Contributed Paper

Effects of an Invasive Plant on Population Dynamics in Toads

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Abstract: *When populations decline in response to unfavorable environmental change, the dynamics of their population growth shift. In populations that normally exhibit high levels of variation in recruitment and abundance, as do many amphibians, declines may be difficult to identify from natural fluctuations in abundance. However, the onset of declines may be evident from changes in population growth rate in sufficiently long time series of population data. With data from 23 years of study of a population of Fowler's toad (Anaxyrus [= Bufo] fowleri) at Long Point, Ontario (1989–2011), we sought to identify such a shift in dynamics. We tested for trends in abundance to detect a change point in population dynamics and then tested among competing population models to identify associated intrinsic and extrinsic factors. The most informative models of population growth included terms for toad abundance and the extent of an invasive marsh plant, the common reed (Phragmites australis), throughout the toads' marshland breeding areas. Our results showed density-dependent growth in the toad population from 1989 through 2002. After 2002, however, we found progressive population decline in the toads associated with the spread of common reeds and consequent loss of toad breeding habitat. This resulted in reduced recruitment and population growth despite the lack of significant loss of adult habitat. Our results underscore the value of using long-term time series to identify shifts in population dynamics coincident with the advent of population decline.*

Keywords: amphibian declines, *Anaxyrus fowleri*, habitat loss, invasive species, *Phragmites australis*, population regulation, time series

Efectos de una Planta Invasora sobre las Dinámica Poblacional de Sapos

Resumen: *Cuando las poblaciones disminuyen en respuesta a cambios ambientales desfavorables, las dinámicas de crecimiento de sus poblaciones se modifican. En las poblaciones que normalmente exhiben niveles altos de reclutamiento y abundancia, como sucede con muchos anfibios, las disminuciones pueden ser difíciles de identificar separadamente de las fluctuaciones naturales de abundancia. Sin embargo el comienzo de las disminuciones puede ser evidente a partir de cambios en la tasa de crecimiento poblacional en series de tiempo de datos poblacionales suficientemente largas. Con datos de 23 años de estudio de una población de Anaxyrus [=Bufo] fowleri en Long Point, Ontario (1989-2011), tratamos de identificar tales cambios en la dinámica. Buscamos patrones de abundancia para detectar un punto de cambio en la dinámica de la población y después los probamos entre modelos poblacionales competitivos para identificar factores intrínsecos y extrínsecos asociados. Los modelos más informativos del crecimiento poblacional incluyeron condiciones para la abundancia de sapos y la extensión de una planta de marisma invasora, Phragmites australis, a lo largo de las áreas de reproducción de los sapos en las marismas. Nuestros resultados mostraron crecimiento dependiente de la densidad en las poblaciones de sapos desde 1989 hasta 2002. Sin embargo, después de 2002 encontramos disminución progresiva de la población de sapos asociada con la extensión de la planta y pérdida consecuente del hábitat de reproducción de los sapos. Esto resultó en el reclutamiento reducido y crecimiento poblacional a pesar de la pérdida significativa de hábitat de adultos. Nuestros resultados resaltan el valor de usar series de tiempo a largo plazo para identificar cambios en la dinámica poblacional coincidentes con el advenimiento de la declinación poblacional.*

Palabras Clave: *Anaxyrus fowleri*, declinaciones de anfibios, especies invasoras, pérdida de hábitat, *Phragmites australis*, regulación de la población, series de tiempo

Introduction

The abundance of amphibians is in apparent decline around the globe (Houlahan et al. 2000; Collins & Storfer 2003). Numerous factors have been invoked to explain this, including emergent diseases, habitat loss, invasive species, climate change, and pollution (Alford & Richards 1999; Pounds et al. 2006; Gardner et al. 2007), but evidence for any particular driving factor is largely correlative and, in numerous cases, the causes of declines remain enigmatic (Stuart et al. 2004). In addition, many amphibian populations, particularly temperate pond-breeding species, may experience large fluctuations in abundance, generally driven by variation in annual recruitment (Alford & Richards 1999; Green 2003). The result is often a boom-and-bust pattern that makes it difficult to distinguish deterministic trends in abundance, due to any number of factors, from natural fluctuations (Pechmann & Wilbur 1994; Beebee & Griffiths 2005; Pellet et al. 2006). To determine whether a population is truly in decline, it is necessary to understand its dynamics under presumed normal conditions, ascertain when it departs from this regime into an uncompensated trend, and determine a probable cause for this shift.

