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Monitoring brown frogs *Rana arvalis* and *Rana temporaria* in 120 south Swedish ponds 1989–2005. Mixed trends in different habitats

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ABSTRACT

The two brown frogs *Rana arvalis* and *Rana temporaria* were monitored at 57 localities (that contained a total of 120 ponds) for up to 17 years each during the years 1989–2005. The analysis summarized below only accounts for trends within sites actually usable for frogs during the analysis period, large scale habitat losses are thus not accounted for. *R. arvalis* populations tended to increase over the study period. *R. temporaria* populations displayed no significant change. However, both species displayed significant fluctuations from year to year. These were not correlated between the two species. Localities with permanent ponds tended to display more positive population trends than localities with temporary ponds and ponds in pastures tended to display more positive trends than those in forests. For ponds in cropped fields, where only *R. temporaria* were found, the trend were also generally negative. Thus, long-term trends suggest that neither species is in decline. Nevertheless, the population trends observed in more exploited habitats are less positive than those in relatively unexploited habitats. We conclude frog populations in agricultural habitats should be more carefully studied to identify the factors behind the decline. The negative trend in temporary ponds are cause for a closer analysis of the effects of weather factors on frog population dynamics.

1. Introduction

The last decades have seen a multitude of reports on declining amphibian populations. These reports include discussions of possible world-wide or regional trends (Blaustein and Wake, 1990; Blaustein et al., 1994; Alford and Richards, 1999; Houlahan et al., 2000). Although no common cause is known, many specific causes have been described and at times shown to be of importance for local declines (Beebee and Griffiths, 2005). These includes effects of diseases (Green, 1994; Daszak et al., 2003), introduced predators (Kupferberg, 1997), increased UV-radiation (Licht and Grant, 1997), acidification (Räsänen et al., 2002), chemical pollution (Sparling and Lowe, 1996) and habitat destruction (Delis et al., 1996). In many cases, multifactorial studies are probably required to understand the cause of declines (Gardner, 2001; Storfer, 2003).

Rana arvalis and *Rana temporaria* are two common frog species in Sweden. They are presently not considered threatened in Sweden, although *R. arvalis* is listed in the EU habitat directive, annex IV. However, they can be considered key species in the sense that they are important prey for many vertebrate species (Lodé, 1996; Zahn, 1997, and references in Loman, 1984) and (as tadpoles) also for invertebrates (Lardner and Loman, 1995). Reduction in their numbers may thus have substantial effects on various animal communities. In addition, they are suitable as non-specific indicator species because

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of their wide geographical distribution and comparatively non-specific habitat requirements. They are likely to react to large scale, non habitat specific, environmental threats like increased pesticide use, general acidification of water bodies, or targeted by non-specific amphibian contagious deceases.

To evaluate potential negative factors on populations it is critical to have good monitoring data, preferably collected before the onset of the factor (Collins and Halliday, 2005). The present study was not started as a response to a suspected decline but to provide such a background, should a decline be suspected in the future.

There is also an ongoing debate related to the nature of amphibian population fluctuations (Pechmann and Wilbur, 1994; Blaustein, 1994; Green, 2003). E.g., Alford and Richards (1999) suggest that there is a tendency in amphibian populations for single years with high population increase to be offset by several years of moderate decrease. This could be a cause for bias when evaluating population trends from real data. Long data series like the one presented here can help elucidate this problem.

To understand the reasons for a possible decline, factors suspected to be responsible should preferably be monitored together with the populations under study. This includes abiotic factors such as pesticide levels and water acidity but also health status of frogs and density of possible predators. This has not been within the scope of the present monitoring program. Some clues can however be gained from separately analysing trends in different categories of ponds. This is possible because records were kept on the hydroperiod status of ponds and of their surrounding habitat. This is a quantitative report of the breeding of *R. arvalis* and *R. temporaria* in 120 Swedish ponds, monitored for up to 17 years. Overall trends for the full data set and for different categories of ponds are analysed.

2. Study area and methods

2.1. Study area and units of study

Monitored ponds were situated in the province Skåne, southern Sweden, except the northern and eastern parts (Fig. 1). They were mainly chosen for accessibility and surveyability. The latter meant that large ponds or ponds with thick reed beds were avoided. Some ponds were the only ones in an area but other were part of a complex. If there were more than one pond within 500 m of another, all ponds in such groups were monitored. Single ponds (without neighbouring ponds) or such groups of ponds were defined as localities. The following analyses are all based on localities. This means that the sampling units more reasonably can be considered independent statistical units than were the case if ponds were used (Petranka et al., 2004). Thus, changes in the number of frogs breeding in a pond because of local between year adult movements do not affect the study. In 1989, 14 ponds distributed at five localities were monitored (Appendix A). In these localities, spawn from *R. temporaria* was found in all five and from *R. arvalis* in two. In 2005, the number had increased to 120 ponds at 57 localities. There was a marked increased in number of ponds monitored from the mid 1990s but the number has since remained fairly constant. In a few ponds, monitoring

