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Direct negative density-dependence in a pond-breeding frog population

Raluca I. Băncilă^{1,2,3}, Arpat Ozgul¹, Tibor Hartel^{4,5}, Tibor Sos⁶, Benedikt R. Schmidt^{1,7}

¹Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

²University Ovidius Constanța, Faculty of Natural Sciences, Al. Universității, corp B, Constanța, Romania

³“Emil Racoviță” Institute of Speleology of Romanian Academy, 13 Sptembrie Road, No. 13, 050711, Bucharest, Romania

⁴Faculty of Sustainability, Leuphana University Lueneburg, Lüneburg, Germany

⁵Department of Environmental Sciences, Sapientia University, Cluj-Napoca, Romania

⁶Milvus Group, Bird and Nature Protection Association, Crinului Road, No. 22, 540343, Târgu-Mureș, Romania

⁷KARCH, Passage Maximilien-de-Meuron 6, CH-2000 Neuchâtel, Switzerland

Corresponding author: Raluca I. Băncilă, “Emil Racoviță” Institute of Speleology of Romanian Academy, 13 Sptembrie Road, No. 13, 050711, Bucharest, Romania. E-mail: raluca.bancila@ieu.uzh.ch

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Abstract

Understanding population dynamics is critical for the management of animal populations. Comparatively little is known about the relative importance of endogenous (i.e. density-dependent) and exogenous (i.e. density-independent) factors on the population dynamics of amphibians with complex life cycles. We examined the potential effects of density-dependent and -independent (i.e., climatic) factors on population dynamics by analyzing a 15-year time series data of the Agile frog (*Rana dalmatina*) population from Târnava Mare Valley, Romania. We used two statistical models: i) the partial rate correlation function to identify the feedback structure and the potential time lags in the time series data and ii) a Gompertz state-space model to simultaneously investigate direct and delayed density dependence as well as climatic effects on population growth rate. We found evidence for direct negative density dependence, whereas delayed density dependence and climate did not show a strong influence on population growth rate. Here we demonstrated that direct density dependence rather than delayed density dependence or climate determined the dynamics of our study population. Our results confirm the findings of many experimental studies and suggest that density dependence may buffer amphibian populations against environmental stress. Consequently, it may not be easy to scale up from individual-level effects to population-level effects.

Key words: amphibian, population dynamics, time series, partial rate correlation function, Gompertz state-space model, density dependence, climate.

Introduction

Understanding the factors regulating the natural populations is of central importance to conservation management. Natural populations can be regulated through endogenous (i.e. density-dependent) and exogenous (i.e. density-independent) factors (Turchin 1999, Bjørnstad and Grenfell 2001, Brook and Bradshaw 2006, Sibly et al. 2005, Knape and de Valpine 2011) and often, these two sources of factors can act together to influence population dynamics (Jaeger 1980, Bjørnstad and Grenfell 2001). Density dependence occurs when the population growth rate increases (i.e. positive density dependence) or decreases (i.e. negative density dependence) with population density due to processes such as

intraspecific competition or disease (Turchin 1999). The most important density independent factors are usually climatic factors (Turchin 1999). Detecting the density-dependent and -independent effects and disentangling the roles of these factors are important for conservation because density dependence implies that populations are buffered to some extent against natural and anthropogenic stressors such as pesticides, invasive species, and harvest (Forbes and Calow 2002, Henle et al. 2004, Lebreton 2005, Rohr et al. 2006).