The natural dynamics of populations, including populations of amphibians, can be strongly affected by intrinsic factors, such as population density, that influence abundance via variable population growth rates (Turchin 2003) or by extrinsic factors that directly affect births and deaths. These extrinsic factors can be stochastic, as with weather events, or deterministic, as with many forms of environmental change (Lande et al. 2003). By characterizing the effect of these various factors on populations under presumably normal conditions, it should be possible to identify deviations from these patterns that may be coincident with population decline.

Density-dependent population growth has a particularly important potential effect on population dynamics (Meyer et al. 1998; Turchin 2003). The occurrence of density-dependent regulation has been demonstrated in many animal groups (Brook & Bradshaw 2006), including some amphibian populations (Meyer et al. 1998; Pellet et al. 2006; Salvidio 2009). Density-dependent growth, assuming it is not overcompensating (May et al. 1974), implies there is an equilibrium size around which a population will naturally fluctuate (Crowley 1992; Turchin 2003). The tendency for a population to return to this equilibrium size results in fluctuations between upper and lower limits. This provides stability through bounded stochasticity (Crowley 1992). In general, amphibian populations appear to be density regulated in this way and characterized by stable, undercompensated dynamics with modest annual return rates (Salvidio 2011). As such, the detection of density-dependent growth may indicate

an amphibian population is neither declining nor increasing. However, long-term time series for amphibian populations are rare (Houlahan et al. 2000; Brook & Bradshaw 2006).

Determining the underlying dynamics of a population requires accurate and unbiased estimates of abundance over many years. If the factors affecting a population's growth remain stable over time, the same underlying model of population growth should be expected to pertain throughout a data time series and during any particular period within it (Turchin 2003). If there were a trend in the time series, however, a change in model likelihood reflective of such a change in population dynamics would be expected. This may indicate a phenomenon of decline, particularly if extrinsic, rather than intrinsic, factors have a greater effect on population dynamics.

We used this principle to investigate the population dynamics of a population of Fowler's toads (*Anaxyrus* [= *Bufo*] *fowleri*) over more than 20 years. We compared the annual abundance of these toads with various models of population growth that incorporated assorted intrinsic and extrinsic factors. Coincident with what appears to be a decline in the abundance of these toads over a decade of study has been the loss of breeding habitat attributable to the expansion of an invasive marsh plant. If this habitat loss has adversely affected the toads' population dynamics, then we expected to be able to detect a shift from the normal pattern of fluctuations in abundance to a deterministic trend of progressive decline.

Methods

Study Species and Area

We used data derived from the study of a population of Fowler's toads (*Anaxyrus fowleri*) at Long Point, Ontario, Canada. Fowler's toads are common and widespread in the eastern United States, but there are only 3 populations in Canada, all located on the northern shore of Lake Erie (Green 2005). Threats to the species' continuing existence in Canada have led to their classification as endangered under both Canadian federal and Ontario provincial legislation. The population at Long Point is of particular conservation interest due to its genetic differentiation from the other Lake Erie populations (Smith & Green 2004).