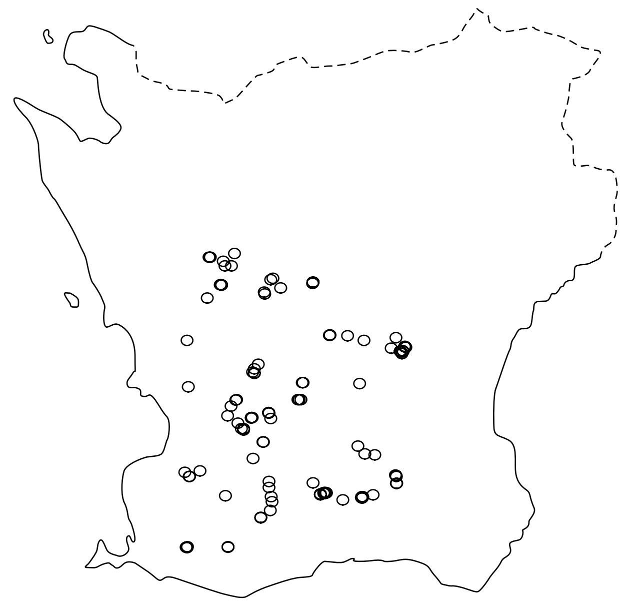

Fig. 1 – Map of the province Skåne and monitored localities.

was discontinued because the pond was drained or else too altered to be considered comparable with previous conditions. If one pond in a complex was drained, this was not considered to affect the use of the rest of the locality as a monitoring unit so surveying was continued.

Localities were classified by two variables. *Permanency* was assessed by checking the status of the ponds at the end of June (about the time for metamorphosis of both species) from 1994 to 2001. Based on this, the ponds were assigned to either of four categories on a subjective scale (Appendix B). Ponds that were not monitored at all or only for some years in this period were also, based on their relevant characteristics, assigned to one of these categories. Localities were assigned to either category based on the classification of the least drought prone pond in the complex, provided this on average contained at least 10% of the spawn. This classification, using four categories, shows the range and distribution of conditions encountered (Appendix B). However, there were few localities in some of the categories. For this reason, the number was reduced to two in the analyses: “Permanent localities” (localities with at least one pond that never dries or does so in extreme years only) and “Temporary localities” (localities where all ponds dry often or in almost all years). On the present sample of ponds, the effect of this simplified classification was that temporary localities contained temporary ponds only and that in permanent localities, more than 70% of the frogs bred in permanent localities. The resulting division was thus quite clear cut.

The localities were also classified according to the *surrounding habitat*. Regard was taken to the terrestrial habitat within 100 m of a pond or (for multi-pond localities) of all ponds at a locality. Categories used were forest (which always was deciduous), pasture and fields. The latter were areas regularly tilled for agriculture. Habitat was scored by visual inspection on site. Ponds at about one third of the localities were surrounded by a mixture of these habitats. These localities were removed from analyses of habitat effects, unless the dominating habitat scored >80% of the surrounding area. This consideration reduced the number of localities available for analysis by about 33% (Appendix B).

2.2. *Egg mass counts*

Spawn clumps of both species are deposited singly or (mostly) in aggregated masses of spawn clumps. The number of clumps in smaller masses is easily counted (Griffith and Raper, 1994) but in large aggregations, this is very time-consuming and involves moving the clumps around. In these situations, the area covered by the mass was measured and a correction factor applied. This factor (215 clumps per m^2 for *R. arvalis* and 140 for *R. temporaria*) was estimated from thorough counts of sample masses. The ponds were visited from the start of breeding in late March each year. The shore-line (or for shallow ponds, the entire pond) was searched for frog's spawn. Any spawn found was noted and its age estimated. Visits were repeated 3–6 times each year (3–7 days interval) and discontinued when only "old" (approximately 5 days and older) spawn was found (unless this happened early in the season; if so an additional search was performed). Similar protocols have been used by Meyer et al. (1998) and Crouch and Paton (2000).

2.3. *Missing data treatment*

Some ponds were frogs usually bred had however too little water (or none) for breeding to take place in dry springs. If there were other ponds present at the locality, the total amount of spawn at these was scored for the locality. However, if all ponds at a locality (including localities with only one pond) were dry in one year, this data was scored as missing for that year. This is because the study is designed with the purpose of monitoring frog population, rather than monitoring the number of breeders *per se*. If all ponds were dry and the number of spawn was zero, this is little cause for assuming that the population is also zero (Alford and Richards, 1999). Probably, the frogs had to skip breeding in that particular year, or possibly, they moved to other localities.

Four of the ponds, that all were the only one at their locality (thus representing four localities), were permanently drained by human activity during the course of the study (1995, 1996, 2004, 2005). All these were used only by *R. temporaria* before draining. These were also set to "missing data" after draining, rather than zero. This means that estimated population trends are slightly bias to the positive side. To look at it another way, what is studied here is the trend for frog populations with access to breeding ponds.

3. Analysis

Population trends are accounted for in two ways in this report.

3.1. *Spawn counts and population indices, direct data*

Some sets of localities were monitored for a common suite of consecutive years. The dynamics of a species in such a set could be analysed without any missing data correction. For example, *R. arvalis* was found in two localities that were monitored all study years, that is from 1989 to 2005, inclusive. From 1995 to 2005, there were 28 localities with this species monitored for all years. The corresponding numbers for *R. temporaria* were 5 and 48. These data were analysed by means of two alternative measurements: (1) total number of spawn clumps in the set of localities or (2) based on an index for each locality and year. Accounting for population variation based on total number of spawn clumps found gives more weight to large localities than to small. The alternative (an index) gives equal weight to all localities included. To compute the index (method (2)), the following procedure was adopted. We calculated first the average number (Av_l, where l is locality #) of spawn clumps found during the respective monitoring period (1989–2005 or 1995–2005) for each locality. Then, for each locality and year, the number relative to that average (Sp_{lt}/Av_l) was calculated. Sp_{lt} is the number of spawn clumps found at locality # l in year t. Finally, for each year, the average of these relative numbers (Sp_{lt}/Av_l) (one value per locality) was calculated. This average is the index value for year t. These yearly indices have the advantage of being directly connected to real data but the drawback is that they do not make use of all data available.

