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Density, climate and varying return points: an analysis of long-term population fluctuations in the threatened European tree frog

Abstract Experimental research has identified many putative agents of amphibian decline, yet the population-level consequences of these agents remain unknown, owing to lack of information on compensatory density dependence in natural populations. Here, we investigate the relative importance of intrinsic (density-dependent) and extrinsic (climatic) factors impacting the dynamics of a tree frog (*Hyla arborea*) population over 22 years. A combination of log-linear density dependence and rainfall (with a 2-year time lag corresponding to development time) explain 75% of the variance in the rate of increase. Such fluctuations around a variable return point might be responsible for the seemingly erratic demography and disequilibrium dynamics of many amphibian populations.

Keywords Amphibian · Density dependence ·
Population fluctuations · Population regulation ·
Population viability analysis · Model selection ·
Weather

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Introduction

There is an increasing interest among conservation biologists to learn about the effects of density dependence on life history traits and the dynamics of natural populations (Grant 1998; Forbes and Calow 2002; Vonesh and De la Cruz 2002; Henle et al. 2004). This is because the response of a natural population to negative anthropogenic impacts, such as habitat loss, pesticides, or harvesting, depends crucially upon density-dependent population responses (Sutherland and Norris 2002). While anthropogenic impacts often only affect a single life history stage or vital rate, population-level responses (e.g., population growth rate) are harder to predict (McPeek and Peckarsky 1998; Biek et al. 2002; Forbes and Calow 2002), especially because density dependence may buffer against such negative impacts (Forbes and Calow 2002; Vonesh and De la Cruz 2002). Thus, even though the study of density (in-)dependence began decades ago (Turchin 1995), it remains important to assess the relative importance of density dependence patterns for population growth (Sutherland 1996; Bjørnstad and Grenfell 2001; Lande et al. 2003) and to evaluate whether these patterns can and do in fact compensate for anthropogenic mortality (Pedersen et al. 2004; Govindarajulu et al. 2005; Rohr et al. 2006).

Amphibians are one group of animals where a better understanding of population-level processes, including density dependence, is necessary (Beebee and Griffiths 2005; Schmidt et al. 2005). This is because amphibians are declining globally for a variety of reasons acting at various spatial scales (Alford and Richards 1999; Houlahan et al. 2000; Collins and Storfer 2003; Stuart et al. 2004). Yet, the evidence for and against many of the proposed mechanisms for population declines is based largely on experimental studies that focused on vital rates of single life history stages (Beebee and Griffiths 2005), and most studies did not include density dependence or other factors that may dampen or enhance the effects of mortality, such as carry-over or time-lagged

effects (Pahkala et al. 2001; Rohr and Palmer 2005). Even though there is good evidence for density independence in some population studies (Jaeger 1980; Beebee et al. 1996; Semlitsch et al. 1996; Grafe et al. 2004), there is also substantial evidence for density dependence in both the aquatic and subsequent terrestrial stages (Jaeger 1980; Smith 1983; Petranka 1989; Berven 1990; Van Buskirk and Smith 1991; Altwegg 2003). Both density-dependent and density independent processes can contribute to population declines in amphibians (Jaeger 1980). Hence, it is unknown whether the effects of factors extrinsic to the population (e.g., pollutants, habitat deterioration, climate change) on tadpoles or adults translate into effects on population growth and ultimately population declines (Vonesh and De la Cruz 2002).

Research into amphibian population declines should adopt a step-by-step analysis incorporating long-term observations, experiments, and models for investigating how any specific anthropogenic stressor affects the population dynamics (Blaustein et al. 2004). Despite the obvious importance of time series analyses in this process, they are still rare in amphibian ecology (Semlitsch et al. 1996; Meyer et al. 1998), and consequently amphibians with their complex life cycles are not included in recent reviews of animal population dynamics (Bjørnstad and Grenfell 2001; Lande et al. 2003; Turchin 2003).

