

Habitat management and global warming positively affect long-term (1987–2011) chorus counts in a population of the European tree frog (*Hyla arborea*)

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We investigated the importance of habitat measures and climate variables on the development of a managed European tree frog (*Hyla arborea*) population based on chorus counts between 1978 and 2011, using Akaike's Information Criterion (AICc) to select the best predictors. Pond area increased over the study period through site management, and was the most important variable in all models. In the density independent models, the annual numbers of calling males were positively correlated with total area of ponds two years before the count, a time lag which corresponds with the time needed for metamorphs to mature. Mean daily temperature, the total amount of precipitation during the breeding season (both with a 2 year time lag) and high winter temperature before the breeding season also had positive effects on the *H. arborea* population. A linear regression of temperature with study years revealed an annual increase of 0.08 °C, whereas precipitation showed no trend. Yearly population growth rates were furthermore density-dependent, and influenced by temperature during breeding season. Our study showed that a combination of habitat management practices and increasing temperatures likely through global warming positively affected the *H. arborea* population.

Key words: AICc, amphibian, density dependence, long term monitoring, model selection, predictors

INTRODUCTION

Amphibians are good indicators of the ecological quality of the habitat in which they live. Survival of pond-breeding species depends on the suitability of the aquatic breeding habitat and the quality of the surrounding landscape. Changes in habitat will have an impact on the viability, abundance and distribution of populations. In recent years, the impact of global climate change on the survival of amphibian populations caused particular concern among amphibian ecologists and conservationists (Reading, 2007; Henle et al., 2008; Bickford et al., 2010; McGrath & Lorenzen, 2010, see Beebee & Griffiths, 2007 for a summary).

In the Netherlands, the European tree frog (*Hyla arborea* L., 1758) formerly occupied large areas but is now suffering from widespread declines and local extinctions (Stumpel & Crombaghs, 1995; Glandt, 2004; Zollinger, 2004; Stumpel et al., 2009). To identify possible causes for declines, it is necessary to discriminate between human and non-human impacts over a long period of time (Pechmann et al., 1991). Long-term field studies on amphibians to identify actual population trends are generally still rare (Meyer et al., 1998; Marsh, 2001; Schuster, 2001; Collins & Halliday, 2005; Pellet et al., 2006).

In our long-term study of a European tree frog population we focus on the following three questions: (1) What is the overall trend of several selected extrinsic variables and the tree frog chorus population during the period of 1978–2011? (2) Can the observed fluctuations of the chorus estimates be explained by management measures, changes in climate (i.e. rainfall and temperature)

or changes in water level? (3) Is there evidence for density dependent population regulation? We discuss in what way our results can contribute to improved conservation management of threatened amphibian populations.

MATERIALS AND METHODS

Study area and conservation management measures

Our study was conducted on an isolated *H. arborea* population in the Doort nature reserve (owned by the Dutch State Forestry Service) near Echt in the province of Limburg (51°05' N, 5°51' E, 25 m above sea level), The Netherlands. The region links a Pleistocene sandy lowland landscape with a Quartair hilly loess landscape. The Köppen-Geiger climate type is Cfb (Peel et al., 2007).

The study site is about 120 hectares in size and lies on an ancient floodplain two kilometres east of the Meuse River. Due to a shipping canal built around 1930, flooding of the area no longer takes place. Forest, strips of trees or shrubs around the breeding site are used for migration or as a summer habitat (Vergoossen, 1991). Between 1920 and 1960, ten large clay pits were created for the local brick and roof tile industry. Since a land consolidation (1975–1978), the clay pits and surrounding farmland has been successively converted into a nature reserve. Much attention is devoted to improve the site for tree frogs through the removal of vegetation, the creation of new reproduction sites and improvement of the land habitat.

Population monitoring

From 1978–2011 we annually counted calling *H. arborea* from mid April to late May under optimal weather conditions. The number of calling sites increased from

three to fourteen over the study period, and all recorded calling males at all sites were considered for population counts. Visits were conducted between two and four times each year. We took the annual maximum count to establish the yearly estimate of chorus size (N_t), a common approach used in tree frog monitoring studies (Stumpel,

1987; Tester, 1993; Carlson & Edenhamn, 2000; Grafe & Meuche, 2005; Pellet et al., 2006). We calculated the yearly growth rate as the natural log-transformed value of N_{t+1}/N_t (following Dennis & Taper, 1994; Meyer et al., 1998; Pellet et al., 2006).