Pond breeding amphibians from the temperate region are a particularly interesting group for exploring the role of density-dependent and -independent factors in population dynamics. First, pond-breeding amphibians have a complex life-cycle, which includes aquatic egg, larval and terrestrial juvenile and adult stages. Experimental and field studies showed that density dependence can affect all life-history stages except the egg stage (e.g., Wilbur 1987, Van Buskirk and Smith 1991, Altwegg 2003, Harper and Semlitsch 2007, Patrick et al. 2008, Berven 2009, Loman and Lardner 2009). Mathematical models of amphibian population dynamics often include density dependence, and predictions depend on the type of density dependence included (Halley et al. 1996, Lampo and De Leo 1998, Hellriegel 2000, Vonesh and De la Cruz 2002, Govindarajulu et al. 2005). Despite the likely importance of density dependence for amphibian population dynamics, there are relatively few studies that assessed the effect of density dependence at the population level using time-series analysis (Meyer et al. 1998, Pellet et al. 2006, Salvidio 2007, Berven 2009, Greenberg and Green 2013). Meta-analyses of multi-species time series data usually involve only a few, if any, amphibians (Sibly et al. 2005, Brook and Bradshaw 2006, Knappe and de Valpine 2012). Time series data and analyses, however, are crucial for a better integration of theory, experiments and field studies (Werner 1998). Second, if density dependence occurs in the larval stage, then this may cause delayed density dependence if the time series is based on estimates of adult abundance. When present, detecting delayed density dependence (second or higher-order negative feedback of density on population growth rate) is particularly important since it allows distinguishing between periodic fluctuations and declines (Salvidio 2009). Third, Pechmann and Wilbur (1994) and Beebee et al. (1996) argued that fluctuations in amphibian population size are largely driven by stochastic variation in recruitment, which would be an alternative to density dependence and the implied population regulation (Sinclair 1989). Last but not least, amphibian populations are in global decline (Houlahan et al. 2000, Stuart et al. 2004). While habitat destruction is a major cause for the declines, particularly in Europe (Stuart et al. 2004), there are many other threats (Beebee and Griffiths 2005) that may be attenuated or exacerbated by density dependence.

In this study, using a 15-year time series data on egg masses and recently developed statistical methods, we explore the roles of density-dependent and -independent factors on the population growth of an anuran amphibian with a complex life cycle: the Agile frog (*Rana dalmatina*). First, we explored whether density dependence occurs, and if so, whether density dependence was direct, delayed or both. Second, we estimated the strength of the density dependence and the effect of climatic conditions during winter on the population growth rate.

Materials and Methods

Study species

The Agile frog (*Rana dalmatina*) has a wide distribution in Europe and in Romania (Fuhn 1960, Sillero et al. 2014) but has a declining population trend in Europe (Temple and Cox 2009). *Rana dalmatina* prefers landscapes with deciduous forests and reproduces in early spring (February - March) typically in ponds of various sizes with aquatic vegetation (Hartel et al. 2009). Adult females, on average, breed twice during their life and each female lays a single egg mass per year (Ficetola et al. 2006). Tadpoles complete metamorphosis within 2–3 months (Günther et al. 1996). Sexual maturity is reached after about two years (Sarasola-Puente et al. 2011).

Study area

The study pond is situated in the Târnava Mare Valley, Romania, north of the town Sighișoara (coordinates: N 46.23094°; E 24.78135°, altitude: 354 m). It is a permanent pond with a surface area of 2.2 ha and a maximum depth of approximately four meters. The pond was formed in the 1970s after the modification of the Târnava Mare river channel. The pond is at 400 m distance from a deciduous forest, and the shoreline of the pond is covered by reeds (*Typha* sp. and *Phragmites* sp.). The landscape around the pond is used for agriculture, mostly unmanaged grassland subject to occasional grazing. The dominant fish species in the pond are *Carassius auratus* and *Pseudorasbora parva* (both were present in high densities during the whole period of the study) and *Esox lucius* (present since 2009). Otherwise, there were no changes in the aquatic or terrestrial habitat.

Population monitoring

Population size was monitored annually from 1997 to 2011. The number of egg masses was counted as a proxy of female breeding population size (Crouch and Paton 2000, Hartel 2008a, Meyer et al. 1998). *Rana dalmatina* attaches its egg masses to aquatic plants and twigs at the pond edge. Therefore, egg masses were counted along the shore of the pond. The water depth was usually below one meter in these

areas. Pond depth sharply increases after about two or three meters from the shore and no egg masses were detected beyond this distance (Hartel 2008a). Egg mass counts started each year in the second part of February and lasted till the middle of April. The number of visits per year varied from six (1997-2007) to four (2008-2011). As egg masses accumulate during the breeding season and egg masses begin to float at the end of the breeding season, the last count was made around the middle of April every year. Detection probability of egg masses is usually high (90%; Grant et al. 2005) but both false positive and false negative can occur in the counting process. False negative can occur when a clutch is overlooked. Although we could usually distinguish old and new egg masses, false positives can occur when an egg mass is counted during more than one visit.

Breeding population size may be influenced by immigration and emigration and the breeding probability. There is another population 600 m away from our study pond and there are breeding aggregations in temporary ponds in the nearby forest (>400 m away). Some dispersal may occur from and to these sites; unfortunately, collecting movement data was not feasible in our study. Because we had no suitable data, we could not test whether breeding probability (i.e., the proportion of females laying eggs) affect breeding population size.