3.2. *Population estimates and trend analysis based on models*

Because different numbers of localities were analysed during the years, a unified analysis that makes an optimal use of all available data requires a model and an estimation of missing data. This has been done using the data analysis package TRIM (Pannekoek and van Strien, 2003) which is intended for use with incomplete monitoring data. The analysis of significance in these trends is of course based on the assumption that the analysed data points are a sample from a larger universe, which is the real object of study. Although the localities studied are not a formally random sample, we will assume they represent localities of these two species in the province of Skåne.

TRIM applies loglinear Poisson regression, a form of GLM. It allows the specification of different models. For the model specified, all data points (year by locality) including missing, are estimated.

In this study, three models are used. A linear trend model assumes one trend (positive or negative) for a suite of years. This analysis answers the question: has there been a significant change in the sampled population during the study period? The actual population sizes estimated for different localities and years are however usually not very realistic.

A more detailed model takes into account different year effects. This model usually gives better estimates than a linear trend model. This model also gives the "best" slope for the change in number between all pairs of consecutive years. Estimated populations slopes from this model will be used to test for synchrony in the two species' population fluctuations. The slopes can be computed separately for groups of ponds classified by a covariate in the model. Such slopes for groups defined by pond permanency or by surrounding habitat will be computed by this model. Slopes for localities differing in permanency or habitat will be compared.

An intermediate model between year effects model and linear trend model is the model where years effect were only applied if statistically significant. If year effects were not significant, they were removed from the model and a linear trend was used for a suite of years. Trends accounted for by this method are all significantly different from each other and the model values used are based on these trends. This analysis will be used to study if the between year variations observed are significant and thus evidence of true variation in the sampled population.

TRIM population indices are of two types. Model indices are estimated for each locality, based on the model. Global model indices are the average of these. When comparing localities by category, model indices only are shown since the variable of interest here is the trend between two consecutive years. These model indices will however somewhat differ from found values for those localities that were actually monitored in a specific year. Even more realistic indices can thus be obtained by using actual values for localities when available and estimated, model, values to substitute missing data for other localities. The global average of these locality specific values are called imputed values. Here, these imputed indices are shown on graphs that account for the variation in the total population.

4. Results

4.1. *Population variation in monitored localities, direct data*

In the two localities that were monitored since the start of the project in 1989, the number of *R. arvalis* spawn clumps increased from about 500 to a maximum of almost 1500 in year 2001 (Fig. 2A). In the larger set of localities monitored all years since 1995, the fluctuations were by and large parallel to those in the smaller set monitored since 1989 ($r = 0.63$, $N = 11$, $P = 0.037$) although there were some discrepancies. There was a similar correlation between the two series based on locality indices (Fig. 2B, ($r = 0.69$, $N = 11$, $P = 0.019$). A similar picture emerged for *R. temporaria* (Fig. 3A and B) but the larger sets of ponds available for this species caused both indices to be closer correlated between them ($r = 0.89$, $N = 11$, $P < 0.001$ for total eggs and $r = 0.93$, $N = 11$, $P < 0.001$ for locality indices).

4.2. *Overall model trend*

The overall model trend for *R. arvalis* was significantly positive (Walds test = 26.9, d.f. = 1, $P < 0.001$) (Fig. 4). For *R. temporaria*, no significant trend could be detected (Walds test = 0.96, d.f. = 1, $P = 0.33$). Based on imputed values, there were 10 years of *R. arvalis* increase and 6 years of decrease. The corresponding values for *R. temporaria* were 8 years of each type (Fig. 4).

4.3. *Between year model trends – power of monitoring program*

For the first 7 years of the study, no significant change in *R. arvalis* could be detected. However, from 1995 to 1999, the population increased, both slopes making up this increase were significantly positive (Fig. 5 and Table 1). This trend was reversed in 1999, starting a four year decrease. However only the first year of this decrease was significant. Also the increase for the last 2 years of the study was not significant.

Also the populations of *R. temporaria* fluctuated. The first 9 years represented significant decreases or non significant trends. During the last 7 years of study, there were short term increases and decreases, most of them significant.