Our study was conducted along 8.5 km of the Lake Erie north shore at the western base of Long Point, Ontario (between $42°34'33''$N–$42°35'3''$N and $80°22'15''$–$80°28'24''$W) (Fig. 1). The study area consisted of a system of sand dunes running parallel to sandy beach along the shore of the lake. North of the dunes were shallow marshes, where Fowler's toads gathered to breed. Beginning in 1995, the area covered by the invasive strain of
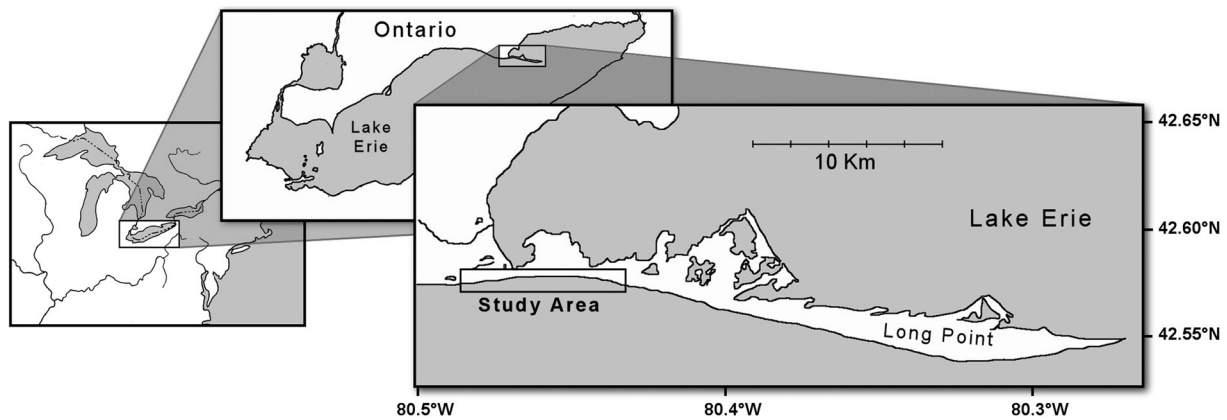
Figure 1. Location of the study site on the Long Point peninsula on the north shore of Lake Erie in Ontario, Canada.

common reed (*Phragmites australis*) rapidly increased at Long Point (Wilcox et al. 2003; Badzinski et al. 2008). This was coincident with what appeared to be a decline in the abundance of Fowler's toads. The area invaded by the reeds included the shallow marshes historically used as breeding habitat by the toads (Green 1997). The reeds filled in these sites, after which the toads no longer used them.

Toad Abundance

We used an intensive mark-recapture method (Donnelly & Guyer 1994) to estimate abundances of adult male Fowler's toads during each breeding season from 1989 through 2011. The protocol was designed to maximize recaptures, minimize effects of individual heterogeneity on detection probability, and obtain the high capture probabilities required for a reliable census (Freckleton et al. 2006). We identified all breeding sites each year by seeking out calling males after their emergence from winter dormancy in early to mid-May (Blaustein et al. 2002) and inspected them nightly through approximately 10 June, by which time chorus activity had waned. We also surveyed on foot 5 km of beach adjacent to the breeding sites to capture males after the end of breeding activity (Green 1997). Animals were captured, individually marked with toe clips, and immediately released. All procedures with the animals were authorized under permits issued by the Ontario Ministry of Natural Resources and Environment Canada and Animal Use Protocol Number 4569 from McGill University.

We used the individual capture histories of all male toads encountered and the closed-capture models embodied in program MARK (White & Burnham 1999) to estimate the number of living animals (*N*) each year. We assumed closure due to the intensity of the survey method, the boundaries imposed on the study area, and the short span of time over which each annual survey was conducted (Table 1). Furthermore, because toads

move only very short distances (Smith & Green 2004), we considered immigration and emigration insignificant for the duration of each census.

To ensure consistency and comparability among years, all estimates of *N* used model M_t (Otis et al. 1978), which incorporated the assumption that capture probability ($\hat{p}$) varied only with time (Darroch 1958). This model was notated {$N, p(t) = c(t)$} by White and Burnham (1999). We chose this model from among a suite of models that incorporated terms for temporal, behavioral, or individual variability. The chosen model had the lowest value of Akaike's (1974) information criterion adjusted for small sample sizes (AIC_c) in 20 of the 23 years of the survey and an average model likelihood of 0.87.

