Brown frog breeding phenology in south Sweden 1990 – 2017: are data subsets robust?

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ABSTRACT - Field data on breeding phenology of *Rana arvalis* and *R. temporaria* for the period 1990- 2017 in Scania, Sweden are presented and analysed. There was no temporal trend for *R. temporaria*. For *R. arvalis* the results were mixed, one out of two approaches found a trend to earlier breeding. The lack of a consistent trend in breeding phenology is unsurprising considering that local mean air temperatures in February, March and April showed no significant trends over the study period. To test the robustness of the conclusion, different subsets of the data (years or ponds) were also analysed for trends. For most subsets the conclusions remained the same. Possible bias arising from the choice of which years to include in an analysis of trends is discussed.

INTRODUCTION

Phenology, especially the progress of spring, has always fascinated people. Arrival of migrating birds (Ekström, 1826), flowering of early plants (Lappalainen, Linkosalo & Venäläinen, 2008) and also the breeding of frogs, for which Terhivuo (1988a) has compiled data collected since 1846, are examples. Spring breeding frogs in temperate areas are particularly suited for such studies (Richter-Boix et al., 2006). Different signs have been used to record the start of spring activities; breeding migration (Gittins et al., 1980; Reading, 1998; Miwa, 2007; Todd et al., 2011; Arnfield et al., 2012; Klaus & Lougheed, 2013; Green, 2017), first calling (Strömberg, 1988; Elmberg, 1990; Blaustein et al. 2001a; Hartel, 2008; Lappalainen et al., 2008; Scott et al., 2008; Klaus & Lougheed, 2013; Steen et al., 2013), or time of spawning (Elmberg, 1990; Beebee, 1995; Gollmann et al., 1999; Blaustein et al., 2001a; Tryjanovski et al., 2003; Hartel, 2008; Scott et al., 2008; Carroll et al., 2009; Neveu, 2009; Loman, 2014). Sensibly, the choice of variable depends mainly upon what is more practical with different species. The subject has received fresh attention as global warming has become a major debate (Beebee, 1995; Blaustein et al., 2001; While & Uller, 2014). Many long-term studies have been compiled over the years and analysed for trends in breeding phenology. These are summarised and discussed below.

The data and analysis in this report are similar to that of Loman (2014) but extend the period from 2010 until the end of 2017 but omit an analysis of pond effect on phenology as previous results were clear enough and were also elaborated (including data until 2015) in Loman (2016).

A problem that is seldom addressed with time series studies is that the outcome partly relies on the, usually random, choice of start year and (hopefully) random choice of end year. A possible solution to this problem is suggested. In addition, an analysis of the robustness of the results is included that considers what the outcome might be if only shorter time series were included or only single ponds. This study is based on a large number of ponds. But would the same conclusions have been reached had only one pond been studied? Analysis of data began after the 2017 field season. Results from the 2018 field season are also included in Figure 2 but are not included in the analyses. This decision is discussed in light of data selection and biases.

METHODS

Field methods

The breeding of *R. arvalis* and *R. temporaria* was monitored from 1990 to 2017 in south-central Scania, the southernmost province of Sweden (Table 1; Fig. 1). In this period the number of ponds varied (maximum 120 but some with no spawn) and most ponds were monitored over several years, occasionally interrupted by a single year when the focal pond was dry in spring.

Within pond 'breeding sites' were identified. A breeding site consists of spawn clumps separated by no more than 1 m although usually all clumps at a site were in physical contact. If breeding took place at the same place but was interrupted by at least 6 days of non-breeding (very rare) this was considered to be two 'breeding sites'. Most ponds had only one or two breeding sites but the number was in some cases much larger. For *R. arvalis* the number of breeding sites per pond ranged from 1 to 17, with a median of 2.5 and for *R. temporaria* the corresponding numbers were 1 to 15 and 1.9. For each site and species the first date of breeding was recorded. This date usually was a good approximation of the time of breeding for all frogs at the site because at any one site most frogs bred in the first two days (pers. obs.; Loman & Håkansson, 2004). The ponds were visited at least every 5 days during the breeding period, often more frequently. Time for the earliest spawn at a site could therefore be extrapolated from the condition of the spawn at the time of visits, taking the effect of water temperature on development

Table 1. Number of ponds monitored. Only ponds where spawn was found are included. Ponds listed under 'Both' are a subset of those listed under either species.

