

## Is There Evidence for Population Regulation in Amphibians and Reptiles?

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**ABSTRACT.**—From the 1950s to the present, many researchers have tested time series data for density dependence. All kinds of organisms have been studied, from microorganisms to insects and vertebrates to plants. A variety of techniques and population growth models were developed, and the conceptual framework to study populations has been improved. We searched for long time series data on amphibians and reptiles in the literature. From 102 population time series, and after filtering the dataset, we tested for density dependence in time series data for 69 populations (52 species) of amphibians (anurans and caudatans), serpents, lacertilians, chelonians, rhynchocephalians, and crocodylians. We used the exponential growth state-space model and the Ornstein-Uhlenbeck state-space model as proxy models for density-independent and density-dependent population growth models, selecting between them with the parametric bootstrap likelihood ratio test. The hypothesis of density independence was rejected for 2 amphibians, 11 serpents, 3 chelonians, 1 rhynchocephalian, and 2 crocodylian populations. Detailed data for serpents and chelonians allowed identification of external factors such as changing food supplies and habitats as drivers of observed changes in population densities. We highlight the need of both long-term and experimental studies on reptile and amphibian populations in semipristine or preserved areas.

**RESUMEN.**—Desde los años 50s hasta nuestros días, diversos investigadores han puesto a prueba denso-dependencia en series temporales de datos. Todo tipo de organismos han sido estudiados, desde microorganismos a insectos, vertebrados y aves. Una variedad de técnicas y de modelos de crecimiento poblacional se han desarrollado, e incluso el marco conceptual de estudios poblacionales fue mejorado. Realizamos búsquedas de datos en series temporales largas para reptiles y anfibios en la literatura. De las 102 poblaciones encontradas y luego de filtrar la base de datos, analizamos 69 poblaciones (52 especies) de anfibios (anura y caudata), serpientes, lagartos, tortugas, tuatara, alligators y caimanes. Utilizamos exponential growth state-space y Ornstein-Uhlenbeck state-space como aproximación a los modelos de crecimiento poblacional denso-independiente y denso-dependiente, seleccionando entre ellos por medio del parametric bootstrap likelihood ratio test. La hipótesis de denso-independencia fue rechazada para poblaciones de 2 anfibios, 11 serpientes, 3 tortugas, 1 tuatara, 1 alligator y 1 caimán. Información detallada disponible para las poblaciones de serpientes y tortugas permitieron identificar factores externos (como cambios en el alimento disponible y en el hábitat) como responsables de los cambios observados en las densidades poblacionales. Resaltamos la necesidad tanto de estudios a largo plazo o experimentales, en poblaciones de anfibios y reptiles en áreas semipristinas o preservadas.

Krebs (1995a) recognized two different paradigms in the study of population regulation: the density-dependent paradigm (Are populations regulated by density?) and the mechanistic paradigm (What factors affect populations?). The density-dependent paradigm relies on the assumption that populations tend to return to an equilibrium when displaced from it and depends on long-term, observational studies. In contrast, the mechanistic paradigm postulates that density is not the relevant variable to study populations and searches for the most meaningful (either biotic or abiotic) variables through short-term, experimental studies (Krebs, 1995a).

Density dependence can be defined as dependence of per capita growth rate on population densities (Murdoch and Walde, 1989). Existence for density dependence has been questioned and discussed at length previously (Andrewartha and Birch, 1954; Smith, 1961; Andrewartha, 1963; Krebs, 1995a,b), although it is now recognized as a widespread mechanism of population regulation (Brook and Bradshaw, 2006; Knape and de Valpine, 2012).

Population size is constrained by energetic requirements (Damuth, 1987). Given that endotherms maintain relatively high and stable body temperatures, metabolic rates vary little with ambient temperature. On the contrary, ectotherm metabolic

rates are closely related to ambient temperatures. Hence, populations of ectotherms are more likely to be affected by external factors such as climate, whereas endotherm populations will likely be regulated by biotic factors, such as density (Buckley et al., 2008). Moreover, amphibians are more susceptible to dehydration because of their permeable skin, making them also dependent on hydric environmental conditions (Spotila and Berman, 1976; Shoemaker and Nagy, 1977).

