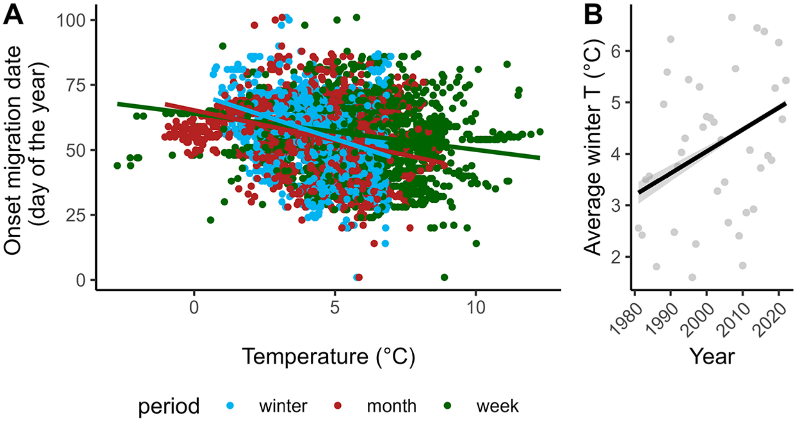

Figure 4. A) Estimated shift in spring migration of the Common Toad (*Bufo bufo*) in Flanders, Belgium based on temperature. The dots represent the onset migration date in different locations and/or years. The line shows the mean estimate of the linear mixed model for the different temperature variables. Blue = the average meteorological winter temperature (°C); Red = average temperature (°C) during the month before the onset of migration; Green = average temperature (°C) during the week before the onset of migration. B) Temporal trend of the average winter temperature, showing the warming in Flanders.

the local variation in the timing of spring migration remains large. Based on the linear mixed model of the onset of the migration, the variance of the random effect was 30.04, while the residual variance was 109.23. This indicates that 21.57% of the total variance in onset migration dates is attributable to differences between populations.

Duration

The similar slopes observed for the different migration timings suggest no change in the overall duration period of the spring migration (fig. 3). This is confirmed by the statistically non-significant result (table 1) obtained from the model assessing the migration duration. However, when examining the effect of the average meteorological winter temperature, the model is statistically conclusive (table 1). For every 1°C increase in the average winter temperature, migration duration was significantly prolonged with 1.25 ± 0.19 days. Additionally, we found that the duration does not directionally change over the considered time interval, but annual variation is considerable as the full and more flexible model showed to be the better fitting model ($\chi^2(6.7) = 104.2$, $p < 0.001$).

Discussion

The Common Toad is an extensively studied species and differences in migration phenology patterns have been reported before (Reading, 1998, 2003; Tryjanowski, Rybacki and Sparks, 2003; Sparks et al., 2007; Arnfield et al., 2012; Lenzi et al., 2023). In this study, we observed a consistent shift of 3.4 ± 0.3 days per decade in the onset of the breeding migration of the Common Toad. This is less than the average shift found in temperate-zone amphibian species of 5.1 ± 0.1 days in a decade (Root et al., 2003). Similar results were found in Poland and Cambridgeshire (UK), where the spring migration of the Common Toad advanced by 3.5 ± 1.3 and 7.4 ± 3.2 days per decade respectively (Tryjanowski, Rybacki and Sparks, 2003; Sparks et al., 2007), while no significant shift was found in arrival dates in south Dorset (UK) (Reading, 1998, 2003; Tryjanowski, Rybacki and Sparks, 2003; Sparks et al., 2007). Conversely delays of 4.3 ± 1.4 days in peak migration have also been noted in Derbyshire, UK (Arnfield et al., 2012). Although these findings concern observations of slightly different migration activities, it still suggests overall that shifts in phenology differ between regions at larger European spatial scales. Such regional variation in migratory phenology is not unique to the Common Toad. Similar patterns have also been observed in the Common Frog (*Rana temporaria*) (Beebee, 2002; Tryjanowski, Rybacki and Sparks, 2003) and in the Common Spadefoot Toad (*Pelobates fuscus*) (Dalpasso et al., 2023). Although species have different reactions to temperature change (Beebee, 2002), their phenology can also be influenced by other factors (microclimate as for instance precipitation, urban heating, humidity) acting at local to regional scales (Hartel, 2008; Phillimore et al., 2010; Mazgajska and Mazgajski, 2020; Dalpasso et al., 2023).