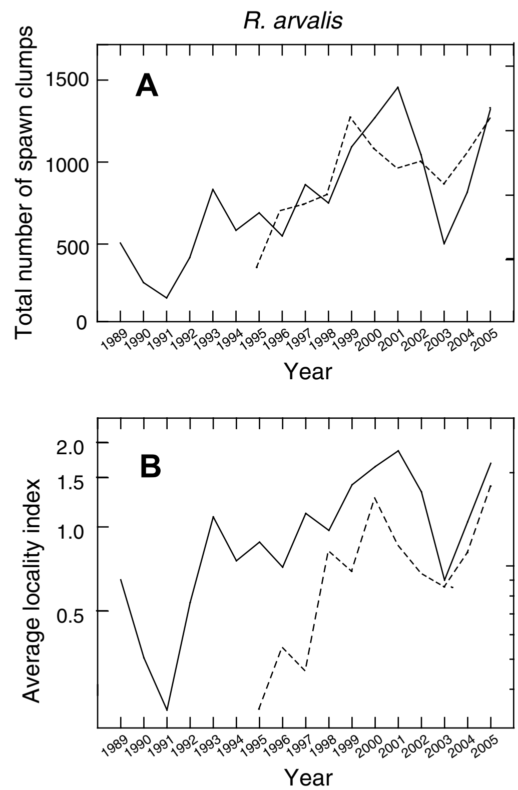

Fig. 2 – (A) Number of spawn clumps from *R. arvalis* counted. The solid line and left scale is based on all (only 2) localities monitored all years from 1989 to 2005. The broken line and the right scale is based on all localities (19) monitored from 1995 to 2005. (B) Average index for number of spawn counted. For each locality included, the average number of spawn clumps is set to 1 and an index for each year assigned in relation to this. The graphs represents the average for included localities of those indices. Localities included are the same as for (A). This graph gives equal weight to all localities while (A) puts more weight on those with much spawn.

4.4. *Pond type effects*

4.4.1. *Pond permanency*

The overall trends for temporary and permanent localities differed significantly for *R. arvalis*, permanent localities had a significantly more positive trend (Fig. 6) (Wald test = 7.28, d.f. = 1, $P = 0.007$). However, no single year showed a significant difference between categories (Fig. 6). There was a significantly increasing trend for permanent localities (Table 2) but a non-significantly decreasing one for temporary (Fig. 6). Also

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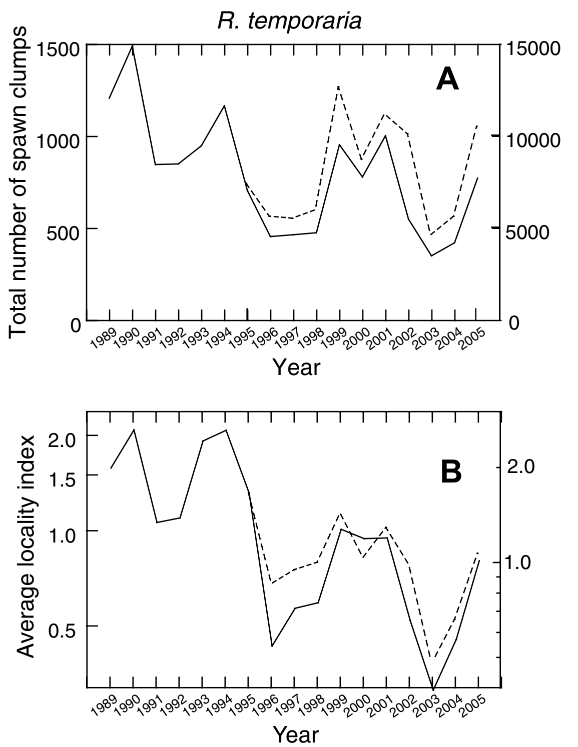

Fig. 3 – Corresponding to Fig. 2 but data for *R. temporaria*. The number of localities included are 5 (1989–2005, unbroken line) and 46 (1995–2005, dashed line).

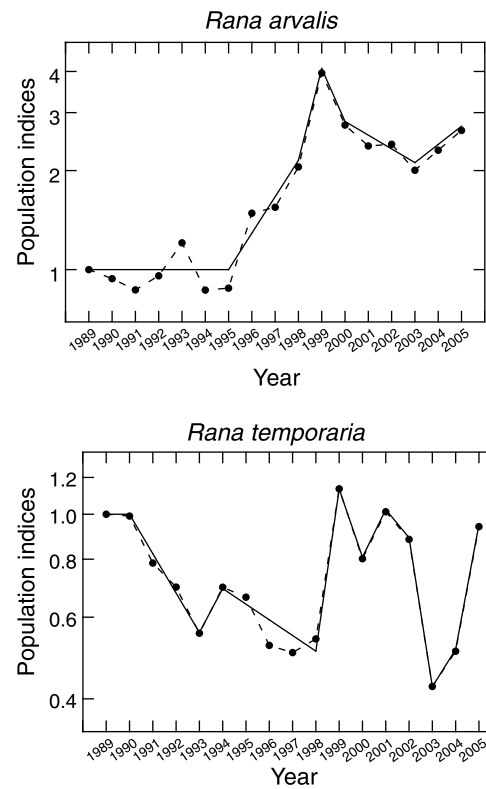

Fig. 5 – As Fig. 4 but based on a model with stepwise selection of significant trends.