Environmental Variables

We obtained daily weather records for 1988 through 2010 from the National Climate Data and Information Archive (Environment Canada 2011) for the Port Colborne weather station located on the north shore of Lake Erie approximately 100 km east northeast of Long Point. This was the closest weather station to Long Point with continuous records from 1988 to the present. Like Long Point, Port Colborne is in the Eastern Lake Erie Basin climatic regime (Sly 1976), and weather patterns at the 2 stations are similar. The weather data included mean maximum summer temperatures (May 1–September 30), summer rainfall (May 1–September 30), and winter snowfall (January 1–March 31). We obtained records on the average monthly water levels of Lake Erie for May through July each year from 1988 through 2010 from the Canadian Hydrographic Service (Fisheries and Oceans Canada 2011).

Common Reed

For quantitative assessments of the area covered by common reed at Long Point, we concentrated on the

Table 1. Capture statistics, capture probabilities and estimated abundances of male Fowler's toads (*Anaxyrus fowleri*) over 23 years within the study area at Long Point, Ontario.

Year	Estimated abundance of male toads (N, SE)	Survey period (nights)	Capture occasions	Animals captured and marked	Total captures	Capture probability ($\hat{p}$)
1989	41, 1	48	20	39	107	0.130
1990	156, 40	35	9	58	68	0.041
1991	393, 24	40	23	253	365	0.035
1992	307, 16	39	18	222	367	0.064
1993	394, 23	36	20	259	389	0.046
1994	93, 4	38	13	83	166	0.144
1995	43, 1	37	19	43	141	0.170
1996	39, 2	39	16	37	95	0.151
1997	31, 1	31	13	31	90	0.218
1998	191, 4	32	28	180	494	0.092
1999	74, 4	35	17	15	45	0.176
2000	63, 5	44	22	50	92	0.065
2001	69, 4	40	21	60	125	0.084
2002	240, 23	46	22	139	197	0.035
2003	134, 14	46	19	85	128	0.049
2004	174, 6	41	30	152	336	0.064
2005	89, 5	40	20	77	162	0.090
2006	48, 4	39	17	38	72	0.090
2007	42, 3	40	18	39	87	0.110
2008	42, 6	40	13	32	51	0.085
2009	37, 2	41	22	34	79	0.095
2010	20, 3	41	16	16	28	0.085
2011	15, 0	41	17	15	45	0.176

central 580-ha Crown Marsh region of our study area. We used the estimated area covered by common reed as calculated by Wilcox et al. (2003) and Badzinski et al. (2008) for 1985, 1995, 1999, and 2006. For 2010 we used ArcMap (version 9.2, ESRI, Redlands, California) to map the extent of the reed beds visible on aerial orthophotographs and calculated their total area within the marsh boundaries. The fine texture and exceptional height of the monospecific common reed stands were readily distinguishable from surrounding vegetation on the photographs (Rice et al. 2000). We derived year-by-year values of common reed extent for the purpose of analyses by assuming linear change between known data points.

Change-Point Analyses

To determine whether and when there might have been a change point in the dynamics of the population over the course of the 23-year time series, we used binary segmentation as implemented in the "change point" package (Killick & Eckley 2012) in R (version 2.13, R Development Core Team 2011). This analysis breaks the series into subsets and tests the hypothesis that the means are the same in each subset with a likelihood ratio test (Scott & Knott 1974). We tested for change points in both the mean and variance of the annual rate of increase in the population (r_t), where $r_t = \ln (N_t/N_{t-1})$ and N_t and N_{t-1} represent the abundance of toads in the current and previous year, respectively.

Density-Dependent Population Regulation and Trends in Abundance

Because periodic cycles in abundance may be the result of complex density-driven dynamics (May et al. 1974), we used an autocorrelation function (ACF) in R (version 2.13) to test the possibility of long-term cycles in the time series. The ACF was estimated through the correlation between pairs of abundance data at multiple time lags, N_t and N_{t-x}, where $x = 1 \ldots 22$, with a significant correlation at lag x indicating the period of abundance cycles (Turchin 2003). We used the Dickey–Fuller test, implemented in the "urca" package (Pfaff 2008) for R (version 2.13), to determine whether the population oscillated in abundance in a manner consistent with stabilizing density-dependent regulation (Dickey & Fuller 1979). We used this test with either a drift constant for the mean or a deterministic trend constant to examine an autoregressive model of the time series with the test statistic, τ, for the presence of a unit root. The unit root, if present, indicates the population was not regulated around a return point.