Climatic variables

From 1996 to 2008 climatic data were collected at a hydrological station from Albești (coordinates: N 46.23333°, E 24.85000°, altitude: 735 m), at ca. 7 km away from the pond. Several climatic variables could be used to account for environmental effects on population regulation. The following climatic variables were recorded and used for the analysis: 1) total amount of precipitation (litres/m²) in January (precipJ), 2) total amount of precipitation (litres/m²) in February (precipF), 3) the total amount of precipitation in the previous year (precipY), 4) the mean monthly air temperature (°C) in January (i.e. around two months before the beginning of reproduction) (tempJ) and 5) the mean monthly air temperature in February (i.e. around one month before the beginning of reproduction) (tempF).

Time series analysis

We used two statistical models to analyse the egg mass time series. We used the partial rate correlation function (PRCF) to identify the feedback structure and potential time lags in the time-series data (Berryman and Turchin 2001). Significance of the PRCF was assessed by Bartlett's criterion, $2/\sqrt{n}$, where n is the length of the time series (Berryman and Turchin 2001). The PRCF analysis suggested that both one- and two-year time lags were important for

describing the population dynamical pattern (see Results). Therefore, we fitted population models with time lags of one and two years for further analysis. For clarity hereafter we refer to one year time lag as direct density dependence and to two-year time lag as delayed density dependence. Given the biology of the species, delayed density dependence corresponds to a minimum of two years delay in the feedback response of adult female population size.

To estimate the effect of density dependence on population growth rate and to quantify the effects of climatic variables, we fitted a Gompertz state-space (GSS) model to the data (de Valpine and Hastings 2002, Dennis et al. 2006). Modelling in WinBUGS (Lunn et al. 2000) followed closely the approach described in Kéry and Schaub (2012) and Tobler et al. (2012). The log-transformed counts of egg masses X_t are described by:

$$X_t \sim \text{Normal}(N_t, \sigma_{obs}^2) \quad (\text{eq. 1})$$

where N_t is the unobserved true population sizes at time t and σ_{obs}^2 is the observation variance.

This part of the model describes the observation process and allows for observation error by assuming that counts sometimes overestimate or underestimate true population size. The biological process was modelled as described by Dennis et al. (2006) and Pasinelli et al. (2011).

N_t was drawn from a normal distribution:

$$N_t \sim \text{Normal}(N_{exp,t}, \sigma_{proc}^2) \quad (\text{eq. 2})$$

where σ_{proc}^2 is the process variance (i.e., unexplained variability in egg mass counts). $N_{exp,t}$ is the expected population size at time t . Direct density dependence was modelled as:

$$N_{exp,t} = N_{t-1} + a + b_1 N_{t-1} \quad (\text{eq. 3})$$

where a is the intercept and b_1 estimates the strength of density dependence. Equation 3 describes Gompertz-type density-dependence and corresponds to equation 2 in Dennis et al. (2006) and Pasinelli et al. (2011). Because the PRCF suggested that the two-year lag may important (see Results), we extended the direct density dependence model to allow for delayed density dependence in addition to direct density dependence:

$$N_{\text{exp}t} = N_{t-1} + a + b_1 N_{t-1} + b_2 N_{t-2} \quad (\text{eq. 4})$$

where b_2 estimates the strength of delayed density dependence.

To assess the effect of climatic variables on population dynamics we used the direct (eq. 3) and the delayed density dependence model (eq. 4) and one climatic variable at a time (Dennis and Otten 2000, Pellet et al. 2006). The models are of the form:

$$N_{\text{exp}t} = N_{t-1} + a + b_1 N_{t-1} + b_3 w_t \quad (\text{eq. 5})$$

$$N_{\text{exp}t} = N_{t-1} + a + b_1 N_{t-1} + b_2 N_{t-2} + b_3 w_t \quad (\text{eq. 6})$$

where w is the climatic covariate at time t and b_3 is the slope. All climatic covariates were standardized to a mean 0 and variance 1. Missing values were replaced with 0. Conducting the analysis using the years for which climate data were available did not lead to different results.