Despite the clear influence of environmental conditions on reptiles and amphibians, previous work has shown that density affects different aspects of reptile and amphibian ecology. In fact, population density affected growth rates in amphibian larvae (Wilbur, 1977; Van Buskirk and Smith, 1991) and yearling lizards (Tinkle et al., 1993). At the population level, some studies have indicated a significant effect of density on population growth rates. For example, Meyer et al. (1998) rejected the hypothesis of density-independent population regulation for *Rana temporaria* by contrasting population growth models using the parametric bootstrap likelihood ratio test (PBLRT) of Dennis and Taper (1994). Brook and Bradshaw (2006) tested for density dependence in 1,198 species by using various methods, and among the 2 lacertilians species, 3 serpents, 3 chelonians, 1 alligator, 13 salamanders, and 13 anurans included, they found evidence of density dependence in 4–20 species.

Detection of density dependence has been hindered by the lack of a method suitable for real ecological data on population

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DOI: 10.1670/16-133

densities as well as the shortage of long time series data. Moreover, differentiating a density-dependent process from a density-independent process seemed almost impossible with real data (Guckenheimer et al., 1977). Separating deterministic from stochastic phenomena has also proven to be difficult (Okamoto et al., 2016) and has given rise to the dichotomy of so-called “explicit density dependence” vs. “density vagueness” (Strong, 1986; Berryman, 1991).

One of the first approaches to detect density dependence was to analyze how population growth rate is related to population density. A significantly negative correlation coefficient (Smith, 1961; Tanner, 1966; Pimm, 1982) or a regression line with a negative slope (Morris, 1963; Solomon, 1964) was interpreted as evidence for density dependence for a wide variety of taxa, including ectotherms (fish and invertebrates, but no amphibians or reptiles were included) and endotherms (birds and mammals). The use of correlation or regression methods as a means to detect density dependence has been criticized because estimation of slope ( $\beta$ ) is unreliable, leading to spurious conclusions of density dependence (Pollard et al., 1987). Moreover, any series with an estimation error (i.e., if the correlation between measurements at different times is not exactly 1) will present a “regression to the mean” effect (Bland and Altman, 1994; Kelly and Price, 2005; Freckleton et al., 2006) because values above the mean tend to be followed by lower values, whereas values below the mean tend to be followed by higher values (“regression towards mediocrity”; Galton, 1886).

From the original approach of plotting change in density vs. density to the present day, different analytical solutions have been proposed to detect density dependence (for reviews of methods, see Wolda and Dennis, 1993; Dennis and Taper, 1994; Dennis and Ponciano, 2014). Population growth models also have been improved. The newer exponential growth state-space (EGSS, density independent) and Gompertz state-space (GSS, density-dependent) models incorporate environmental process noise and observation error through state-space implementation (Dennis et al., 2006; Knappe, 2008). Further development of the Ornstein-Uhlenbeck state-space (OUSS) model improved GSS to the point of allowing its application to ecological data, where generations may overlap and missing information may occur in the time series (Dennis and Ponciano, 2014).

Different methods were also developed to select among alternative population growth models (Bulmer, 1975; Pollard et al., 1987; Wolda and Dennis, 1993; Dennis and Taper, 1994; Brook and Bradshaw, 2006; Dennis et al., 2006; Dennis and Ponciano, 2014). The use of state-space population growth models and the PBLRT to select among models emerged as the best candidates to detect “return tendencies” that can be interpreted as density dependence (“tests of statistical density-dependence”; Wolda and Dennis, 1993; Dennis and Ponciano, 2014).