|	*R. arvalis*	*R. temporaria*	Both	Ponds with spawn
1990	8	25	7	26
1991	7	27	6	28
1992	8	30	8	30
1993	10	28	8	30
1994	25	65	24	66
1995	**26**	60	18	68
1996	28	70	28	70
1997	32	79	30	81
1998	43	80	38	85
1999	40	86	40	86
2000	42	83	38	87
2001	46	81	39	88
2002	44	82	39	87
2003	34	69	29	74
2004	42	71	33	80
2005	47	76	41	82
2006	20	40	19	41
2007	26	47	25	48
2008	23	45	23	45
2009	7	29	6	30
2010	10	31	10	31
2011	13	31	12	32
2012	13	30	13	30
2013	10	26	9	27
2014	7	25	6	26
2015	9	28	9	28
2016	4	7	4	7
2017	3	4	3	4
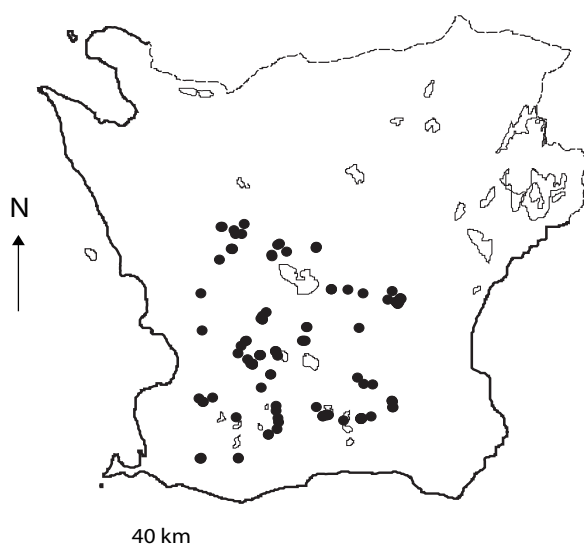
Figure 1. Map of study ponds in the province Scania, south Sweden. Lakes are outlined for easier orientation.

into account. This can usually be done with a certainty of one or at most two days. A similar approach was adopted by Tryjanowski et al. (2003). Frequent visits, observing fresh spawn, also made it easier to separate the spawn of the two species. After a few days this tends to be difficult. The number of spawn clumps at each breeding site was counted or estimated from the area of the egg mass at the breeding site (Loman & Andersson, 2007).

Analysis of trends
For each pond, breeding time was computed as the average breeding time for all sites in the pond, weighted by the number of female frogs breeding (assumed equal to number of spawn clumps) at each site. Thus the measure approximated to the actual average breeding time for all frogs at each pond. This use of breeding sites in the present context explains why a breeding site was counted as 'new' after 6 days of interrupted breeding (a rare occurrence).

For each year, breeding time was calculated as the average time for all ponds studied in that year (raw means). This suffered from the fact that different ponds were studied in different years. To account for this an alternative measure of yearly breeding time was also used. The ponds were subject to an ANOVA (with ponds and year as categories). Data was weighted by number of frogs breeding at a pond and the least square mean was used to represent each year. Trends were analysed as the correlation between year and breeding time. For an alternative approach, the combined effect of pond and year on breeding time was also analysed as an ANCOVA.

Subset analysis
Trend analyses depend much on the starting year. If data collection starts in a year with late breeding there is a bias for a negative trend (earlier breeding in later years), and vice versa. Analyses were therefore done for subsets of the complete data set, assuming data collection had started in 1991 (rather than 1990), 1992, 1993 etc. The shortest data set analysed used 5 years of data, starting in 2013. Subsets based on single ponds were also analysed. Trends for all ponds monitored for at least 20 years and starting no later than 1995 were therefore also analysed.

RESULTS

Trends?
There was no significant trend in the time for breeding for either species (Fig. 2). This was true both using raw year means (Both n=28: *R. arvalis*: r=-0.28, p = 0.16; *R. temporaria*: r = -0.18, p = 0.37) and least squares means (Both n=28: *R. arvalis*: r = -0.25, p = 0.20; *R. temporaria*: r = -0.07, p = 0.72) as a measure of the start to breeding. For both species there were non-significant negative slopes. Although the slope was steeper for *R. arvalis* there was no significant difference between the species (ANCOVA, Year*Species interaction; Raw means: d.f. = 1:52, F = 0.14, p = 0.71; Least squares means: d.f. = 1:52, F = 0.46, p = 0.50).