Table 1. Descriptive statistics and linear regression of environmental variables against year of observation (1978–2011). Temp.=mean day temperature; R^2 =explained variance; SD=Standard deviation; n.s.=non significant at $P>0.05$.

	Descriptive statistics						Linear regression (variable against year)			
	Abbr.	N	Minimum	Maximum	Mean	SD	R^2	F-ratio	slope	P-slope
Chorus estimate	Nt	34	20	430	154.12	95.29	52%	34.922	6.912	<0.001
Yearly growth rate	Growth	33	-0.96	1.24	0.05	0.55	2%	0.462	-0.007	n.s.
Pond area (m ²)	Pa	34	1000	2810	1936.18	617.65	63%	54.089	49.163	<0.001
Temp. winter =Jan–March (Celcius)	Tw	34	-0.17	6.90	3.96	1.80	13%	4.670	0.064	<0.05
Hellmann	He	34	7.90	238.10	69.11	59.87	8%	2.697	-1.676	n.s.
Temp. breeding season =April–July (Celcius)	Tb	33	12.09	15.96	14.21	1.00	59%	44.343	0.080	<0.001
Temp. activity season =April–Sept (Celcius)	Ta	33	13.08	16.57	14.88	0.86	56%	39.445	0.067	<0.001
Sunshine activity season =April–Sept (sum hours)	Sa	33	825.60	1391.20	1061.72	128.61	47%	27.061	9.080	<0.001
Rain winter =Jan–March (mm)	Rw	34	72.50	297.60	162.47	47.75	<1%	0.058	-0.204	n.s.
Rain breeding season =April–July (mm)	Rb	33	146.10	337.30	243.96	52.03	8%	2.686	-1.519	n.s.
Meuse level March (m above sea level)	MM	34	21.59	25.59	23.37	0.97	7%	2.334	-0.025	n.s.
Meuse level June (m above sea level)	MJ	33	20.97	23.21	21.71	0.54	47%	27.027	-0.038	<0.01

Environmental parameters

We defined ten predictor variables to explain trends and fluctuations in chorus estimates (Table 1). New ponds (1.5–2 m deep and 100–450 m² in area) were created in 1983, 1985 and 1993. A pond was only taken into account as a potential chorus site when it contained no fish (except the sticklebacks *Gasterosteus aculeatus* and *Pungitius pungitius*), had sufficient water in April–May and was not shaded by shrubs or trees (Grosse & Nöllert, 1993). These aspects varied over the years, and total pond area therefore fluctuated during the study period. Total pond area was expected to affect the number of calling males with a two-year time lag ($t-2$) because most juvenile males reach sexual maturity after two seasons (Moravec, 1993). New ponds were included into the models after the second season of digging, when at least some water vegetation important for egg deposition was present (Fog, 1988; Grosse, 2009).

Climate data were obtained from KNMI (2011). Temperature and sunshine data were obtained from the Beek-Maastricht weather station (50°54'N, 5°46'E at a distance of 20 km), and rainfall levels were obtained from the Echt weather station (51°05'N, 5°54'E at a distance of 3.9 km). Since winter temperature might affect the survival of hibernating frogs (e.g. Anholt et al., 2003; Reading, 2007), we calculated the mean daily temperature for the three winter months (January–March) before the start of the breeding season. We also considered the Hellmann criterion, which is the sum of all mean day temperatures below zero between November in the previous year until March. Mean daily temperature during the breeding season (April–July) at year $t-2$ was calculated since high temperatures might positively affect development and survival of tadpoles. As growth and survival of sub adults and adults during the activity season (April–September) can be also a relevant factor (e.g. Moravec, 1993; Grosse, 2009), we further calculated mean day temperature and total amount of sunshine at year $t-1$. We expect a positive influence of rainfall in the winter period of year $t-2$ (January–March), since this contributes to assure sufficient water in the ponds at the beginning of the calling season. Furthermore, rainfall during the breeding season (April–July) might prevent the breeding sites from early drying, and maintains sufficient carrying capacity for tadpoles (e.g. Pearman, 1993). Water levels also depend on the nearby Meuse River with a lag of one month (Pearson's $r > 0.70$; $P < 0.05$), and we used Meuse River levels in March and in June as an additional indicator for pond water levels. The groundwater and river levels were provided by the Ministry of Transport, Public Works and Water Management and by the regional Water Authority Roer en Overmaas.