Knowing whether amphibian and reptile populations are regulated by density would allow researchers to better predict the responses of these animals to external factors affecting their populations, such as climate change or disease. Given the present availability of a powerful method to test the hypothesis of density independence (Dennis and Ponciano, 2014) and indications that density is actually affecting amphibian and reptile populations, we searched the literature extensively for time series population data. Our objective was to determine the extent of density-dependent regulation processes in reptile and amphibian populations and to make these data available so they can be included in future meta-analyses.

## MATERIALS AND METHODS

We used time series abundance data on amphibians and reptiles, including papers published in scientific journals, books, our own data, and in the Global Populations Dynamics Database (GPDD; NERC Centre for Population Biology and Imperial College, 2010). We found data on 102 time series corresponding to 77 species (11 anurans, 14 salamanders, 22 serpents, 22 lacertilians, 4 chelonians, 1 rhynchocephalian, and 3 crocodylians) (Appendix 1). To increase accuracy, we only used time series that met the following conditions: 1) the series must include at least 10 yr, and 2) the origin of the data and the conditions on how they were obtained must be known. Given that a very small proportion of the time series we found for anurans has a known bibliographic source, we decided to include the species listed in the GPDD even when sampling conditions were not known. Although the models used allow inclusion of time series with missing years, we divided time series for *Agkistrodon contortix*, *Coluber constrictor*, *Diadophis punctatus*, and *Thamnophis sirtalis* into two series each because a gap of about 10 yr occurred between the ~50 yr of sampling (Fitch, 1999). For *Sphenodon punctatus* (rhynchocephalian), we used only female data and divided the time series in two because of an 8-yr gap of missing data (Moore et al., 2007). After filtering the dataset, we ended up with 69 time series (10 for 10 anurans species, 12 for 12 salamanders species, 31 for 20 serpents species, 4 for 3 lacertilians species, 6 for 4 chelonians species, 1 for rhynchocephalian, and 5 for 2 crocodylians species) (Appendix II).

We used the PBLRT because it has greater power than alternative methods at rejecting the hypothesis of density independence (Dennis and Ponciano, 2014). We performed PBLRT contrasting the EGSS model against the OUSS model, testing the hypothesis of density-independent population growth, with 2,000 bootstraps, and at a significance level of  $P < 0.05$ . Model parameters  $\mu$  (mean stationary log abundance),  $\theta$  (rate of approach to stationarity),  $\beta^2$  (variability of process noise), and  $\tau^2$  (variability of sampling) were extracted, calculating strength of density dependence  $c$  (Dennis et al., 2006) with the formula  $c = \exp^{-\theta}$  (Dennis and Ponciano, 2014). Absolute values of  $c$  range from 0 to 1, with  $c = 1$  being complete density independence and  $c = 0$  being complete density dependence. PBLRT calculations and parameter estimations were performed using the R script RUNNING-PBLRT.R as provided by Dennis and Ponciano (2014). All analyses were made in R version 3.2.5 (R Core Team, 2016).

## RESULTS

The hypothesis of density independence was rejected for 19 of the 69 time series analyzed, corresponding to populations of 2 anuran, 11 serpent, 3 chelonian, 1 rhynchocephalian, and 2 crocodylian species (Table 1). In the case of *T. sirtalis*, density independence was rejected for both parts of the time series. For *A. contortix*, *C. constrictor*, and *S. punctatus*, density independence was rejected for only a part of the time series, whereas for *D. punctatus* density independence was not rejected for any part of the time series analyzed (Table 1). Model parameters and strength of density dependence showed large estimation errors (Appendix 3).

## DISCUSSION

We rejected density-independent population growth for some populations of anurans, serpents, chelonians, rhynchocephalian,

TABLE 1. Populations tested for density-dependent growth by using PBLRT (Dennis and Ponciano, 2014). Bold *P* values indicate rejection of the density-independence hypothesis (PBLRT method). Bibliographic sources for each population are included.