We used randomization tests on the toad abundance data to determine whether the average annual rate of increase (r_t) significantly deviated from zero, which would mean the null hypothesis of no trend was rejected. We used the whole data set ($n = 23$ years) and subsets of varying duration. Using a custom program written in BASIC, we randomized the abundance values in each of these data sets, without substitution, 1000 times and computed the average r_t for each randomization. We

computed the mean and variance of these 1000 random average r_t values and computed the one-tailed probability that the average r_t obtained from the real temporal sequence of data was not more extreme than any value in this distribution. To test for the absence of a trend in the data, we also performed the 2-part test for a return point developed by Schmidt and Meyer (2008). In this test, the presence of a return point indicates there is no trend.

Model Selection and Evaluation

We employed both an information theoretic approach (Akaike 1974; Burnham & Anderson 2002) and leave-one-out cross-validation (Turchin 2003), implemented in the package DAAG (Maindonald & Braun 2012) in R (version 2.13), to evaluate candidate models of the population dynamics of the Fowler's toad population. The models variously incorporated terms for environmental variables, the extent of common reed in the marshes and the intrinsic factor of population density, which we modeled on the basis of our estimates of abundance either as N or $\ln(N)$ according to the Ricker (1954) or Gompertz (1825) logistic models of population growth, respectively. Density-dependent models were included on the basis of Dickey–Fuller test results. Each model represented the hypothesis that its particular combination of factors most strongly influenced the annual rate of increase of the population. As such, the null model contained only a stochastic term (ε_t) and a drift constant (i.e., $r_t = a + \varepsilon_t$). To avoid the unnecessary proliferation of uninformative models, we did not investigate multiyear time lags or complex interactions among factors that would not have been expected a priori. For each model, we calculated AIC_c scores, ΔAIC_c, and Akaike weights, which we used to identify the most informative model(s). From cross-validation, we calculated ΔCV (mean square error across all folds) and R^2_{pred}, which estimates the ability of the model to predict the test value relative to the mean of the series (Turchin 2003). Using the same set of models each time, we applied both methods of model selection for the entire 23-year time series and identified subsets of the time series to investigate those factors related to shifts in the dynamics of the population.

Results

Toad Abundance

In 909 evening surveys over 23 years of data collection, we made 3729 captures of 1957 individual male Fowler's toads. The number of toads captured each year ranged from 15 to 259, and individual capture probabilities ranged from 0.035 to 0.218 (Table 1). The estimated abundance of male toads went through a series of peaks
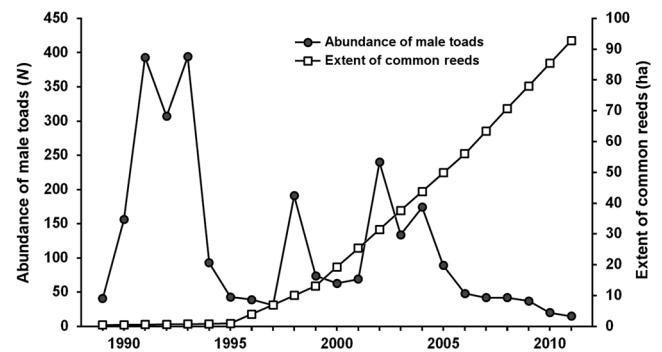

Figure 2. Estimated abundance of male Fowler's toads and extent of invasive common reed over 23 years, 1989–2011, at Long Point, Ontario.

and troughs over the 23 years of our study (Table 1 & Fig. 2). The highest of 5 peaks in abundance were in 1991 and 1993. The lowest abundances were in 1997 and 2011, when $N = 15$ (SE 0) individual males. From 1989 to 2002, there was a pattern of fluctuating abundance (Fig. 2). During this time, 6 of 13 changes (46.2%) were increases and 7 (53.8%) were decreases. However, after 2002 only one increase in abundance, in 2004, was recorded out of 9 population changes (11.1%).