The ANCOVA found no interaction between pond and time (year) on breeding date for either species (*R. arvalis*: d.f. = 16:199, F = 1.32, p = 0.19; *R. temporaria*: d.f. = 42:577,
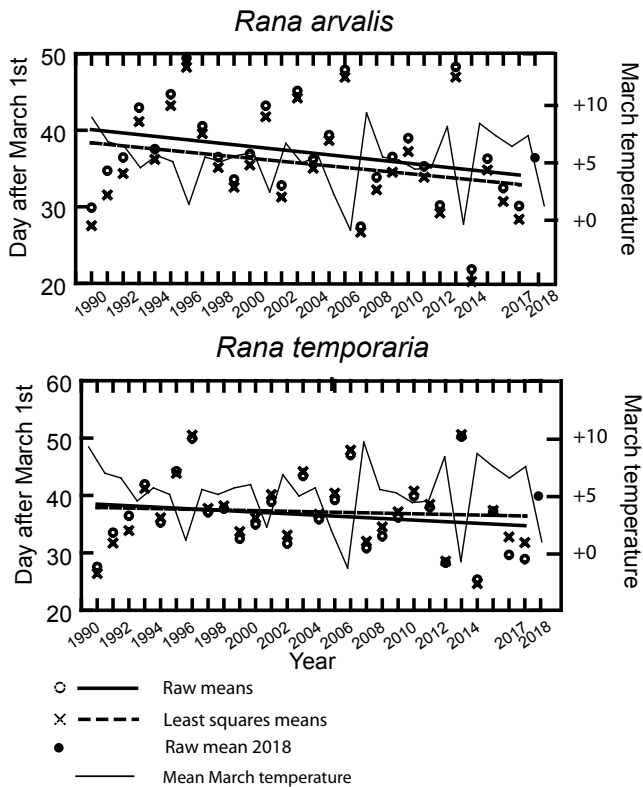
Figure 2. Mean breeding date and linear trends for years 1990 to 2017. The computation of the two types of yearly mean is explained in the Methods. Data for 2018 are not included in the regression lines.

F = 1.36, p = 0.07). However removing the interactions, both pond and time (year) had a significant effect on breeding date in *R. arvalis* (Pond: d.f. = 16:215, F = 2.52, p<0.001; Year: d.f. = 1:215, F = 7.61, p = 0.006). For *R. temporaria* only pond but not year had a significant effect on breeding date (Pond: d.f. = 42:619, F = 3.46, p<0.001; Year: d.f. = 1:619, F = 1.53, p=0.217).

Temperature effects
Among years, the trend in phenology for both species were negatively correlated to February, March and (almost so to) April temperatures (n=28; *R. arvalis*: r=0.43, p = 0.02, r = 0.84, p<0.001, r = 0.48, p = 0.11; *R. temporaria*: r=0.46, p = 0.016, r = 0.85, p<0.001, r = 0.35, p = 0.07 respectively), with earlier breeding in warmer years. During the study period 1990 to 2017 there were no trends in spring (February, March or April) temperatures (all n=28: r=0.14 p=0.48; r=0.01, p=0.94; r=0.15, p=0.43, respectively) in the study region.

Subsets
Had the data collection started in any of the years 1992, 1993, 1994 or 1995 (rather than in 1990, analyzed above) one would have found a significant negative trend (p<0.05) for the breeding start of *R. arvalis* (Table 2). For these years the negative trend was almost significant for *R. temporaria* (p = 0.05 - 0.10). Had the study started in 1996 or later, the conclusions were the same as for the present study; with no significant trend for either species.

The results from the ANCOVA for successive subsets of years are similar (Table 3). If the analysis started from any of

Table 2. Tests for significance of trends in phenology, using alternative starting year. All sequences end with 2017. Trends are based on raw pond breeding dates within years.