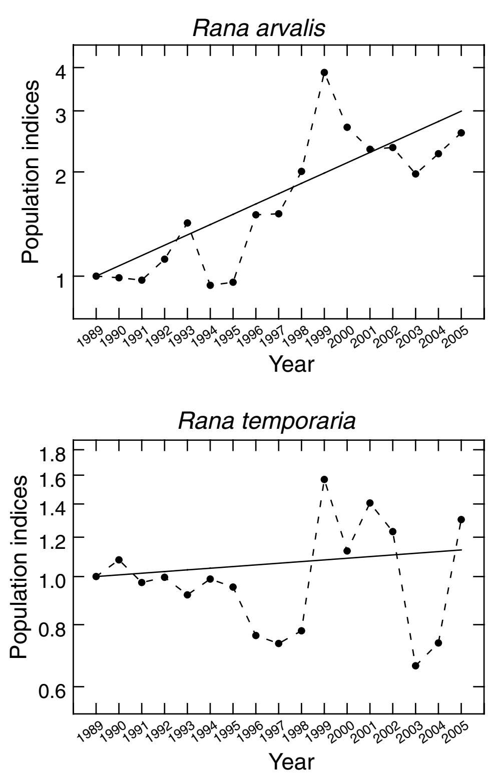

Fig. 4 – Model (solid line) and imputed (dashed line, dots) indices for *R. arvalis* and *R. temporaria*.

for *R. temporaria* there was a significant difference (Wald test = 7.92, d.f. = 1, $P = 0.005$). There was also a significant differences in the tendency for one of the years, in 1994–1995 permanent localities were more successful than temporary ones (*t*-test, $P < 0.01$). The positive trend for permanent localities was not quite significant but the negative one for temporary localities was (Table 2).

4.4.2. *Pond surroundings*

For *R. arvalis* only localities in forest and pasture were sufficiently common for inclusion in a test. Localities in pasture landscapes showed a more positive population trend than those in forest habitats (Wald = 9.72, d.f. = 1, $P = 0.0018$). The positive trend in pasture landscapes was significant but the negative one in forest not so. There was also a difference in the trends for *R. temporaria* (Wald = 9.68, d.f. = 2, $P = 0.0079$). There was an overall tendency for an increase in localities in pastures but decreases in the other two habitats, more so in field localities than in forest localities (Fig. 7). Only the negative trend in field localities was significant (Table 2).

4.4.3. *Combined*

Testing the simultaneous effects of both permanency and surrounding, that for surrounding was significant for *R. arvalis* (Wald = 6.43, d.f. = 1, $P = 0.112$) but not that for permanency (Wald = 3.24, d.f. = 1, $P = 0.072$). However, both were significant for *R. temporaria* (Wald = 6.80, d.f. = 1, $P = 0.0091$ and Wald = 11.41, d.f. = 2, $P = 0.0033$, respectively).

Table 1 – Significance of trends and changepoints

From:	*R. arvalis*			*R. temporaria*		
	Trend	Significance of		Trend	Significance of	
		Trend	Change		Trend	Change
1989	0			0		
1990				Negative	**	0.033
1991						
1992						
1993				Positive	n.s.	0.055
1994				Negative	**	0.095
1995	Positive	***	<0.001			
1996						
1997						
1998	Positive	***	0.029	Positive	***	<0.001
1999	Negative	**	<0.001	Negative	***	<0.001
2000	Negative	n.s.	0.085	Positive	**	<0.001
2001				Negative	*	0.012
2002				Negative	***	<0.001
2003	Positive	n.s.	0.059	Positive	n.s.	<0.001
2004				Positive	***	0.035

Trends included (Fig. 6) are those that represent a change at least at the 0.05 level ("significance to enter" = 0.05, Pannekoek and van Strien, 2003) and were not removed during the stepwise selection of changepoints ("significance to remove" = 0.10). "Year" indicates the starting year for an included trend. Years when there was no significant change in trend are left blank. "Trend" indicates if the trend, starting the indicated year, is positive or negative. "Significance of trend" indicates if the slope is significantly positive or negative. "Significance of changepoint" indicates the significance of a change in trend, compared to the preceding trend. Significances are tested with Walds test. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

4.5. *Between species correlation – synchrony*

There was no correlation between the yearly trends, as estimated by the model, of the two species (Pearson $r = 0.15$, d.f. = 15, $P = 0.59$). There was further no correlation between the species when localities with permanent ponds only were included (Pearson $r = 0.10$, d.f. = 15, $P = 0.72$). However, for temporary localities only, there was a tendency for positive correlation, i.e. between year fluctuations tended to be in parallel for the two species (Fig. 8, Pearson $r = 0.50$, d.f. = 15, $P = 0.060$).

5. Discussion

5.1. *What is measured?*

The direct subject of this monitoring is the number of spawn clumps. This may be a valid measure in its own right as a measure of reproductive potential but is also useful as an indicator of the adult population size. It would be a perfect index if sex ratios were fixed and all females bred each year from a population specific age. The former is probably not always true. Yearly variation in sex-ratios has been shown for *Rana sylvatica* by Berven (1981) and for *R. arvalis* by van Gelder and Wijnands (1987). However, in some respects, a measure of the female segments only may be as useful as one for the whole adult population.

There is however also increasing evidence that the relation between number of adult females and number of egg masses deposited is quite variable over years. Examples were documented for *Rana sevosa* (Richter et al., 2003), for *Scaphiopus hoolbroki* (Greenberg and Tanner, 2005) and has repeatedly been documented for fish (review by Rideout et al., 2005) and also for marine turtles (Hays, 2000; Solow et al., 2002). A variation of this phenomenon is present if "adult female" is defined as any female exceeding a fixed (for the population) age, as age at maturity may depend on year specific weather factors. E.g., in a spring after a summer with favourable weather most young females may breed at age T but after poor weather, some may postpone first breeding until age $T + 1$. However, a short term study in one pond within the present study are failed to find indications of skipped breeding opportunities in *R. temporaria* (Eekhout, 2000). The same was concluded by Ryser (1988), also for *R. temporaria*, based on a study in Switzerland. A potentially important source of variation, skipped breedings due to dry ponds, is eliminated in this study as years when all ponds at a locality were dry in spring were treated as missing data, rather than zero spawn.