Environmental Variables and Common Reed

Of the extrinsic environmental variables (Supporting Information), only Lake Erie water level exhibited a discernible trend over the study period. Although water levels averaged 174.4 (SE 0.2) m above mean sea level overall, all records prior to 1999 were above that level and all records thereafter, except for 2009 and 2011, were below. Summer air temperature averaged 22.9 °C (SE 1.0) and increased 0.05 °C/year. Summer rainfall ($\bar{X} = 419.6$ mm/year [SE 23.0]) and winter snowfall ($\bar{X} = 85.5.6$ cm/year [SE 37.0]) showed no patterns or trends.

The area of the Crown Marsh covered by common reeds remained <1 ha until the advent of the invasive strain around 1995 (Fig. 2 & Supporting Information). After 1995 the extent of common reeds increased by approximately 11.1%/year. By 2010 common reeds covered 85.4 ha (15% of the total marsh area). The reeds were concentrated primarily adjacent to the toads' overwintering habitat and where the toads had been known to breed.

Change Point

There was a significant change in the mean and variance of r_t in the toad population in 2002. From 1989 to 2002, mean r_t was 0.136 and year-to-year variance in r_t was 0.920. Thus, overall abundance was increasing, but it was highly variable. After 2002, however, mean

r_t was −0.308, and its variance was 0.110, indicating abundance was consistently decreasing. Accordingly, our subsequent analyses examined both the entire 23-year time series and the 2 consecutive subsets, 1989–2002 and 2002–2011.

Density Dependence and Trends in Abundance

There were no significant correlations in the ACF beyond a 1-year time lag in both the complete 23-year data set ($ACF_{[1]} = 0.572$) and the 2002–2011 subset ($ACF_{[1]} = 0.629$). These results indicate no evidence of long-term cycling or periodicity in the population during these periods. For 1989–2002, there were no significant correlations in the ACF.

Results of the Dickey–Fuller test showed the null hypothesis of the presence of a unit root could not be rejected when the test included a drift constant for the mean ($\tau = -2.46$, $p > 0.10$). However, the inclusion of a deterministic trend constant returned marginal evidence that abundance was regulated around a shifting return point ($\tau = -3.46$, $0.05 < p < 0.10$). Results of this analysis indicated that an initial carrying capacity of 176 male toads (SE 59) in 1989 declined by an average of 8 toads/year over time.

Over the entire time series, the average r_t of the male toad population was −0.046. Randomizing the abundance data produced a distribution of average r_t values with a mean of −0.002 and variance of 0.003. The one-tailed probability that the actual average r_t of the data set was not more extreme than any value in this distribution was $p = 0.226$. When we partitioned the data into 2 subsets and repeated the randomization test for each, the distribution of average randomized r_t values for 1989–2002 had a mean of −0.004 and variance of 0.010. This result was not much different from actual average r_t of 0.043 for the same period ($p = 0.350$). For the period 2002–2011, the distribution of average randomized values of r_t was −0.005 with a variance of 0.020; however, the actual average r_t was −0.308 ($p = 0.015$). Thus, we rejected the null hypothesis of no trend.

The Schmidt–Meyer test returned a low probability that there was no trend ($p = 0.037$) over the entire time series. However, the results of this test differed significantly for the population on either side of the 2002 change point. The probability of no trend during the period 1989–2002 was $p = 0.96$, and the return point for abundance of male toads was 111 individuals (CI 68–181 individuals). But the probability of no trend during the subsequent period, 2002–2011, was $p < 0.01$ and there was no return point for the abundance of the toads.