Population	Length of time series (yr)	PBLRT, <i>P</i>	Data source
<b>AMPHIBIA</b>			
<b>ANURA</b>			
<i>Bufo bufo</i>	11	0.433	GPDD
<i>Bufo canorus</i>	12	< <b>0.001</b>	GPDD; Sherman and Morton, 1993
<i>Bufo terrestris</i>	16	0.125	GPDD
<i>Gastrophryne carolinensis</i>	16	0.388	GPDD
<i>Pseudacris nigrita</i>	16	0.076	GPDD
<i>Pseudacris ornata</i>	16	0.267	GPDD
<i>Pseudacris regilla</i>	15	0.38	GPDD
<i>Rana clamitans</i>	16	0.544	GPDD
<i>Rana damaltina</i>	12	<b>0.001</b>	GPDD
<i>Scaphiopus holbrookii</i>	16	0.466	GPDD
<b>CAUDATA</b>			
<i>Ambystoma opacum</i>	14	0.183	GPDD; Hairston and Wiley, 1993
<i>Ambystoma tigrinum tigrinum</i>	16	0.449	GPDD; Hairston and Wiley, 1993
<i>Desmognathus aeneus</i>	15	0.114	GPDD; Hairston and Wiley, 1993
<i>Desmognathus monticola</i>	15	0.359	GPDD; Hairston and Wiley, 1993
<i>Desmognathus ochrophaeus</i>	15	0.404	GPDD; Hairston and Wiley, 1993
<i>Desmognathus quadramaculatus</i>	15	0.36	GPDD; Hairston and Wiley, 1993
<i>Eurycea quadridigitata</i>	16	0.309	GPDD; Hairston and Wiley, 1993
<i>Notophthalmus viridescens</i>	16	0.448	GPDD
<i>Plethodon cinereus</i>	13	0.382	GPDD; Hairston and Wiley, 1993
<i>Plethodon glutinosus</i>	15	0.396	GPDD; Hairston and Wiley, 1993
<i>Plethodon jordani</i>	15	0.126	GPDD; Hairston and Wiley, 1993
<i>Triturus helveticus</i>	19	0.303	GPDD
<b>REPTILES</b>			
<b>TESTUDINES</b>			
<i>Chelydra serpentina</i>	18	< <b>0.001</b>	GPPD; Congdon and Gibbons, 1996
<i>Chrysemys picta</i>	18	0.235	GPPD; Congdon and Gibbons, 1996
<i>Chrysemys picta 2</i>	17	< <b>0.001</b>	GPPD; Congdon and Gibbons, 1996
<i>Chrysemys picta 3</i>	17	< <b>0.001</b>	GPPD; Congdon and Gibbons, 1996
<i>Dermochelys coriacea</i>	25	0.656	Dutton et al., 2005
<i>Emydoidea blandingii</i>	18	0.141	GPPD; Congdon and Gibbons, 1996
<b>RHYNCHOCEPHALIA</b>			
<i>Sphenodon punctatus</i>	27	<b>0.03</b>	Moore et al., 2007
<b>SQUAMATA</b>			
<b>Sauria</b>			
<i>Anolis limifrons</i>	19	0.175	GPDD;
<i>Cyclura cychlura</i>	23	0.21	Iverson et al., 2006
<i>Cyclura cychlura 2</i>	23	0.442	Iverson et al., 2006
<i>Sceloporus graciosus</i>	11	0.387	Tinkle et al., 1993
<b>Ophidia</b>			
<i>Agkistrodon contortrix</i>	16	< <b>0.001</b>	Fitch, 1999
<i>Agkistrodon contortrix 2</i>	21	0.144	Fitch, 1999
<i>Bitis gabonica</i>	14	0.123	Reading et al., 2010
<i>Bitis nasicornis</i>	14	<b>0.002</b>	Reading et al., 2010
<i>Coluber constrictor</i>	17	<b>0.002</b>	Fitch, 1999
<i>Coluber constrictor 2</i>	20	0.288	Fitch, 1999
<i>Coronella austriaca</i>	13	< <b>0.001</b>	Reading et al., 2010
<i>Crotalus viridis</i>	11	0.304	GPPD; Julian, 1951
<i>Dendroaspis jamesoni</i>	14	0.431	Reading et al., 2010
<i>Diadophis punctatus</i>	21	0.28	Fitch, 1999
<i>Diadophis punctatus 2</i>	19	0.359	Fitch, 1999
<i>Elaphe obsoleta</i>	18	0.391	Weatherhead et al., 2002
<i>Elaphe obsoleta 2</i>	16	0.531	Weatherhead et al., 2002
<i>Hierophis viridiflavus</i>	15	0.09	Reading et al., 2010
<i>Hierophis viridiflavus 2</i>	13	0.483	Reading et al., 2010
<i>Masticophis taeniatus</i>	11	0.408	GPPD; Julian, 1951
<i>Natrix natrix</i>	12	0.468	Reading et al., 2010
<i>Natrix natrix 2</i>	15	0.227	Reading et al., 2010
<i>Notechis scutatus</i>	13	0.353	Reading et al., 2010
<i>Python regius</i>	14	< <b>0.001</b>	Reading et al., 2010
<i>Thamnophis atratus</i>	16	0.568	Lind et al., 2005
<i>Thamnophis sirtalis</i>	21	<b>0.002</b>	Fitch, 1999
<i>Thamnophis sirtalis 2</i>	21	<b>0.02</b>	Fitch, 1999
<i>Vipera aspis</i>	17	0.419	Reading et al., 2010
<i>Vipera aspis 2</i>	20	<b>0.001</b>	Reading et al., 2010
<i>Vipera aspis 3</i>	21	<b>0.02</b>	Reading et al., 2010
<i>Vipera berus</i>	19	0.063	Madsen et al., 1999
<i>Vipera ursinii</i>	22	<b>0.001</b>	Reading et al., 2010
<i>Vipera ursinii 2</i>	22	<b>0.009</b>	Reading et al., 2010