Within the region of Flanders, populations are consistently shifting their timing (i.e., at the same rate). This indicates that the observed shift is predominantly caused by macroclimatic factors (Visser and Gienapp, 2019; Iler et al., 2021). Although macro- and microclimatic factors are largely correlated, significant deviations may nevertheless be due to spatiotemporal variability caused by topography and land use (Klinges et al., 2024). Such deviations deserve more attention by directly measuring all relevant microclimatic factors. Previous studies found no significant effect of precipitation on migration activity for the Common Toad (Tryjanowski, Rybacki and Sparks, 2003; Arnfield et al., 2012), but warmer temperatures serve as cues for an earlier onset of amphibian migration (Arnfield et al., 2012; Ficetola and Maiorano, 2016). Our temperature-based model confirmed these findings, indicating an earlier onset of migration of 2.29 ± 0.12 days per 1°C increase in the average monthly temperature. However, it is probable that other related microclimatic factors are influencing the trigger of toad migration, such as soil temperature, wind speed and wind direction (Scott, Pithart and Adamson, 2008; Dalpasso et al., 2023; Lenzi et al., 2023).

While shifts in the onset of migration are commonly observed across species (Root et al., 2003; Arnfield et al., 2012), changes in the duration of the migration period are rarely looked into. The timing of arrival is crucial for individuals of the Common Toad as the short breeding season is highly synchronised to optimise reproductive success and recruitment (Wells, 1977; Trenham et al., 2003; Grant, Halliday and Chadwick, 2013; Dalpasso et al., 2023). A wider migration window could disrupt this synchronization, potentially leading to cannibalism of eggs and larvae by larger tadpoles (Petranka and Thomas, 1995). In our study, we did not observe any directional changes in migration duration over the considered period, while annual variation was large. However, based on the temperature-based model, there is a significant elongation of migration duration of 1.25 ± 0.19 day per 1°C temperature increase in the meteorological winter. This indicates that an increase in winter temperatures might increase migration duration, but no general shift through time can be detected. A possible explanation could be that early spring events cause accidental early awakening, with no detectable consistent effect (yet) over time.

The observed shift in migration phenology might result in extensive implications on the population level of the Common Toad, due to phenological mismatches with the environment (Reed, Jenouvrier and Visser, 2013; Visser and Gienapp, 2019). Usually, such mismatches occur when cues for the initiation of a life history event are not reliable anymore. For example, prey species themselves might not be available at the time of toad emergence, as the phenological responses of prey themselves might vary greatly (Visser and Both, 2005; Primack et al., 2009; Forrest, 2016; Thackeray et al., 2016). This disturbance in toad-prey interaction might possibly lead to substantial costs and eventually reduced fitness and fecundity. Furthermore, temperature instability (early spring events, followed by sudden frost periods) can cause mortality in adult toads and eggs, resulting in lower survival and recruitment (Schmidt et al., 2024). Both mismatches with the environment, prey availability and temperature instability, could eventually impact demography and population dynamics. Further research should explore in greater detail such population-level impacts of phenological shifts and related mismatches.

In conclusion, we have observed an advancement in the migration phenology of the Common Toad in the region of Flanders. The shift in spring migration phenology is consistent across all locations in this region, indicating that it is a consequence of temperature change linked to climate change. The link with climate change is further supported with the explicit connection between migration shifts and regional temperature data. Nevertheless, local variation in the timing of spring migration remains considerably large. The causes and consequences of this local variation need to be studied in more detail and might explain trends in population decline at national and international levels.

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