We do not think we can state for certain if variation in breeding frequency (skipped reproduction) occurs in the presently studied populations. It may not be important but must be taken into account as a possibility. However, even if present, this is a small problem if the object of the analysis is to detect multi-year, long term, trends. Spurious trends would require a long-term trend in the proportion breeding (but no corresponding trend in the actual population size). This, to us, seems far fetched.

5.2. *Potential biases*

The bias for ponds that are easily and quickly monitored could be a problem if trends were different in localities close to public roads than in those more remote. This is in principle possible, there might, e.g., be a negative bias because of increased traffic during the study years. However, few of the sampled localities were situated in the vicinity of major roads. Also, we see no obvious bias by using surveyability as a criterion for inclusion. If there were any bias with respect to hab-

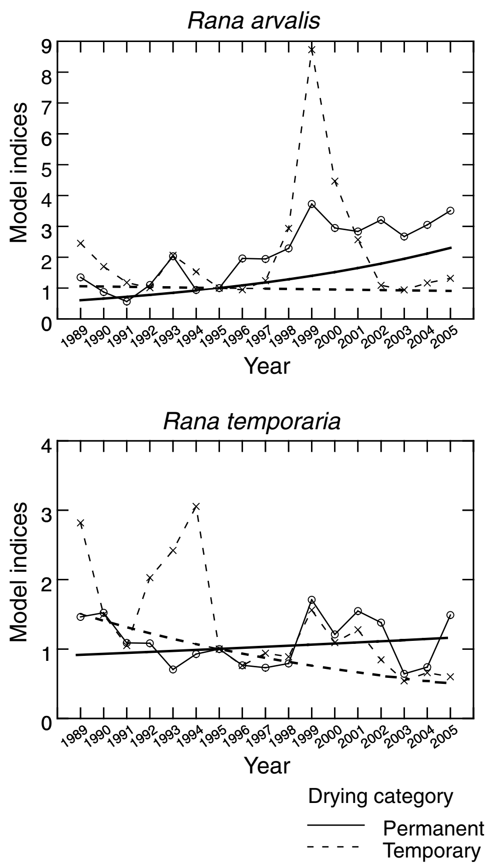

Fig. 6 – Model indices for spawn clumps in permanent and temporary ponds. Indices with yearly symbols are based on a model with all years included as switchpoints. The models for the total 17 year trends are indicated without yearly symbols. For base year, 1995 is chosen. This does not affect slopes but means this year is set to "1". This facilitates comparison of models for the period after 1995, which is the more reliable one, due to more sites available.

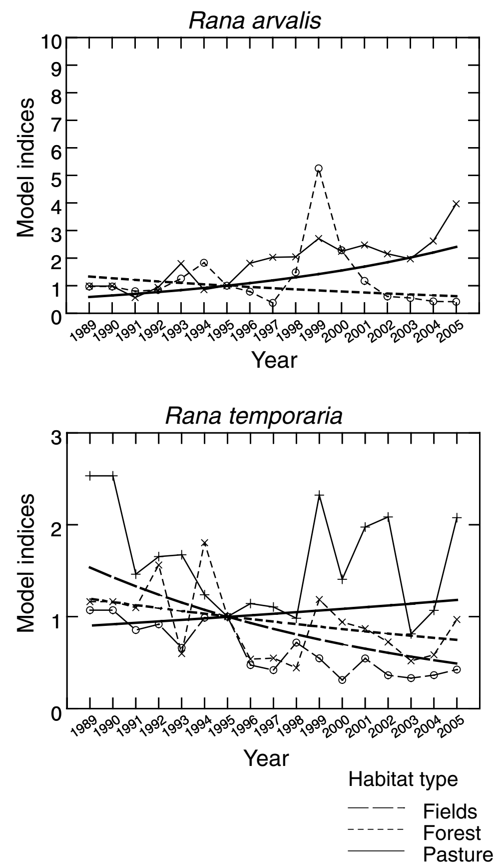

Fig. 7 – As for Fig. 6 but ponds classified by surrounding habitat. *R. arvalis* were only found in forest and pasture ponds. 1995 is set as base year.

Table 2 – Significance of trends for subset of localities based on pond hydroperiod or surrounding habitat classification

			Slope	P
Hydroperiod	Permanent	*R. arvalis*	Positive	<0.001
		R. temporaria	Positive	<0.10
	Temporary	*R. arvalis*	Negative	n.s.
		R. temporaria	Negative	<0.05
Habitat	Forest	*R. arvalis*	Negative	n.s.
		R. temporaria	Negative	n.s.
	Pasture	*R. arvalis*	Positive	<0.05
		R. temporaria	Positive	n.s.
	Field	*R temporaria*	Negative	<0.10

Tests based on SD for slope estimates (Pannekoek and van Strien, 2003).