|	*R. arvalis*			*R. temporaria*		
	n	r	p	n	r	p
1990 - 2017	28	-0.28	0.16	28	-0.17	0.37
1991 - 2017	27	-0.37	0.055	27	-0.29	0.14
1992 - 2017	26	-0.42	0.03	26	-0.35	0.081
1993 - 2017	25	-0.46	0.02	25	-0.38	0.064
1994 - 2017	24	-0.44	0.032	24	-0.35	0.095
1995 - 2017	23	-0.46	0.026	23	0.39	0.066
1996 - 2017	22	-0.42	0.052	22	-0.34	0.12
1997 - 2017	21	-0.32	0.16	21	-0.21	0.36
1998 - 2017	20	-0.29	0.22	20	-0.21	0.37
1999 - 2017	19	-0.31	0.2	19	-0.2	0.41
2000 - 2017	18	-0.37	0.13	18	-0.28	0.27
2001 - 2017	17	-0.4	0.12	17	-0.32	0.21
2002 - 2017	16	-0.33	0.21	16	-0.3	0.26
2003 - 2017	15	-0.42	0.12	15	-0.41	0.12
2004 - 2017	14	-0.32	0.26	14	-0.34	0.24
2005 - 2017	13	-0.34	0.26	13	-0.37	0.21
2006 - 2017	12	-0.3	0.34	12	-0.35	0.26
2007 - 2017	11	-0.06	0.86	11	-0.16	0.65
2008 - 2017	10	-0.26	0.46	10	-0.28	0.44
2009 - 2017	9	-0.32	0.39	9	-0.38	0.31
2010 - 2017	8	-0.32	0.44	8	-0.41	0.31
2011 - 2017	7	-0.22	0.63	7	-0.34	0.46
2012 - 2017	6	-0.2	0.7	6	-0.27	0.6
2013 - 2017	5	-0.42	0.48	5	-0.61	0.27
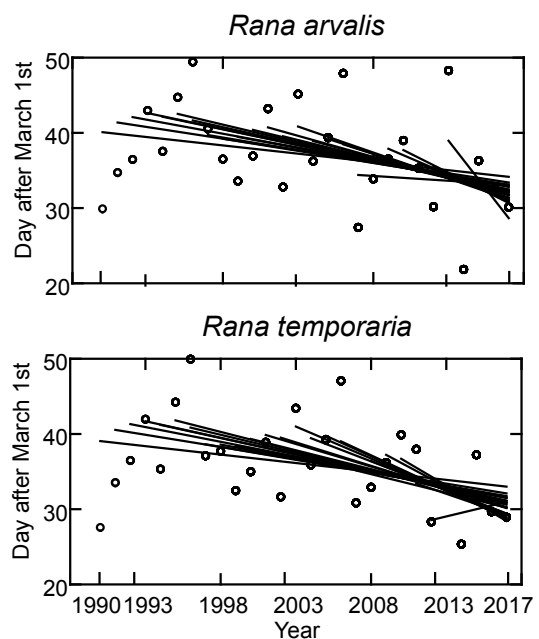
Figure 3. Trends in breeding, based on raw means of breeding date within ponds and years. The starting year for each trend is evident from the left end of each line. The shortest trend analysed was 2013 to 2017 inclusive.

Table 3. As Table 2 but analysis based on a 2-way ANCOVA; pond and year effects on breeding date. Only year effects are accounted for in the table. All interactions are non-significant and were removed before final analysis.

	R. arvalis			R. temporaria		
	d.f.	F	p	d.f.	F	p
1990 - 2017	1:227	7.7	0.006	1:679	0.92	0.34
1991 - 2017	1:221	15.1	<0.001	1:660	8.59	0.004
1992 - 2017	1:216	20.5	<0.001	1:639	17.7	<0.001
1993 - 2017	1:208	27.7	<0.001	1:613	26.8	<0.001
1994 - 2017	1:200	21.9	<0.001	1:591	23.8	<0.001
1995 - 2017	1:188	26.3	<0.001	1:553	36.1	<0.001
1996 - 2017	1:175	16	<0.001	1:519	18.9	<0.001
1997 - 2017	1:163	5.14	0.025	1:485	0.36	0.55
1998 - 2017	1:149	2.32	0.13	1:446	0.17	0.68
1999 - 2017	1:134	2.75	0.1	1:407	0.081	0.78
2000 - 2017	1:121	6.2	0.14	1:368	3.22	0.073
2001 - 2017	1:108	7.81	0.006	1:330	6.66	0.01
2002 - 2017	1:94	3.48	0.065	1:293	1.66	0.199
2003 - 2017	1:78	7.87	0.006	1:257	10.6	0.001
2004 - 2017	1:66	2.35	0.13	1:225	2.1	0.15
2005 - 2017	1:52	2.72	0.11	1:188	5.51	0.02
2006 - 2017	1:42	0.56	0.45	1:164	2.65	0.11
2007 - 2017	1:35	1.68	0.2	1:145	1.42	0.23
2008 - 2017*				1:121	0.17	0.68
2009 - 2017	1:20	0.58	0.46	1:102	1.21	0.27
2010 - 2017	1:18	0.53	0.48	1:85	2.63	0.11
2011 - 2017	1:15	0.13	0.72	1:68	0.53	0.47
2012 - 2017	1:11	0.048	0.83	1:52	0.051	0.82
2013 - 2017	1:7	1.6	0.25	1:36	9.73	0.004
2014 - 2017	1:4	1.68	0.26	1:22	3.46	0.076