Model Selection and Evaluation

The 10 most informative models for the entire data set included ln(N), and the top 8 of those also included the term for the extent of common reed (Supporting Information). For all models better than the null model, those with ln(N) had a cumulative AIC_c weight of 0.967 and those incorporating common reed had a cumulative weight of 0.938. The model with the lowest AIC_c value (Table 2) included the 4 terms ln(N), common reed, spring rainfall, and winter snowfall and had a significantly greater predictive capability compared with the null model ($R^2_{pred} = 0.27$). Several models differing only in their inclusion of particular environmental variables provided a similar level of information ($\Delta AIC_c < 2$). The simplest model in which all terms were significant (i.e., the most parsimonious model) contained only ln(N) and the term for common reed, which was always negative. Comparing the predictions of models parameterized on the basis of all years of data (Fig. 3), the model containing only ln(N) performed poorly mainly because it predicted positive growth in the population after 2002 instead of the actual negative growth. Adding common reed to this model increased the accuracy of predictions relative to the realized negative values of r_t after 2002. The environmental variables such as rainfall and snowfall increased the variance in r without markedly changing this pattern, a result that suggests these variables did not add substantially to model likelihood.

All models better than the null model that explained variation in r_t from 1989 to 2002 included ln(N) (Table 2). Environmental factors, which performed relatively poorly as single-factor models, added significantly to models that also accounted for toad abundance. The most informative model ($w = 0.682$) included ln(N) and winter snowfall and predicted observed r_t significantly better than the null model ($R^2_{pred} = 0.33$). However, the next most informative model ($\Delta AIC_c = 1.78$) included only ln(N). When we compared the 2 models of density-dependent growth, ln(N) provided a better fit than N ($\Delta AIC_c = 2.74$, evidence ratio = 2.61). Models parameterized on the basis of data from 1989 to 2002 all performed poorly in predicting r_t after 2002 (Fig. 3). This result is a further indication that the dynamics of the population changed at that time and that it no longer responded to ln(N), common reed, or the environmental factors that had held sway previously.

The only model more informative than the null model to explain variation in r_t following 2002 incorporated only Lake Erie water level ($w = 0.78$, $R^2_{pred} = 0.21$) (Table 2). Even so, ΔAIC_c for the null model was 1.51 ($w = 0.17$), indicating that defining r_t as a function of lake level between 2002 and 2011 was not a substantial improvement over simple stochastic growth. Models that included ln(N) or common reed all had values of $\Delta AIC_c > 3$, a result that indicated the population was responding largely to extrinsic, stochastic factors.

Table 2. Summary of the most informative models predicting the annual rate of change (r_t) in the abundance of Fowler's toad (*Anaxyrus fowleri*) at Long Point, Ontario.[a]

Period	Model: $r_t =$[b]	ΔAIC_c	w	ΔCV	R^2_{pred}
1989–2011					
1	$2.521 - 0.551 \ln(N_{t-1}) - 0.0159 P_{t-1} + 0.0023 R_{t-1} - 0.0078 S_t + \varepsilon_t$	0.00	0.412	0.432	0.27
2	$3.392 - 0.547 \ln(N_{t-1}) - 0.0152 P_{t-1} - 0.0073 S_t + \varepsilon_t$	0.68	0.209	0.472	0.20
3	$2.749 - 0.550 \ln(N_{t-1}) - 0.0140 P_{t-1} + \varepsilon_t$	1.50	0.092	0.531	0.10
4	$1.905 - 0.554 \ln(N_{t-1}) - 0.0146 P_{t-1} + 0.002 R_{t-1} + \varepsilon_t$	1.76	0.071	0.491	0.17
5	$191.4 - 0.578 \ln(N_{t-1}) - 0.0193 P_{t-1} - 0.0080 S_{t-1} - 1.076 L_{t-1} + \varepsilon_t$	1.87	0.063	0.657	−0.11
Null	$-0.0457 + \varepsilon_t$	4.62	0.004	0.590	—
1989–2002					
1	$4.258 - 0.683 \ln(N_{t-1}) - 0.0116 S_t + \varepsilon_t$	0.00	0.682	0.551	0.33
2	$2.837 - 0.591 \ln(N_{t-1}) + \varepsilon_t$	1.78	0.115	0.771	0.06
3	$0.652 - 0.0037 N_{t-1} + \varepsilon_t$	2.74	0.044	0.813	0.01
4	$9.100 - 0.622 \ln(N_{t-1}) - 0.314 T_{t-1} - 0.0108 S_t + \varepsilon_t$	3.01	0.034	0.630	0.24
5	$3.091 - 0.630 \ln(N_{t-1}) + 0.002 R_{t-1} - 0.0104 S_t + \varepsilon_t$	3.04	0.033	0.649	0.21
Null	$0.0846 + \varepsilon_t$	3.86	0.014	0.824	—
2002–2011					
1	$522.75 - 3.00 L_{t-1} + \varepsilon_t$	0.00	0.811	0.077	0.21
Null	$-0.308 + \varepsilon_t$	1.51	0.179	0.098	—