To fit the models we used vague normal priors with a mean zero and a precision of 0.0001 for a , b_1 , b_2 , and 0.01 for b_3 , respectively. WinBUGS parameterizes normal distributions using a precision parameter = $1/\text{variance}$. We also fitted the model with more precise priors, but this did not affect the results substantially. We here report the results with the least vague priors. We used vague uniform priors in the interval 0 - 10 for the standard deviations of σ_{obs}^2 and σ_{proc}^2 . In all three models, the first value of the time series had a normal prior with mean equal to the log-transformed count and a variance of 100. We ran three parallel MCMC chains with 200'000 iterations and a burn-in of 100'000. Chains were thinned by a factor 20. Convergence was assessed using the Gelman-Rubin statistic Rhat. Convergence was satisfactory when R-hat values were smaller than 1.1 (Brooks and Gelman 1998, Gelman and Hill 2007).

Results

Figure 1 shows the relationship between the population size (log-transformed counts of egg masses, $\log(C_{[t]})$) and population growth rate for direct ($\log(C_{[t+1]}/C_{[t]})$) and delayed ($\log(C_{[t+2]}/C_{[t]})$) density dependence. The PRCF indicated the presence of a negative feedback at both one- and two-year lags, but only the one-year lag was significant (Fig. 2). The state-space model estimated population sizes that were close to the observed population counts (Fig. 3). The density dependence estimate for the one-year lag and both one and two-year lag (b_1 in equation 3 and 4) was negative and the 95% credible interval did not include zero (Table 1). The two-year lag effect (b_2 in equation 4) was negative but the 95% credible interval included zero. None

of the climatic variables had a strong effect on population dynamics as the 95% credible intervals of the slope estimates (b_3 in equation 5 and 6) included zero for all variables (Table 2).

Discussion

Our study showed that negative direct density dependence is present in the dynamics of Agile frog populations (Fig. 1 and Table 1). There was some evidence for delayed density dependence (Fig. 2, Table 1). In contrast, density independent factors (climate) did not affect the dynamics of this population (Table 2). Knappe (2008) used simulations to show that density dependence can be difficult to demonstrate reliably. We believe that our results are robust because observation error in counts of egg masses is generally low (Grant et al. 2005) and two different models, one simple and one complex, give qualitatively the same result.

If density dependence in the larval stage is indeed as common as suggested by experiments (Wilbur 1980), then we would expect to observe delayed density dependence in time series of adult abundance. Female agile frogs reach sexual maturity at the age of two or three years (Sarasola-Puente et al. 2011). Hence, an effect larval density dependence on population dynamics would lead to delayed density dependence in time series of adult frogs (such as ours). In general, longer time series (> 25 years) are needed to detect delayed density dependence (Holyoak 1994). Meyer et al. (1998), however, argued that some time-series models may not be able to distinguish between density dependence in the larval and other stages. It is important to note that delayed density dependence as used here differs from delayed density dependence in insects. In amphibians, it arises from the time lag between metamorphosis and maturity, whereas in insects it can arise from interactions with natural enemies or from effects on fecundity (Turchin 1990).

In contrast to Hartel (2008b), we found no effect of climate on population dynamics (Table 1). Climate conditions can certainly affect animal populations (Anholt et al. 2003, Reading 2007, Grosbois et al. 2008) and others have observed that climatic conditions affected amphibian population dynamics (Pellet et al. 2006). The difference between the result of Hartel (2008b) and our result may simply reflect the problems generally associated with detecting an effect of climate on animal time series (Krebs and Berteaux 2006, Knappe and de Valpine 2011). The effects of variability in weather and climate are often too complex to be picked up from population abundance time series (Knappe and de Valpine 2011).

Although our study does not address the biological mechanisms behind the observed density effect, many experimental studies revealed the importance of density dependence at multiple life history

stages. In experiments, exploitative competition for food in the larval stage is common (Wilbur 1980) and leads to increased larval mortality or to reduced size at metamorphosis, which may affect juvenile and adult performance (Altwegg and Reyer 2003, Morey and Reznick 2005, Schmidt et al. 2012). In fact, since adult body size can vary with abundance in adult amphibians (Green and Middleton 2013), similar mechanisms may also cause density dependence in terrestrial stages.

The literature documenting the effects of density dependence on amphibians comes from studies carried out in artificial ponds or in the laboratory (Wilbur 1980, 1997). The observation of density dependence at the population level in this study corroborates the results of a few other field studies (Meyer et al. 1998, Pellet et al. 2006, Salvidio 2007, Berven 2009, Greenberg and Green 2013) and thereby confirms experimental studies and supports the use of density dependence in mathematical population models (Werner 1998).