* This test for *R. arvalis* signalled 'Lost degrees of freedom'

the years 1990 to 1996 then there was a significant effect of YEAR (with earlier breeding in later years) for *R. arvalis* (Fig. 3). For *R. temporaria* this was only true for the series starting from 1991 to 1996. For shorter time series (starting later than 1997 or 1996 respectively), usually no year effect could be detected. An exception (for both species) was starting in 2003, a year in which breeding started very late, when a year effect was found.

A study was also made to investigate what conclusions would be reached if only one pond was sampled. For this analysis it is assumed that the study started in 1993. This choice is motivated by the fact that this starting year yielded 'the most significant' result (p<0.02) for *R. arvalis* and was almost significant (p = 0.064) for *R. temporaria* (Table 2). This analysis included all ponds for which monitored starting no later than 1995 and continued until at least 2015. For only one of these 20 ponds there was a trend to earlier breeding (*R. arvalis*: n = 23, r = -0.53, p = 0.009, all others ponds p>0.11; *R. temporaria*: n = 23, r = -0.44, p = 0.035, all other ponds p>0.08). The fact that the ANCOVA test never found any interactions between pond and year confirms that the conclusions are robust with respect to the choice of ponds.

DISCUSSION

Trends
In the previous analysis of this data set up to 2010, a significant trend to earlier breeding could not be detected with certainty. Adding another 7 years of data has allowed a more powerful and/or reliable analysis. The more simplistic analyses still do not find any trends towards earlier breeding, using the full data set. However, taking advantage of the large number of ponds included in the study and with pond identity included in the analysis, accounting for possible concordance among pond trends (by means of an ANCOVA), there is a significant trend to earlier breeding for *R. arvalis*. However, not even this approach finds any trend in breeding phenology in *R. temporaria*. The weak trends come as no surprise as there were no trends in spring temperatures during the study period.

Causes for lack of trends
Several other studies have documented trends to earlier breeding in frogs but there are also exceptions (Table 4). If no trend is found, it could simply mean that there has been no climate trend in the study area. This seems to be the explanation in the present case. Actually, one of the main lessons from this study is that climate trends are geographically very heterogeneous, and one should not automatically assume everything is happening earlier in all areas! Another reason could be that the organisms are date conservative, date is as important a clue to phenology as short term weather, as shown by Harri & Koskela (1997) in a common garden study of *R. temporaria*. There are two reasons. Although early breeding is the key to a head start for the offspring, eventually resulting in a larger size of young frogs at the time of first hibernation, the effect is not as strong as one might suspect; a few days difference in egg laying and hatching make for even less difference later in the season (Loman, 2009, Steen et al., 2013, Benard, 2015). There is also a strong incentive not to respond too strongly to an occasional warm spring as the likelihood of a set back with later low temperatures is not to be neglected (Loman, 2009). The price to pay in these cases is high as the spawn risks destruction by freezing of the breeding pond.

Robustness
Shortening the study period did not affect the conclusion reached for *R. temporaria*. For *R. arvalis* the outcome was ambiguous. By chance (starting the study one or a few years later) it could have been concluded that there was indeed a trend for earlier breeding. The large number of years for this study gave an opportunity to put the main conclusion in perspective. Also, studying only one pond had in almost all cases resulted in reaching the same conclusion. Again, the large number of ponds studied gave an opportunity to test the robustness of the conclusions in this respect.