Data analyses

We used SPSS v19.0, SAM v4.0 (Rangel et al., 2010) and R (R Development Core Team, 2004) to explore correlations between environmental variables, chorus estimates and yearly growth rates. The level of significance was 0.05.

We determined four descriptive statistics for each variable (mean, standard deviation, minimum and maximum), and related each variable with study years

(1978–2011) using linear regressions. All variables were tested for multicollinearity by Pearson product-moment correlation coefficient r (Pearson's r). High degrees of correlations were found between winter temperature and the Hellmann criterion ($r = -0.84$), temperature and sunshine during the breeding season ($r = 0.79$) and precipitation during the winter period with water level of the Meuse River in March ($r = 0.71$). All variables except total pond area (normally distributed after log-transformation) were normally distributed (Kolmogorov-Smirnov tests, detailed data not shown).

We built generalized linear models (GLM) with the natural log-transformed chorus estimates (X_t) as the response variable using the equation:

$$X_t = a + cWt - n + \sigma Z_t,$$

where W is the covariate, n is 0, 1 or 2 (depending on the specified time lag) and Z is a normal random noise variable at time t . For all variables we calculated the coefficients (a , c , σ), F -ratio (ANOVA) and explained variance (R^2).

After this we compared original, log- and square transformed values. To select the candidate model or type of transformation that best supported the data, we used the second-order Akaike's Information Criterion corrected for small samples ($AICc$) and $\Delta AICc$ (Burnham & Anderson, 2002, 2004; Mazerolle, 2006). Neither log-transformed nor square-transformed values performed significant better than original values (all $\Delta AICc < 2$). To select the best multivariate density independent candidate models we calculated the $AICc$ of all 1023 possible combinations of the ten predictors. Models with $\Delta AICc > 2$ were considered to receive unsubstantial support from the data (Burnham & Anderson, 2004).

We used the following general log-linear form for modelling yearly growth rate considering density dependency (N_t):

$$\ln(N_{t+1}/N_t) = a + bN_t + cWt - n + \sigma Z_t$$

We applied the same covariates, methods and statistics as in the density independent models. We tested the data with the Ricker-type model and the Gompertz-type model, which uses X_t instead of N_t at the right hand of the equation. We also used a parametric bootstrap likelihood ratio (PBLR) to test a density independent model 1 ($b = 0$) against a density dependent model 2 ($b < 0$) while $c = 0$. For a detailed description and discussion we refer to Dennis & Taper (1994) and Pellet et al. (2006). The yearly growth rate was tested for autocorrelation using the Box-Ljung method (Ljung & Box, 1978), an autoregressive-moving average methods for time series analyses (e.g. Ryding et al., 2007).

RESULTS

Trends in chorus estimates and environmental variables

At the beginning of the study period, the chorus estimates resulted in about fifty calling males. After this, the

Table 2. Model selection and parameter estimates of ten univariate and four multivariate density independent generalized linear models (GLM), with ten predictors variables and the log-transformed chorus estimates (X_t) of the *Hyla arborea* population (1978–2011) as the response variable. $AICc$ = Akaike's Information Criterion corrected for small sample sizes; for abbreviations see Table 1.