Here, we present an analysis of a long-term time series (22 years) of an isolated population of the European tree frog (*Hyla arborea* L., 1758). The population that we studied was not declining. Our goal was therefore not to explain a specific decline or the causes thereof, but rather to contribute to a better understanding of amphibian population dynamics that should be useful for amphibian conservation biology and population ecology in general. The time series analysis allowed us to evaluate the relative importance of intrinsic density dependence and extrinsic factors (i.e., weather), either alone or in combination, for population growth rate (Dennis and Taper 1994; Dennis and Otten 2000; Burnham and Anderson 2002). Thus, the first goal of the analysis was to answer the question whether the dynamic of the population was driven by intrinsic density dependence, extrinsic factors, or both. This question matters because we wanted to know whether density dependence could buffer the population against extrinsic perturbations. The second goal was to evaluate which type of density dependence was operating (Saitoh et al 1997), namely linear (Ricker 1954) or log-linear (Gompertz 1825). Because the type of density dependence strongly affects predictions of population models (Henle et al. 2004), such knowledge should greatly enhance the value of predictive amphibian population models. This would allow a feedback from time series analysis to population models and thereby allow closing the loop between experiments, observational studies, and population models (Werner 1998; Blaustein et al. 2004). The third goal was to investigate the mechanisms behind the seemingly erratic fluctuations that often characterize amphibian populations (Marsh and Trenham 2001; Green 2003) and may render them especially vulnerable to local and global extinction (Leigh 1981; Schoener and Spiller 1992; Inchausti and Halley 2003).

Materials and methods

Tree frog monitoring

The European tree frog is listed as "near threatened" in the global IUCN Red List, and is highly vulnerable in most of its distribution range (IUCN 2004), including Switzerland where the status on the Swiss Red List is "endangered" (Schmidt and Zumbach 2005). *H. arborea* first breeds at 2 years of age and has a life expectancy of 5–6 years (Friedl and Klump 1997). Tadpole growth and juvenile metamorphosis usually take place between early June and late September. Juveniles disperse before the first night frosts to their terrestrial overwintering habitats (Stumpel 1993), where they will remain until late March. As with most frogs and toads, males of the European tree frog exhibit a conspicuous breeding behavior by calling from pond shores to attract gravid females (Giacoma et al. 1993). Counts of calling males is considered an appropriate technique for evaluations of tree frog population density (Carlson and Edenhamn 2000; Tester 1993) and is one of the most widely used methods to assess population size in anuran populations (Heyer et al. 1994). Visiting ponds regularly during the breeding season (mid-March–late May in Switzerland; Pellet et al. 2004) provides several counts of calling males, from which the highest value for a given year is generally used as an index of breeding population size (Tester 1993; Edenhamn 1996; Carlson and Edenhamn 2000; Schmidt and Pellet 2005).

We studied an isolated population in western Switzerland (Lerchenfeld near Thun, 46°45′N, 7°35′E) from 1979 until 2004. Calling males were counted between one and four times (mean = 1.5) during the season by the same observer (K. Grossenbacher) in all years. The maximum count was used for analysis. In our population, breeding choruses were small, making it easy to accurately count individual calling males . We assume that the proportion of satellite males, the mean time spent at the pond, and the overall probability of breeding remained roughly constant through years. Because new breeding ponds were created in the area in the winter of 2000, the dataset was restricted to the time frame where carrying capacity of the habitat was expected to have remained stable (1979–2000, thus reducing it to a 22-year-long time series; Fig. 1).

Statistical analysis and candidate models

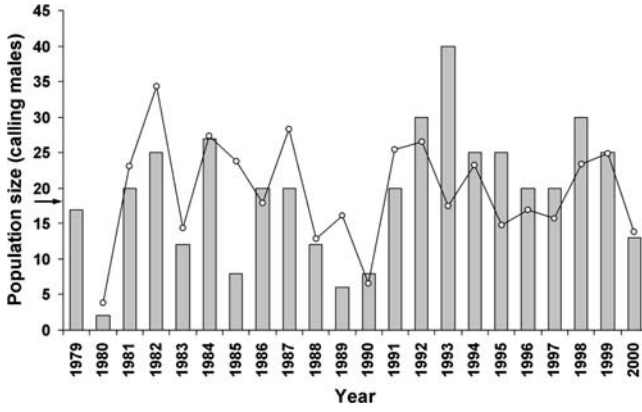We used standard statistical models developed for inference from short time series developed by Dennis

Fig. 1 Tree frog (*Hyla arborea*) calling males counts in Lerchenfeld from 1979 to 2000 (*bars*) and expected return point (*dots*). The return points are based on model H10 which has an AIC_c weight of 0.980 (Table 1). The *arrow* on the *y*-axis indicates the position of the mean return point (based on model H10)

and Taper (1994) and Dennis and Otten (2000). They are of the general form:

$$\ln\left(\frac{N_{t+1}}{N_t}\right) = a + bN_t + cW_t + \sigma Z_t, \tag{1}$$

where N_t is population size at time t, W_t is a climatic covariate, Z_t is a normal ($N \sim 0, 1$) random noise variable, and a, b, c and σ are the coefficients to be estimated. Dennis and Taper (1994) provide a detailed account of the properties of these models.