Our results are in contrast to other studies arguing that fluctuations in amphibian population size are largely driven by stochastic variation in recruitment (Pechmann and Wilbur 1994, Beebee et al. 1996). While seemingly erratic fluctuations in abundance are common in amphibian populations (Green 2003, Marsh 2011), our results show that these fluctuations are at least partially determined by density dependence. Using an analysis that did not account for observation error, Salvidio (2009) found evidence for density dependence in 12 out of 16 amphibian population time series, suggesting that density dependence may be common in amphibian populations. As more time series analyses of amphibian populations become available, a meta-analysis on the frequency, strength and form of density dependence would be worthwhile. Overall, amphibian population dynamics do not appear to be any different from other vertebrates (Salvidio 2011). This suggests that both density dependence and extrinsic stochastic factors (i.e. climate) may determine population dynamics, as observed in other systems (Higgins et al. 1997, Leirs et al. 1997, Bjørnstad and Grenfell 2001).

Conclusions

Many experimental studies have demonstrated density dependence in amphibian populations. Our results confirm the occurrence of density dependence in a natural population. We believe that amphibian natural populations may be buffered against environmental stressors, with important implications for amphibian conservation. Similar to populations that are harvested, amphibian populations may be able to tolerate some mortality induced by environmental stressors as long as this mortality is (at least partially) compensatory rather than additive. Density dependence and compensatory mortality imply that increased

mortality caused by an environmental stressor leads to reduced mortality in another stage of the life cycle such that there is little or no net effect of the stressor (Burnham and Anderson 1984, Forbes and Calow 2002, Lebreton 2005). While a stressor may affect individuals, there may be no effect on the viability of the population (Vonesh and De la Cruz 2002). Therefore, it may not be easy to scale up from individual-level the effects of stressors to population-level effects because the interplay between stressors, density dependence and compensatory/additive mortality is not yet sufficiently understood.

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Table Legends

Table 1. Estimates and 95% credible intervals (CRI) of the parameters for the GSS model with one (equation 3) and both one and two-year lag (equation 4), respectively. σ_{obs}^2 = the observation variance, σ_{proc}^2 = the process variance, a = intrinsic rate of increase, b_1 and b_2 = the strength of direct and delayed density dependence, respectively.

Parameter	<i>One-year lag</i>			<i>One and two-year lag</i>		
	Estimate	CRI		Estimate	CRI	
		2.5%	97.5%		2.5%	97.5%
σ_{obs}^2	0.068	0.000	0.222	0.046	0.000	0.164
σ_{proc}^2	0.059	0.000	0.226	0.044	0.000	0.171
a	6.311	1.027	11.170	9.752	3.068	15.950
b_1	-1.059	-1.877	-0.177	-0.992	-1.908	-0.305
b_2				-0.642	-1.268	0.221

Table 2. Estimates and 95% credible intervals (CRI) of the parameters for the model with one-year (equation 5) and both one- and two-year lag and one climatic variable (equation 6). σ_{obs}^2 = the observation variance, σ_{proc}^2 = the process variance, a = intrinsic rate of increase, b_1 and b_2 = the strength of direct and delayed density dependence, respectively, b_3 = strength of the effect of the climate variable; precipJ = total amount of precipitation (litres/m²) in January, precipF = total amount of precipitation (litres/m²) in February, precipY = the total amount of precipitation in the previous year, tempJ = the mean monthly air temperature (°C) in January and tempF = the mean monthly air temperature in February.