Single variable candidate models							
	<i>Abbr.</i>	R^2	F -ratio	Slope	P -slope	$AICc$	$\Delta AICc$
Pond area (2-year lag)	Pa	48%	29.710	1.468	<0.001	64.039	0.000
Temperature winter	Tw	13%	4.819	0.160	0.024	81.598	17.559
Hellmann	He	7%	2.227	-0.003	n.s.	84.080	20.041
Temp. breeding season (2-year lag)	Tb	34%	16.446	0.444	<0.001	72.267	8.228
Temp. activity season (1-year lag)	Ta	34%	16.306	0.514	<0.001	72.365	8.326
Sunshine activity season (1-year lag)	Sa	23%	9.436	0.003	0.002	77.581	13.542
Rainfall winter (2-year lag)	Rw	<1%	0.179	0.001	n.s.	86.177	22.138
Rainfall breeding season (2-year lag)	Rb	<1%	<0.001	<0.001	n.s.	86.367	22.328
Meuse level March (2-year lag)	MM	<1%	0.060	0.036	n.s.	86.303	22.264
Meuse level June (2-year lag)	MJ	6%	1.983	-0.361	n.s.	84.322	20.283
Multivariate candidate models		R^2	F -ratio	Slope	P -slope	$AICc$	$\Delta AICc$
Model 1	Pa	59%	14.501	1.139	<0.001	61.242	0.000
	Tb			0.284	0.006		
	Rb			0.003	0.046		
Model 2	Pa	54%	18.506	1.133	<0.001	62.233	0.991
	Tb			0.226	0.031		
Model 3	Pa	61%	11.500	1.262	<0.001	62.371	1.129
	Tb			0.275	0.006		
	Rb			0.004	0.026		
	Rw			-0.003	n.s.		
Model 4	Pa	60%	11.038	1.035	<0.001	63.220	1.978
	Tb			0.284	0.005		
	Rb			0.004	0.026		
	Tw			0.056	n.s.		
All other tested models		-	-	-	-	>63.220	>2.000

chorus gradually increased, however with intermittent short-term declines. In the last ten years of study, chorus estimates were between about 150 and 400 males (Fig. 1A). The overall linear trend is positive ($R^2=0.52$). The mean yearly growth rate is above zero, and shows no linear trend ($R^2=0.02$). The total pond area increased in a stepwise fashion, due to the digging of ten ponds in three different years (Fig. 1B). The mean ground water levels (and thus pond water levels) ranged from about 95 cm below the surface in April to about 145 cm below the surface in July between 1984 and 2009. The depth of the new ponds usually guaranteed about a water level of one

metre in April and several decimetres at the end of the breeding season. However, the ground water level trend is negative, with a slope of 2.3 cm per year in the month of July ($R^2=27\%$, $F_{1,24}=8.724$, $P=0.007$). The water level of the Meuse River also shows a negative trend, whereas the total amount of precipitation shows no trend. From 1990 onward, the pond water levels show large fluctuations and early drying of ponds became a major problem.

Temperature change is reflected in milder winters and warmer summers. The temperature rose linearly over the study period by about 0.08 degrees per year, resulting in a 2.7 degree difference between the beginning and the end

of our study period. The total amount of sunshine shows a similarly positive trend.

Density independent and dependent candidate models

The summary statistics for the density independent candidate models for X_t , ten univariate predictor variables and four multivariate models are presented in Table 2. Multivariate models with $\Delta AICc$ differences below 2 from the best performing model are not listed.

The predictor that best explained the variation in X_t is total pond area at year $t-2$ ($R^2=0.48$). Also the temperature variables and sunshine appear to be important (R^2 between 0.13 and 0.34). The total amount of rainfall and water level of the Meuse River are not correlated with X_t ; except for the Hellmann criterion, all other slopes have a positive sign. All four best performing multivariate GLM models include pond area and mean day temperature during the breeding season, both with a 2-year time lag.

Winter temperature in year t is included in one model. The total amount of rainfall in the breeding season at year $t-2$ is part of three models, and winter rainfall is included in one model. The range of explained variance for these best performing models is 54–61%.