We built a set of candidate models and used information-theoretic model selection to determine which model describes the data best (Burnham and Anderson 2002). We first built a density independent null model which assumes stochastic exponential growth or decline, where slopes of N_t (b) and W_t (c) in Eq. 1 were constrained to be zero (model H0; Dennis and Taper 1994). We then tested for linear and loglinear density dependence (Saitoh et al. 1997). The linear function between growth rate ($\ln(N_{t+1}/N_t)$) and N_t corresponds to Ricker's (1954) density dependence model (model H1), while the loglinear model is obtained by replacing N_t in the right-hand part of Eq. 1 with the log-transformed abundance index $X_t = \ln(N_t)$ (Gompertz 1825; Saitoh et al. 1997, model H2). The third group of candidate models tested the effect of climatic variables.

The first climatic model (H3) tests the hypothesis that rainfall during the breeding season (from April to July) affects adult breeding probabilities and thus positively affects observed population growth rate (e.g., Semlitsch 1985). Similarly, the hypothesis under our second climatic model (H4) is that rainfall at year $t-2$ positively influences population growth rate with a 2-year time-lag which is the time to sexual maturity. Rainfall could either affect breeding population size as under model H3 or it may affect tadpole development (e.g., Reading and Clarke 1999; Reading 2003). The third climatic model

(model H5) represents the hypothesis that population growth rate is positively affected by pond water level during the period of tadpole development. The underlying hypothesis is that water level reflects pond volume which in turn is supposed to reflect the carrying capacity of the pond for tadpoles (e.g., Pearman 1993) which may positively affect population growth. Since the pond under study is located close to the river Aare (< 50 m) and shares its water table, we used the mean river water level from April to July (with a 2-year lag which is the time to maturity). Both rainfall and water level are weakly correlated by 13%, suggesting that pond water level is not influenced by atmospheric precipitation. The fourth climatic model (model H6) tests the effect of winter temperature (October–March) on population growth rate. Cold winters are known to negatively affect the survival of adult frogs (e.g., Anholt et al. 2003). Mean temperatures (°C) during winter months (October through March) and total amount of rainfall (mm) during spring and summer (April through July) were calculated for each year. For rainfall and temperature, we assumed a non-linear response of population growth rate and thus square-transformed both variables. Climatic data were provided by MeteoSwiss (Payerne weather station: 46°49′N, 6°56′E). Data on the river Aare water level (untransformed monthly means) were provided by the Swiss Federal Office for Water and Geology.

The fourth group of models represented the hypotheses that both intrinsic (density) and extrinsic (weather) variables affect population growth (model H7–H14). These candidate models combined density and weather variables as shown in Table 1.

We used the second-order Akaike information criterion (AIC_c; Hurvich and Tsai 1989) and Akaike weights (a posterior model probability; Burnham and Anderson 2002) for ranking candidate models, and R^2 to estimate the proportion of variance explained. The analysis was implemented in the statistical package R (R Development Core Team 2004).

Results

All 15 candidate models, parameter estimates (Eq. 1), model selection criteria and R^2 are presented in Table 1, in increasing AIC_c order. Models that include both density (Ricker or Gompertz type) and rainfall at time $t-2$ perform best among our candidate models with a cumulated weight of 0.998. Gompertz-type density dependence was far better supported by the data than Ricker-type density dependence (evidence ratio = 54; Burnham and Anderson 2002, p. 77). The best model thus reads:

$$\ln\left(\frac{N_{t+1}}{N_t}\right) = a + b\ln(N_t) + cW_t, \tag{2}$$

Table 1 Model selection and parameter estimates of all candidate models

	Predictors	Type of density dependence	Intercept	Density slope	Rain slope	Temp. slope	Water level slope	σ	R^2 (%)	AIC_c	ΔAIC_c	w
H10	Density and rainfall $(t-2)$	Gompertz	4.036	−1.035	−8.23E-6	–	–	0.1917	75	34.314	0.000	0.980
H9	Density and rainfall $(t-2)$	Ricker	2.274	−0.060	−8.59E-6	–	–	0.2810	64	42.352	8.0382	0.018
H12	Density and water level	Gompertz	872.236	−1.188	–	–	−1.582	0.3900	50	47.801	13.487	0.001
H8	Density and rainfall (t)	Gompertz	1.894	−0.902	5.866E-6	–	–	0.3783	51	48.592	14.278	0.001
H2	Density	Gompertz	2.745	−0.955	–	–	–	0.4518	42	49.576	15.262	0.000
H14	Density and temperature	Gompertz	2.756	−0.957	–	−0.003	–	0.4518	42	52.321	18.006	0.000
H7	Density and rainfall (t)	Ricker	0.174	−0.049	6.53E−6	–	–	0.4693	39	53.121	18.807	0.000
H5	Water level	–	−177.840	–	–	–	0.324	0.7700	0	53.266	18.952	0.000
H11	Density and water level	Ricker	858.718	−0.069	–	–	−1.562	0.5050	35	53.266	18.952	0.000
H1	Density	Ricker	0.997	−0.051	–	–	–	0.5607	28	54.11	19.796	0.000
H4	Rainfall $(t-2)$	–	0.927	–	−7.31E-6	–	–	0.5670	27	54.345	20.031	0.000
H13	Density and temperature	Ricker	0.939	−0.050	–	0.024	–	0.5591	28	56.797	22.483	0.000
H3	Rainfall (t)	–	−0.869	–	7.21E-6	–	–	0.6619	14	57.596	23.282	0.000
H0	Random walk	–	−0.013	–	–	–	–	0.7738	0	58.422	24.107	0.000
H6	Temperature	–	−0.142	–	–	0.101	–	0.7443	4	60.061	25.747	0.000

Models are ranked in an increasing AIC_c order. Type refers to the form of density dependence
w is the Akaike weight of the model

and explains a large part of the variance ($R^2 = 75\%$). Models including both density dependence effects and all three other climatic covariates (rainfall at time t, water level and winter temperatures) were weakly supported by the data, while models including density only or environmental covariates only had virtually no support from the data (all Akaike weights < 0.002).

As expected under the hypothesis of density dependence, the effect of density on population growth rate was negative (Table 1); the stronger support for the Gompertz model suggests that density dependence in tree frogs is loglinear. Rainfall at time $t-2$ negatively influenced population growth rate (Table 1).

Under deterministic settings, the negative relationship between density and population growth rate would make the population stabilize at its carrying capacity. Under stochastic settings, this capacity behaves as a return point, around which the population fluctuates (Dennis and Taper 1994). In the population under study, the return point is itself fluctuating owing to variance in extrinsic factors (rainfall). The return point can be computed by setting to zero the right-hand side of Eq. 2 as

$$R_t = \exp\left[\frac{-(\hat{a} + \hat{c}W_t)}{\hat{b}}\right],$$

with W_t being the total amount of rainfall 2 years before surveys; $\hat{a}$, $\hat{b}$, $\hat{c}$ being the estimated intercept and coefficients (Dennis and Otten 2000). The return point, R_t, fluctuates between 4 and 34 callers depending on the amount of rainfall 2 years before (rounded to the nearest integers; Fig. 1). The mean return point

$$\hat{R} = \exp\left[\frac{-(\hat{a} + \hat{c}\bar{W})}{\hat{b}}\right]$$

(where, $\bar{W}$ is the mean amount of rainfall during the study interval), is 18 (to the nearest integer).

Discussion

Our results show that the magnitude of population fluctuation in the European tree frog is affected by both intrinsic and extrinsic factors. Hence, the population fluctuates around a return point and the extrinsic factor causes the return point to fluctuate itself. While there is abundant evidence that density and/or extrinsic factors affect single vital rates or life cycle stages (e.g., Smith 1983; Petranka 1989; Berven 1990; Van Buskirk and Smith 1991; Beebee et al. 1996; Anholt et al. 2003; Altwegg 2003; Reading 2003; Grafe et al. 2004), our study is one of the few to show that these factors also affect population growth rate (e.g., Jaeger 1980; Semlitsch et al. 1996; Meyer et al. 1998).