	precipJ		precipF		precipY		tempJ		tempF	
Parameter	Estimate	CRI	Estimate	CRI	Estimate	CRI	Estimate	CRI	Estimate	CRI
<i>One year-lag</i>										
σ_{obs}^2	0.072	(0.000, 0.247)	0.076	(0.000, 0.258)	0.073	(0.000, 0.249)	0.072	(0.000, 0.250)	0.070	(0.000, 0.248)
σ_{proc}^2	0.064	(0.000, 0.253)	0.068	(0.000, 0.268)	0.069	(0.000, 0.268)	0.070	(0.000, 0.270)	0.073	(0.000, 0.270)
a	6.665	(-0.482, 12.130)	6.479	(0.809, 11.450)	6.068	(0.671, 11.110)	5.576	(-0.381, 10.740)	5.756	(-0.243, 11.230)
b_1	-1.118	(-2.022, -0.077)	-1.088	(-1.928, -0.141)	-1.019	(-1.867, -0.108)	-0.935	(-1.806, 0.061)	-0.966	(-1.886, 0.040)
b_3	0.045	(-0.200, 0.339)	0.019	(-0.239, 0.283)	0.046	(-0.208, 0.286)	-0.044	(-0.335, 0.204)	0.036	(-0.212, 0.298)
Deviance	-8.793	(-24.857, 16.430)	-8.096	(-82.050, 17.120)	-10.094	(-91.871, 17.150)	-9.888	(-90.200, 17.100)	-11.390	(-93.435, 16.810)
<i>One and two-year time lag</i>										
σ_{obs}^2	0.052	(0.000, 0.183)	0.052	(0.000, 0.180)	0.050	(0.000, 0.178)	0.051	(0.000, 0.184)	0.050	(0.000, 0.191)

σ_{proc}^2	0.046	(0.000, 0.200)	0.044	(0.000, 0.193)	0.042	(0.000, 0.194)	0.052	(0.000, 0.214)	0.056	(0.000, 0.221)
a	10.703	(1.911, 17.560)	10.595	(3.153, 16.960)	10.630	(2.161, 16.580)	9.857	(1.635, 17.240)	9.432	(1.431, 16.51)
b_1	-1.183	(-2.075, -0.084)	-1.104	(-1.933, -0.297)	-1.060	(-1.823, -0.299)	-0.978	(-1.935, -0.111)	-0.962	(-1.930, -0.085)
b_2	-0.611	(-1.250, 0.275)	-0.673	(-1.305, 0.257)	-0.720	(-1.401, 0.292)	-0.674	(-1.392, 0.279)	-0.618	(-1.318, 0.335)
b_3	0.072	(-0.225, 0.337)	0.079	(-0.164, 0.320)	-0.055	(-0.262, 0.198)	0.018	(-0.259, 0.274)	0.008	(-0.221, 0.249)
<i>Deviance</i>	-12.170	(-75.403, 12.080)	-11.894	(-74.717, 12.440)	-12.109	(-75.040, 12.460)	-14.211	(-83.847, 13.010)	-15.458	(-89.271, 13.040)

Figure Legends

Fig. 1. The relationship between population growth rate for one-year lag ($\log(C_{[t+1]}/C_{[t]})$) (open circles) and two-year lag ($\log(C_{[t+2]}/C_{[t]})$) (closed circles), respectively, and the population size (number of egg masses counted, $C_{[t]}$) in the Agile frog, *Rana dalmatina*.