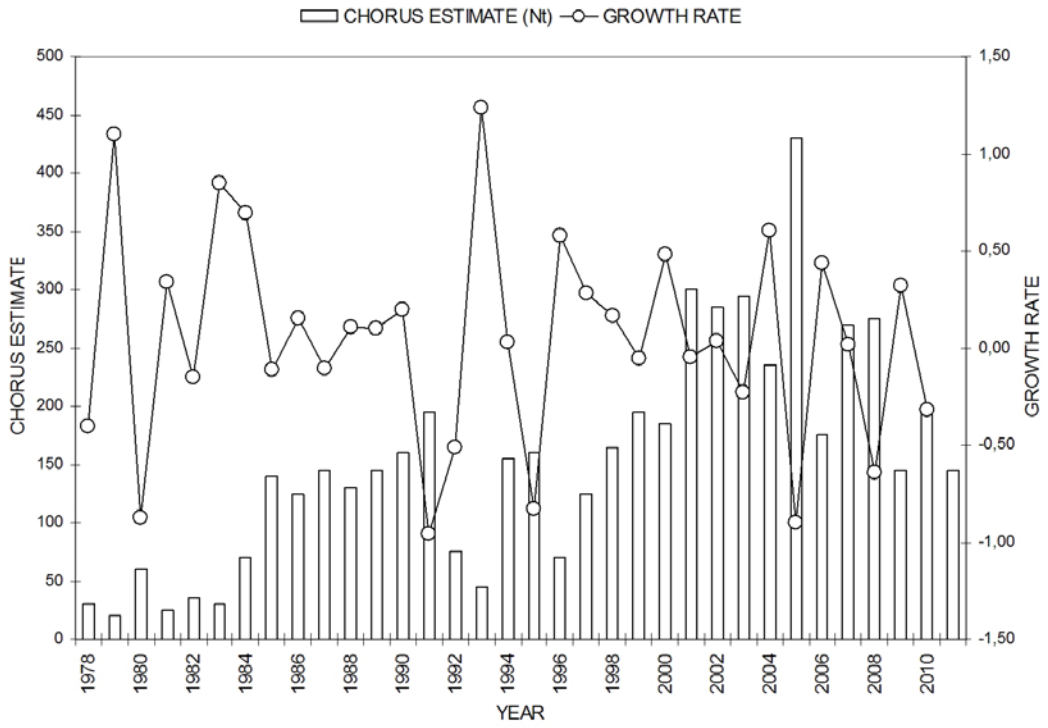
The summary statistics for the density-dependent candidate models for yearly growth rate are presented in Table 3. Univariate Ricker- (N_t) and Gompertz models (X_t) perform best and are equally supported by the data. The explained variance is rather low ($R^2=0.17$). All other variables support the yearly growth rates only weakly. Three multivariate models with low $AICc$ all contain N_t or X_t (with negative slopes) and temperature during the breeding season (with a 2-year time lag and a positive slope). One model includes the Hellmann criterion, however with an insignificant regression slope.

The results of the PBLR test of the chorus estimates show no significant evidence of density dependence (Table 4). The result of the autocorrelation test of the yearly

Table 3. Model selection and parameter estimates of twelve univariate and three multivariate density dependent generalized linear models (GLM), with yearly growth rate $\ln(N_{t+1}/N_t)$ as the dependent variable (see Tables 1 and 2).

	<i>Abbr.</i>	R^2	F	Slope	P -slope	$AICc$	$\Delta AICc$
Nt (Ricker-type model)	Nt	17%	6.506	-0.002	0.016	53.460	0.000
Xt (Gompertz-type model)	Xt	17%	6.293	-0.280	0.018	53.648	0.188
Pond area (2-year lag)	Pa	2%	0.489	-0.185	n.s.	59.231	5.771
Temperature winter	Tw	2%	0.746	-0.046	n.s.	58.962	5.502
Hellmann	He	1%	0.335	<0.001	n.s.	59.392	5.932
Temp. breeding season (2-year lag)	Tb	<1%	0.135	0.035	n.s.	59.603	6.143
Temp. activity season (1-year lag)	Ta	<1%	0.243	-0.056	n.s.	59.439	5.979
Sunshine activity season (1-year lag)	Sa	4%	1.150	<0.001	n.s.	58.545	5.085
Rainfall winter (2-year lag)	Rw	2%	0.665	-0.002	n.s.	59.046	5.586
Rainfall breeding season (2-year lag)	Rb	<1%	<0.001	<0.001	n.s.	59.747	6.287
Meuse level March (2-year lag)	MM	<1%	0.119	0.036	n.s.	59.621	6.161
Meuse level June (2-year lag)	MJ	3%	1.047	0.190	n.s.	58.651	5.191
Multivariate candidate models		R^2	F	Slope	P -slope	$AICc$	$\Delta AICc$
Model 1 Gompertz-type	Xt Tb	32%	6.910	-0.472 0.249	<0.001 0.017	49.844	0.000
Model 2 Ricker-type	Nt Tb	29%	6.251	-0.472 0.217	0.001 0.031	50.852	1.008
Model 3 Gompertz-type	Xt Tb He	34%	5.070	-0.476 0.299 0.002	<0.001 0.010 n.s.	51.227	1.383
All other tested models		-	-	-	-	> 51.905	> 2.000