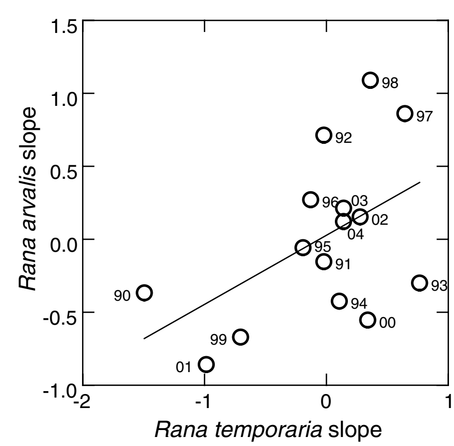

Fig. 8 – Correlation between yearly trends for *R. temporaria* vs *R. arvalis*. Only localities where both species were found in at least one year are included. The slopes used are thus not exactly the same as those shown in Fig. 7. Year labels indicate the starting year of each trend. 1989 is not included as there was no temporary pond with *R. arvalis* monitored in this year.

itat this will be accounted for in the analyses including covariates (surrounding habitat or drying status).

The use of a correction factor to count spawn in large masses was employed to save time and minimize disturbance to breeding sites. In particular, walking around much at the site would risk stepping on frogs hiding at the bottom. The practice might result in some bias when comparing sites. This is because the number of clump layers in a mass depends on the pond structure and water depth at the actual breeding site. However, for any single pond, breeding sites were usually constant in topography from year to year, minimizing within pond, between year, variation in the correction factor. If the standard factors were wrong, this could somewhat distort the actual count at large breeding sites but should have very little effect on between year trends, which are the object of this analysis.

5.3. *Overall trends*

The present study does not give reason for alarm with respect to the local survival of these two species. Actually, for one of them, *R. arvalis*, an increasing population trend was found.

There are a few other long term monitoring series for these two species. van Gelder and Wijnands (1987) and Ishchenko (1994) monitored *R. arvalis* for 17 years in Holland and 11 years in the Ural. *R. temporaria* was monitored by Cooke (1972), Elmberg (1990), Meyer et al. (1998) and van Buggenum (2004) for 13 years in England, 10 years in northern Sweden, 28 years in Switzerland and 16 years in Holland, respectively. The only significant decrease noted in these studies was for one out of three ponds in the Swiss study. This was explained by the introduction of fish into the breeding pond. These studies support an optimistic view. However with only six studies, it is not possible to state that these frogs are secure in all parts of their range. Also, most of the studies were conducted in one or a few ponds. This means that ponds that have been lost were systematically not part of the study sets and some localities abandoned for this reason did not affect the computation of trends. In the present study, a few ponds were indeed permanently lost due to antropogenic draining.

For frogs at large, a meta study by Houlahan et al. (2000) suggest global decline since the beginning of available data in the 1950s but with variation between periods and between regions. In western Europe, there was however no significant decrease during the period 1966–1997. A contrasting interpretation of the same data set (Alford et al., 2001) only found a global decline since 1990. Another meta study (Stuart et al., 2004) was based on subjective assessments by field researchers, rather than (as for study by Houlahan et al. (2000)) published data series. This gives a more balanced cover of the global situation today but may be more subject to various biases. Also, the basis for the study is not actually trends, rather red list status. However, a comparison is relevant. This suggest that the situation in Europe is at the average global level or better. For Europe they (Stuart et al., 2004) conclude that habitat destruction is the main cause of decline. The same was concluded for frog populations in New York state, USA (Gibbs et al., 2005). In the present study, this aspect was excluded from analysis because destroyed, usually drained, localities were excluded from analysis. Thus, our analysis does not contradict the possibility that habitat destruction is a problem for amphibian populations, including the species studied by us.

The ratio of increase to decrease years did not support a pattern suggested by Alford and Richards (1999) for amphibian populations). They suggested that yearly population *increases* should typically have greater magnitude (per year) but (in a zero trend population) be fewer than *decreases*. This did not apply and a conclusion similar to ours was reached in a review by Green (2003).

5.4. *Short term trends*

The general pattern is one of fairly large population fluctuations. The statistical analysis shows that many of these between year trends represent significant changes in the trend for the region. However, because there was a variation among localities, a substantial number is needed to detect such trends. Only when more localities were added in 1994 and 1995, it seemed the study had sufficient power to detect trends in the populations of *R. arvalis*. Still, in general, the variation in the small initial samples of localities were in agreement with that of the larger samples in later years.

There was little agreement in single year trends between the two species. This suggest that different processes affect their population dynamics. Only in the temporary localities was there some agreement. In these, episodes of drought may contribute to synchronizing the dynamics.

5.5. *Effects of pond permanency and habitat*

Analysing different categories of ponds (here localities) increases the resolution of the results and gives som clues to the cause of changes. For both species, some populations in localities with permanent ponds increased and the trend was significantly more positive than that for temporary ponds. For *R. arvalis* but not *R. temporaria* this result may be confounded by covariation between hydroperiod and habitat. The effect of pond hydroperiod may be the result of a trend in water regime but it may also be because localities classified as temporary usually were smaller. Actually, the average number of ponds in “temporary” localities was 1.5 while it was 2.3 in “permanent” localities. The average number of spawn clumps was 45 and 59 (for *R. arvalis* and *R. temporaria*, respectively) in the former and 108 and 202 in the latter type of localities. This size bias is partly an effect of the way localities were defined as “temporary” or “permanent” (with more ponds, it is more likely that at least one is permanent). Thus, it is not quite clear if the difference in trend is an effect of pond hydroperiod or an effect of smaller populations being more sensitive to effects causing a negative trend. However, whatever the interpretation, it is clear that localities made up only of temporary ponds (that tend to be part of small localities) have shown a negative trend for *R. temporaria* during the last 17 years. These localities may thus be in need of special protection.