TABLE 1. Continued.

Population	Length of time series (yr)	PBLRT, <i>P</i>	Data source
<i>Zamenis longissimus</i>	16	0.281	Reading et al., 2010
<i>Zamenis longissimus</i> 2	13	0.26	Reading et al., 2010
CROCODYLIA			
<i>Alligator mississippiensis</i>	14	0.122	Joanen and McNease, 1987
<i>Alligator mississippiensis</i> 2	12	<0.001	Joanen and McNease, 1987
<i>Alligator mississippiensis</i> 3	18	0.224	GPDD; Brandt, 1991
<i>Caiman crocodilus</i>	16	<0.001	GPDD; Smith, 1981
<i>Caiman crocodilus</i> 2	10	0.324	GPDD; Smith, 1981

and crocodylians. No lizard or salamander populations were density dependent, possibly because of specific ecological traits of these animal groups (*r*-*K* selection related; Pianka, 1972), the length of the time series used, the power of PBLRT, or other uncontrolled variables. Estimation of model parameters ( $\mu$ ,  $\theta$ ,  $\beta^2$ , and  $\tau^2$ ) and strength of density dependence (*c*) had wide confidence intervals (Appendix 3). Population growth models used here sometimes have ridge-like likelihoods, or likelihoods with multiple local maxima, that can affect parameter estimation for short time series (Dennis et al., 2006; Knape, 2008; Dennis and Ponciano, 2014). Even though the model proposed by Dennis and Ponciano (2014) seems to be a useful method for real ecological data, length of time series apparently is still a limitation. Dennis et al. (2010) suggested replicating the sampling process one or more times at selected sampling times improves parameter estimation.