A



B

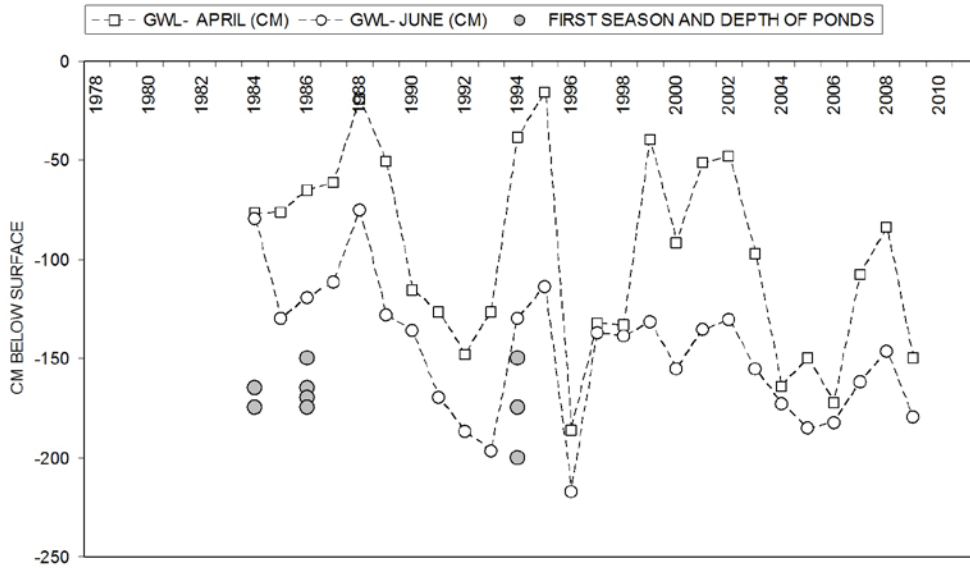


Fig. 1. (A) Chorus estimates and the yearly growth rate $\ln(N_{t+1}/N_t)$ of the European tree frog (*Hyla arborea*) in the Doort-area, the Netherlands, from 1978–2011. (B) Ground water levels (GWL) in centimetre below surface are shown for April and July from 1984–2009. The larger circles symbolize the depth and year of digging of the new amphibian ponds. At the start of the study in 1978 clay pits with a depth of 1 metre were present.

Table 4. Parametric bootstrap likelihood ratio (PBLR) test of density dependence for the European tree frog chorus estimates in the Doort-area (the Netherlands). Number of bootstrap samples=2000. a, b, σ =estimated coefficients (see the quotation in the text about data analyses).

Maximum likelihood parameter estimates
density independent model ($b_1 = 0$)

$a_1 = 0.048$; $\sigma_1^2 = 0.291$

Maximum likelihood parameter estimates
density dependent model

$a_2 = 0.411$; $b_2 = -0.002$; $\sigma_2^2 = 0.241$

Likelihood ratio statistics

$T = -2.551$; $P = 0.111$

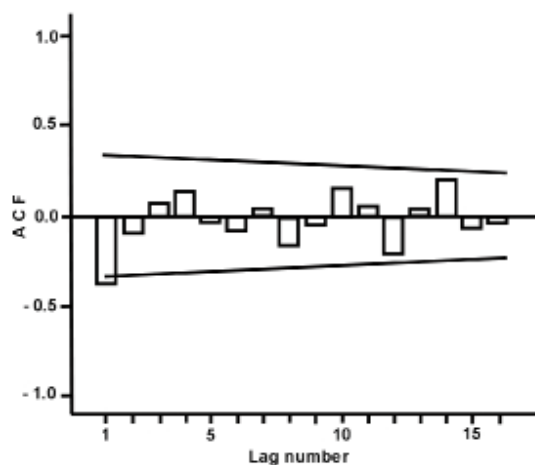


Fig. 2. Autocorrelation function (ACF) based on moving average time series of yearly growth rates of estimates of calling European tree frog males in the Doort-area (the Netherlands) in the period 1978–2011.

growth rate is presented in Fig. 2. The only significant correlation of the count data was with lag 1 year. The Box-Ljung value of lag 1 is 4.920 ($df=1$; $P=0.027$). The autocorrelation is negative (-0.369 ; $SE=0.166$).