For both species, localities on pastures showed an overall population increase. The cause for the relative decrease in forest and field (agricultural areas) localities is not clear. At least for *R. temporaria* it was not due to covariation with pond hydroperiod status. Actually, field localities were typically made up of permanent pond that in this respect actually had a more positive trend than temporary ones. The decrease may be related to the smaller number of ponds in forest localities (1.2 vs 2.1 in pasture localities) or the smaller populations sizes in forest (78 and 103 for *R. arvalis* and *R. temporaria*, respectively) and field localities (48 *R. temporaria*) compared to pasture localities (129 and 147 for *R. arvalis* and *R. temporaria*, respectively). It may also be an indication of some deterioration in the forest and field habitats, although no obvious changes were noted. If the population size of localities in this study are typical of those in the area, which seems likely, the change is however real and it is clear that the relatively small and isolated localities in forest and, in particular, fields in agricultural areas suffer a decrease in frog populations. These may thus be in need of special protection.

Several studies have documented the adverse effects of intensive agriculture on amphibian distribution (Bonin et al., 1997; Lehtinen et al., 1999; Kolozsvary and Swihart, 1999; Bishop et al., 1999). This may be due to fragmentation or adverse effects of agriculture *per se* (pesticides, deterioration of summer foraging habitat) or a combination of these factors. No previous study shows an on-going decline in this habitat. Thus, this study seems to be the first to demonstrate a poorer trend in some habitats, including agricultural ones, than in less intensively exploited habitats, like pastures.

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Appendix A

Spawn found in the study ponds/localities. A locality is a group of ponds where no pond is more than 500 from at least one other in the group (and all ponds are separated from ponds in other localities by at least 500 m).

Year	No spawn	Only *R. arvalis*	Only *R. temporaria*	Both species	Only spawn indet.	Total
Ponds						
1989	1	0	10	3	0	14
1990	2	1	18	7	0	28
1991	3	1	21	6	0	31
1992	3	0	22	8	0	33
1993	3	2	20	8	0	33
1994	5	1	43	24	0	73
1995	24	5	41	19	9	98
1996	45	0	42	28	3	118
1997	38	2	49	30	0	119
1998	34	5	42	38	0	119
1999	33	0	46	40	0	119
2000	32	4	45	38	0	119
2001	32	7	42	39	0	120
2002	34	5	43	39	0	121
2003	46	5	40	29	0	120
2004	41	9	38	33	0	121
2005	38	6	35	41	0	120
Localities						
1989	0	0	3	2	0	5
1990	0	0	7	4	0	11
1991	0	0	9	4	0	13
1992	0	0	9	4	0	13
1993	0	0	8	5	0	13
1994	0	0	27	12	0	42
1995	7	1	26	11	6	51
1996	11	0	27	18	3	59
1997	10	0	30	19	0	59
1998	7	1	28	23	0	59
1999	9	0	27	22	0	58
2000	7	2	26	23	0	58
2001	9	2	23	24	0	58
2002	9	3	26	20	0	58
2003	15	1	21	20	0	57
2004	10	4	24	20	0	58
2005	10	2	21	24	0	57

Appendix B

Dry and habitat classification of study localities. Only localities where spawn was found in at least one of the study years are included. A locality has been assigned to the least dry prone category of the included ponds, provided this on average has contained at least 10% of spawn found at the locality. The two lower sections refer to localities that have been studied in all years 1989–2005 and 1995–2005, respectively.

	Forest	Pasture	Fields	Other and mixed	Total
R. arvalis					
All localities					
Never dries[a]	0	2	1	4	**7**
Dries in extreme years[a]	2	8	0	6	**16**
Dries often[b]	1	4	0	2	**7**
Dries in almost all years[b]	0	0	0		**0**
Total	**3**	**14**	**1**	**12**	**30**
Localities 1989–2005					
Never dries	0	1	0	0	**1**
Dries in extreme years	0	1	0	0	**1**
Dries often	0	0	0	0	**0**
Dries in almost all years	0	0	0	0	**0**
Total	**0**	**2**	**0**	**0**	**2**
Localities 1995–2005					
Never dries	0	2	0	3	**5**
Dries in extreme years	1	6	0	3	**10**
Dries often	0	4	0	0	**4**
Dries in almost all years	0	0	0	0	**0**
Total	**1**	**12**	**0**	**6**	**19**
R. temporaria					
All localities					
Never dries	1	5	5	6	**17**
Dries in extreme years	2	10	2	9	**23**
Dries often	6	9	1	2	**18**
Dries in almost all years	0	1	1	1	**3**
Total	**9**	**25**	**9**	**18**	**61**
Localities 1989–2005					
Never dries	0	1	2	0	**3**
Dries in extreme years	0	1	0	0	**1**
Dries often	0	1	0	0	**1**
Dries in almost all years	0	0	0	0	**0**
Total	**0**	**3**	**2**	**0**	**5**
Localities 1995–2005					
Never dries	1	5	4	5	**15**
Dries in extreme years	1	7	2	5	**15**
Dries often	5	8	1	0	**14**
Dries in almost all years	0	1	0	1	**2**
Total	**7**	**21**	**7**	**11**	**46**

a In the analyses, these two categories are pooled into one; permanent ponds.
b In the analyses, these two categories are pooled into one; temporary ponds.

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