Other studies had found evidence for density dependence in lizards (Tinkle et al., 1993; Brook and Bradshaw, 2006) and in salamanders (Van Buskirk and Smith, 1991; Brook and Bradshaw, 2006) by using some other methodology or population growth models. Brook and Bradshaw (2006) got different results when comparing multimodel inference (MMI), Bayesian Information Criterion ([BIC], Zeng et al., 1998), Jack-knifed cross-validation ([C-V], Turchin, 2003), Bulmer's *R* (Bulmer, 1975), randomizations (Pollard et al., 1987), and PBLRT (Dennis and Taper, 1994). Of the 35 reptile and amphibian species included in the analysis of Brook and Bradshaw (2006), 16 showed evidence of density dependence with MMI, 32 with C-V, 23 with BIC, 15 with Bulmer's *R*, 8 with a randomization method, and 9 with PBLRT. The proportion of density-dependent populations (about 25%) was similar between this study and the PBLRT made by Brook and Bradshaw (2006), but the population growth models we used were different. Brook and Bradshaw (2006) used the Gompertz logistic growth model as a density-dependent model (Dennis and Taper, 1994), which is less suitable for real ecological data compared with the OUSS model (Dennis and Ponciano, 2014) used here. Not including measurement error in population growth models could lead to spurious detection of density dependence (Knape, 2008; Knape and de Valpine, 2012).

Detailed studies on snakes by Fitch (1999) allowed identification of density-dependent factors affecting snake populations between years. Habitat modification, both natural or induced by humans, is the most plausible factor driving population changes. In the case of *Agkistrodon contortix*, livestock removal led to an increase of small rodents in the study site, thereby increasing food supply for the snakes, with a concomitant increase in the snake population. Later, shrub encroachment reduced the availability of grasses and the number of rodents fell, thereby reducing food supply and negatively impacting (reducing) the snake population abundance. Finally, new

management practices aimed at producing crops and pastures led to a second increase in rodent populations that also increased abundance of *Agkistrodon* snakes (Fitch, 1999). For *C. constrictor*, abundance varied according to land management in a similar way to that observed for *A. contortix*. Shrub encroachment continued for a longer period in the *C. constrictor* habitat and almost led to the disappearance of the species from the area (Fitch, 1999). For *D. punctatus*, changes in vegetation structure in sampling areas led to changes in snake abundance, although in a more complex way. Snake abundance seemed to be associated with availability of refuges and open areas for thermoregulation (Fitch, 1999). In *T. sirtalis*, modifications in the habitat (creation of artificial water bodies, preferred habitat for the species) may account for variation in abundance among years. For the chelonian *Chrysemys picta*, however, differences in abundance among years in all studied populations seem to be because of migratory events between water bodies during dry periods (Congdon and Gibbons, 1996).

Density independence was rejected for several snake populations reported to be in a sustained decline for the past 10–15 yr (*Bitis nasicornis*, *Coronella austriaca*, *Python regius*, *Vipera aspis*, and *Vipera ursinii*) (Reading et al., 2010). By taking logarithms for species abundance, PBLRT seems to be insensitive to population general trends (increasing or decreasing) and still is able to find a return tendency in the time series, even when it may be ecologically meaningless. In the same way that correlation does not imply causation, rejecting the hypothesis of density independence does not necessarily imply a density-dependent mechanism of population regulation (Wolda and Dennis, 1993). PBLRT can reject density independence for any kind of data—even temporal series of rainfall data—if it has a “return tendency,” the quality searched for by the test (Wolda and Dennis, 1993). This leads to the need for both an ecological interpretation of test results and a knowledge of the time series data used to avoid spurious conclusions.

*Caiman crocodilus* also showed a significant density-dependent regulation. Time series for this species is hosted in the GPDD database (NERC Centre for Population Biology and Imperial College, 2010). The author of the original article on *C. crocodilus* (Smith, 1981) strongly recommended not using those time series data in population dynamic studies because the data were not reliable estimates of population abundance. Data for caimans in Smith (1981) are based on voluntary reports by hunters for an extensive area (populations were not clearly delimited), during a period of time when hunting and skin trade regulations changed (hunters would adapt their methods and reports according to their needs, but there was no actual audit). Work using time series hosted on the GPDD would conduct meta-analyses on population dynamics using the extensive amount of data available (Inchausti and Halley, 2001) and conduct some kind of data filtering to avoid including deficient

data on their analyses (Sibly et al., 2005; Brook and Bradshaw, 2006; Knape and de Valpine, 2012). Still, not knowing the origin of these data may lead researchers to base their conclusions on unsuitable information. We advise caution when using data in bulk to enhance accuracy of results and to improve its future applicability.