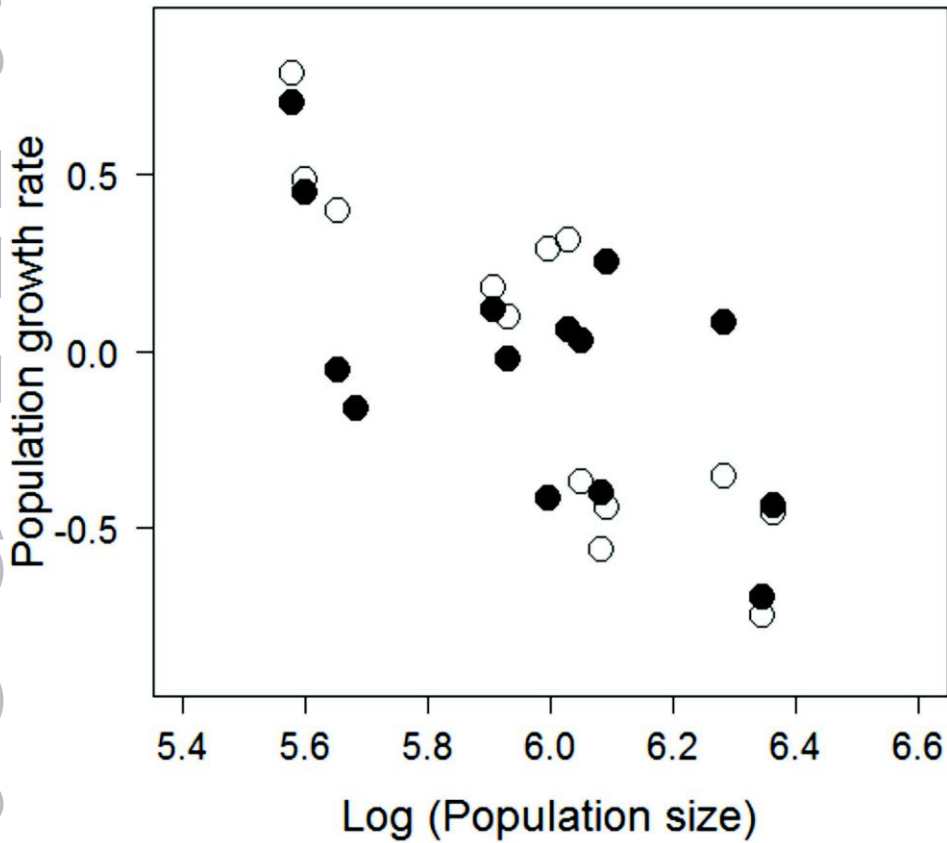


Fig. 2. Partial rate correlation function (PRCF) for the Agile frog, *Rana dalmatina*, time series data.

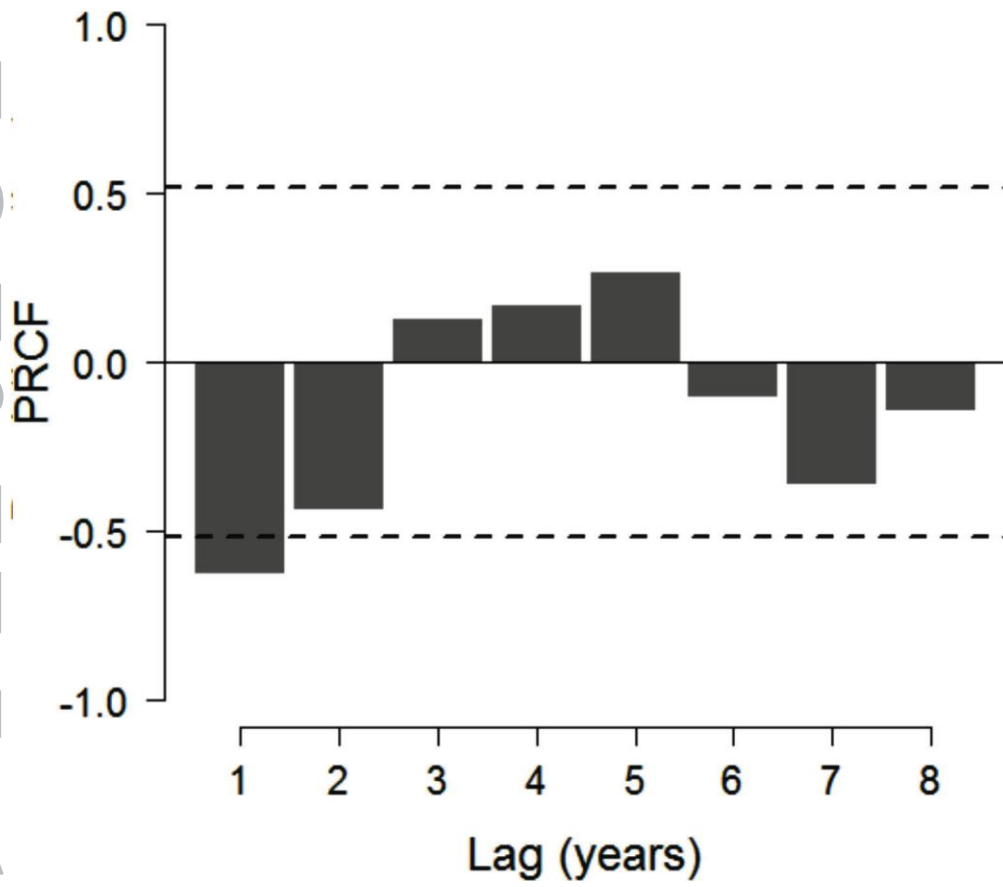


Fig. 3. The observed counts of egg masses of Agile frog, *Rana dalmatina*, from 1997 to 2011 (solid line), the estimated abundance based on the model with one-year lag (equation 3) (dotted line) and, the estimated abundance based on the model with both one- and two-year lag (equation 4) (dashed line).

The shaded area is 95% CRI.