DISCUSSION

Our tree frog population was able to increase after a major decrease in numbers that occurred before the onset of our study (Broen & Vergoossen, 1983), however without the genetic signature of a bottleneck (Vos et al., 2005). Our study shows that management, i.e. the digging of new small ponds, was the most important variable to explain the increase and variance in chorus estimates with a 2-year time lag. This measure seems to have a direct and positive impact on the population size. The increase of the total pond area from about 1000 m² to 2810 m² appeared to be the most crucial factor for population recovery. The effect of new terrestrial habitat mitigation (about 4000 m² of land with brambles and shrubs; Heimbucher, 1991; Stumpel, 1993; Junck & Schoos, 2000) however remained unmodelled in the present study.

Mean daily temperature during the breeding season is the most important climate variable to predict the size of the tree frog population. Higher mean day temperature had a positive effect on water temperature, and thus apparently improved breeding conditions for eggs and tadpoles (Tester, 1990; Sayim & Kaya, 2006). Therefore, in the case of our study population, the tree frog population has benefited from climate change in recent decades. Also higher winter temperature at year t has a positive effect. Anholt et al. (2003) found that, for the water frogs *Pelophylax* (*Rana*) *lessonae* and *P. esculenta*, cold winters were negative for survival, and McCaffery & Maxell (2010) documented positive effects of mild winters for a mountain frog (*Rana luteiventris*). However, on the other hand Reading (2007) and Griffiths et al. (2010) found that mild winters reduced annual survival in the common toad (*Bufo bufo*) and the crested newt

(*Triturus cristatus*), respectively. How milder winters might influence survival and viability of amphibians still needs further research (Henle et al., 2008).

Temperature and the correlated amount of sunshine in the activity season of year $t-1$ are only significant in the univariate models. However, they were not part of the best multivariate GLMs. Subadult and adult individuals might grow faster and have more survivors under better climatic conditions in their summer habitat (Stumpel & Hanekamp, 1986; Grosse, 2004), although in our case such effects were overridden by other factors. The univariate models for rainfall show no significant correlation with chorus counts, and tadpoles might adapt their metamorphosis to drying (Crump, 1989; Loman, 1999). The total amount of rainfall in the breeding season is however part of the best multivariate models, suggesting that the prevention of early drying during the breeding season has a positive effect (see e.g. Piha et al., 2007; McGrath & Lorenzen, 2010). Pellet et al. (2006) found that rainfall had a negative impact on *H. arborea* populations, whereas Hartel & Moga (2007) found a positive effect.

Pellet et al. (2006) demonstrated that both intrinsic and extrinsic factors affected their *H. arborea* population. They showed that, over a period of twenty years, yearly growth rate was negatively influenced by density, thus stabilizing it at its carrying capacity. Their Gompertz-type model appeared to be the best, whereas we did not find a difference between Ricker-type and Gompertz-type models. Our best density dependent models for yearly growth rates also included temperature during breeding season with a 2-year time lag. We conclude that a density dependent growth mechanism is present, but rather weak and probably overruled by habitat management and climate (see also Henle et al., 2004).

Although we support the use of capture-mark-recapture methods for population monitoring (Pellet et al., 2007), our chorus estimates provided useful information for evaluating conservation management measures as well as analyses of intrinsic and extrinsic factors that influence population size. Long-term monitoring should be labour-efficient and with the intention that it can be carried out over decades. The use of chorus estimates in (post-hoc) modelling involve uncertainties (Schmidt, 2004; Schmidt & Pellet 2009), and there is a need for meta-analyses of long-term data from different populations and environments (Henry et al., 2008).

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