Our best model suggests a negative effect of rainfall on population size, which runs counter to our expectations of a positive effect of rainfall on adult reproduction and/or larval development. However, it should be underlined that species normally exhibit non-monotonic, unimodal responses to environmental gradients (in fact,

this is one of the foundations of the ecological niche), so that negative effects are expected above some optimal value. Future research should focus on capturing a wider part of the rainfall gradient, and test curvilinear responses. For the time being, we refrain from speculating about biological mechanisms a posteriori.

The large variance (75%) explained by our model is worth underlining. Little scope is left for alternative environmental variables or for demographic stochasticity, which is somewhat surprising given the small size of the study population.

The result that density dependence matters has important implications when modeling structured demographic amphibian (meta)populations. So far, most models deal rather simply with density dependence. Conroy and Brook (2003), Griffiths (2004) and Hatfield et al. (2004) included ceiling type density dependence when modeling population and metapopulation dynamics. Since the results of population viability analyses may critically depend on the way density dependence is modeled (Henle et al. 2004), we believe that incorporating linear and/or loglinear density dependence is a key to improve these population models.

Density affects population growth rate directly, but it also acts in combination with lagged climatic variables. This might be seen as good news for this threatened species since density dependence is known to buffer small populations against extinction (Henle et al. 2004). However, Gompertz-type density dependence will also lead to a lognormal distribution of population size (Halley and Inchausti 2002) which in turn leads to a higher extinction risk (Halley and Inchausti 2002; Lande et al. 2003). This is even more the case when the amplitude of population fluctuation is wide (Leigh 1981; Schoener and Spiller 1992; Inchausti and Halley 2003). Populations are likely to show very large amplitude of fluctuations when the return point around which they fluctuate is fluctuating itself. In the case of the tree frog population we analyzed, the return point was not fixed ($\hat{R}_t = 18$) but varying through time [$R_t \subset (4;34)$; Fig. 1)]. It is therefore no surprise that populations of the tree frog are very likely to go extinct, especially when small (Carlson and Edenhamn 2000; Schmidt and Pellet 2005).

If the dynamics of a natural population are driven by both intrinsic and extrinsic factors, then the likely effect of a novel anthropogenic stressor is not easy to predict. The population may or may not be able to compensate for additional mortality; potential compensation is determined by the strength of density dependence. An extrinsic factor could lead to a population decline if it causes the return point to decline or it may lead to stronger fluctuations. Under either scenario, demographic or environmental stochasticity may then cause the population to collapse and go extinct.

Our evidence for density dependence contrasts with other studies on the population dynamics of amphibians breeding in temporary ponds. Pechmann and Wilbur (1994) and Alford and Richards (1999) argued that the dynamics of anurans breeding in temporary ponds is largely driven by stochastic, density-independent variation in recruitment. Detailed long-term studies have indeed found support for strong temporal variation in recruitment (e.g., Shoop 1974; Berven 1990; Semlitsch et al. 1996). Green (2003), however, argued that this model for amphibian population dynamics is unlikely to be general because positive and negative population growth rates were equally common. Population fluctuations driven by stochastic variation in recruitment, such as under the models of Pechmann and Wilbur (1994) and Alford and Richards (1999), would not show such a pattern (Houlahan et al. 2001; Green 2003). The distribution of population growth rates as described by Green (2003) is consistent, however, with fluctuations around a return point.

Varying return points under the influence of extrinsic and intrinsic factors may provide a general explanation for the seemingly erratic fluctuations that often characterize amphibian populations (Green 2003). Population dynamics might appear driven by stochasticity, but still be determined by intrinsic or extrinsic factors. This should induce fluctuations that go beyond those caused by demographic stochasticity alone, leading to frequent local extinctions (Leigh 1981; Schoener and Spiller 1992; Inchausti and Halley 2003). Rescue effects are required in such cases for the regional persistence of metapopulations, since recolonization events must balance local extinctions. Evidence is emerging that dispersal in amphibians may not be as uniformly limited as previously thought (Smith and Green 2005), but current levels may not suffice in present-day fragmented landscapes if the environmental correlates responsible for the fluctuations in return point synchronize population dynamics across large scales (Bjørnstad et al. 1999). Landscape-level studies of habitat connectivity and environmental autocorrelations should complement analyses of local dynamics, if conclusions are to be drawn in terms of viability prospects.

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