There are two reasons for not redoing the analyses after the 2018 field season. First, it had meant more work and sometimes you have to decide that something is finished, no more data collection and time to start compilation. This decision should be (and was) taken regardless of the last data point (2017) being late or early. Second, 2018 was a late year

Table 4. Results from long-term studies of frog phenology

Species	Site	Measure	Time span	Trend	Ref.
R. temporaria	Finland	Spawn	1846 - 1986	Earlier	Terhivuo, 1988a, Terhivuo, 1988b
B. bufo	S England	Migration	1980 - 1998	No trend	Reading, 1998
Rana cascadae (site 1 and 2)	Oregon, USA	Spawn	1982 - 1999	No trend	Blaustein et al., 2001
Bufo boreas (site 1)	Oregon, USA	Spawn	1982 - 1999	Dubious earlier	Blaustein et al., 2001
Bufo boreas (site 2 and 3)	Oregon, USA	Spawn	1982 - 1999	No trend	Blaustein et al., 2001
Pseudacris crucifer	Michigan, USA	Call	1967 - 1994	No trend	Blaustein et al., 2001
Bufo fowleri	Oregon, USA	Call	1980 - 1998	No trend	Blaustein et al., 2001
Pseudacris crucifer	New York, USA	Call	1900-1912 comp. to 1990-1999	Early trend	Gibbs & Breisch, 2001
Rana sylvatica	New York, USA	Call	1900-1912 comp. to 1990-1999	Early trend	Gibbs & Breisch, 2001
Rana catesbeiana	New York, USA	Call	1900- 1912 comp. to 1990-1999	Possibly early trend	Gibbs & Breisch, 2001
Hyla versicolor	New York, USA	Call	1900 - 1912 comp. to 1990-1999	Early trend	Gibbs & Breisch, 2001
Bufo americanus	New York, USA	Call	1900 - 1912 comp. to 1990-1999	No trend	Gibbs & Breisch, 2001
Rana clamitans	New York, USA	Call	1900-1912 comp. to 1990-1999	No trend	Gibbs & Breisch, 2001
R. temporaria	Poland	Spawn	1978 - 2002	Earlier	Tryanowski, Rybacki & Sparks, 2003
Bufo bufo	Poland	Spawn	1978 - 2002	Earlier	Tryanowski, Rybacki & Sparks, 2003
R. temporaria	Central Finland	Call	1952 - 2005	Earlier	Lappalainen, Linkosalo & Venäläinen, 2008
Rana temporaria	Eastern England	Spawn	1978-2005	Weak early trend	Sparks et al. 2007
Rana temporaria	Wales	Spawn	1978-2005	No trend	Sparks et al., 2007
Bufo bufo	Eastern England	Migration	1978-2005	Early spawning	Sparks et al., 2007
Rana ornativentris	Tokyo, Japan	Spawning	1992 - 2007	Earlier	Kusano & Inouse, 2008
Rhacophorus arboreus	Tokyo, Japan	Spawning	1992 - 2007	Earlier	Kusano & Inouse, 2008
R. temporaria	United Kingdom	Hatching	Starting 1994-99, lasting 5-12 y.	No trend	Scott, Pithart & Adamson, 2008
R. temporaria	United Kingdom	Spawning	Starting 1994-99, lasting 5-12 y.	Earlier	Scott, Pithart & Adamson, 2008
R. temporaria	NW France	Spawn	1984 - 2007	Earlier	Neveu, 2009
Bufo americanus	Ontario	Call	1970 - 2010	Earlier	Klaus & Lougheed, 2013
Rana pipiens	Ontario	Call	1970 - 2010	Earlier	Klaus & Lougheed, 2013
Rana sylvatica	Ontario	Call	1970 - 2010	Dubious earlier	Klaus & Lougheed, 2013
Hyla versicolor,	Ontario	Call	1970 - 2010	No trend	Klaus & Lougheed, 2013
Pseudacris crucifer,	Ontario	Call	1970 - 2010	No trend	Klaus & Lougheed, 2013
Rana catesbeiana	Ontario	Call	1970 - 2010	No trend	Klaus & Lougheed, 2013
R. arvalis	South Sweden	Spawn	1990 - 2010	Dubious earlier	Loman, 2014
R. temporaria	South Sweden	Spawn	1990 - 2010	No trend	Loman, 2014

and thus supports the main conclusion; there is no or a very weak trend to earlier breeding for these species in this region. Adding the 2018 data, knowing the outcome of the season, could justifiably be considered a bad statistical practice. But it is worthwhile to present the data (Fig. 2) and point out that this season certainly does not weaken the conclusion!

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