Although our effort fits in the first paradigm proposed by Krebs (1995a) and tried to find evidence for density dependence in studied populations, the analysis of well-known populations by using appropriate techniques should be useful to answer questions for both paradigms. The outstanding fieldwork of Fitch (1999) provided enough data to test for density dependence, whereas detailed information provided in his study sheds some light on density-dependent factors acting on snake populations. Inclusion of external factors such as food availability, predators, and environmental variables (Dennis and Otten, 2000; Hone and Sibly, 2002) are major variables to take into account to better understand population dynamics.

No similar studies have been published for lizards, and more detailed demographic information probably would be needed to capture variation in short-lived lizard populations. Evidence of density dependence in lizards was offered by Tinkle et al. (1993) for *S. graciosus* in an experiment where hatchling snout-vent length was larger after removing individuals from the experimental population. In our work, PBLRT did not reject density independence for this species. Similarly, although we could not reject density independence for any salamander, Van Buskirk and Smith (1991) found a positive correlation between survival and density in larvae of *Ambystoma laterale*. Mechanisms regulating amphibian species might differ between adults and larvae because different factors affect populations in terrestrial and aquatic environments (Wilbur, 1980; Berven, 1990). Moreover, temporal ponds may be subjected to higher pressures than larger and more stable bodies of water, because larval density increases as the pond dries, triggering different larval responses to crowding and predation (Wilbur, 1980; Leips et al., 2000).

The scarcity of long-term monitoring studies on reptiles and amphibians in pristine (or at least well-protected habitats) highlights the difficulty of analyzing density dependence in these groups. Some evidence exists that snake and anuran populations are regulated, and the combination of both experimental and long-term observational studies may be the way to gather more information on the subject. Analytic methods to detect density dependence have improved since the times of Tanner and Pimm, but we still do not have data of sufficient quality to use for such analyses. Moreover, the probability of type I and type II errors increases with small sample size (number of years in the time series), requiring a minimum sample of at least 30 generations to reject density independence with high probability (Solow and Steele, 1990). Even the methodology proposed by Dennis and Ponciano (2014) is sensitive to small sample sizes, by affecting accuracy in estimation of parameters. Still, data do provide insight into the existence of population regulation in reptiles, mediated by availability of food (*A. contortix* and *C. constrictor* as examples) and preferred habitats (as in the snakes *D. punctatus* and *T. sirtalis* and the turtle *C. picta*). Inclusion of environmental covariates in long-term monitoring studies may also enhance the sensitivity of analytical methods aimed at detecting density dependence in natural populations (Dennis and Otten, 2000).

Given that conditions on Earth are changing at a rapid pace (with climate change and habitat loss as major driving factors),

many reptile and amphibian populations likely will disappear (Huey et al., 2010; Sinervo et al., 2010; Li et al., 2013; Nowakowski et al., 2016). Although a significant influence of density on amphibian and reptile population regulation was not a widespread result of our analyses, density dependence should not be discarded as a regulation factor on these ectothermic animals.

*Acknowledgments.*—We dedicate this paper to the memory of the late H. S. Fitch in recognition of his dedication and pioneering long-term studies of Kansas snake populations. SML thanks Conselho Nacional de Desenvolvimento Científico e Tecnológico and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) for granting doctoral fellowships. NP thanks CONICET for an external postdoctoral fellowship to carry out research activities at the University of Texas at Austin and G. R. Colli for helpful discussion of ideas. ERP thanks the Denton A. Cooley Centennial Professorship in Zoology at the University of Texas at Austin for continuing support. We sincerely thank J. Knape, anonymous reviewers, and the journal's subject editor for helping us improve this manuscript.

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Accepted: 5 September 2017.

Published online: 25 January 2018.

#### SUPPLEMENTARY DATA

Supplementary data associated with this article can be found online at <http://dx.doi.org/10.1670/16-133.s1>.