[a] *For each period, the 5 most informative models are presented, except for 2002–2011 for which only one model had an AIC_c value less than the value for the null model.*
[b] *Abbreviations: N, toad abundance; P, extent of common reeds; R, spring rainfall; S, winter snowfall; T, summer temperature; L, lake level.*
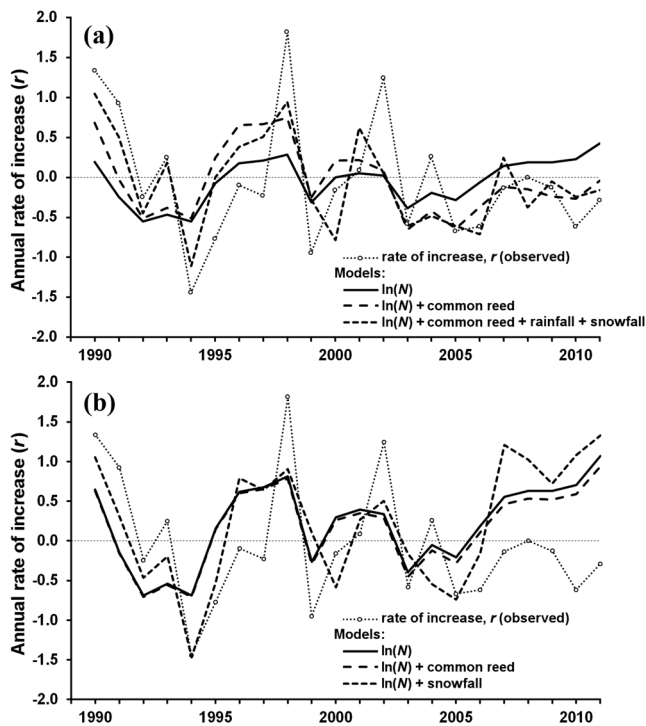
Figure 3. Variation in observed annual rate of change (r) in Fowler's toad abundance relative to predictive models of abundance (Table 2): (a) models parameterized on the basis of data from 1989 to 2011 and (b) models parameterized on the basis of data from 1989 to 2002.

Discussion

Population decline is the invariable prelude to population loss. Decline may be catastrophically rapid or so slow as to be nearly imperceptible but, in all cases, populations will decline in response to extrinsic causes of unfavorable environmental change. They shift from their previous, regulated dynamics into a period of adjustment to whatever levels of abundance the new environmental conditions may support. On the basis of over 2 decades of accurate census data, we successfully identified this shift in Fowler's toads at Long Point as they were affected by a major environmental perturbation: the loss of breeding habitat due to expansion of invasive common reeds.

The dynamics of the Fowler's toad population at Long Point from 1989 to the early 2000s is characterized by considerable fluctuations in abundance, which is entirely as expected for a pond-breeding anuran (Green 2003) and consistent with a hypothesis of density dependence. Such undercompensating regulation would be stabilizing, thereby increasing population persistence (Crowley 1992; Turchin 2003). It would also counteract stochastic environmental factors that would serve to increase variance in the rate of increase, exaggerate fluctuations in abundance, and foster higher probabilities of extinction (Lande et al. 2003). Yet density-dependent regulation is exceeding difficult to demonstrate (Dennis & Taper 1994), even with time series of data longer than ours, and we are unable to prove it conclusively despite the precision of our data. Detection is confounded when

time series are short and highly variable, and rendered nearly impossible when changes in environmental carrying capacity induce trends in abundance. Thus, we used a battery of tests to investigate the dynamics underlying our 23-year time series of abundance data, including the Dickey–Fuller test, which is conservative but lacks statistical power for short time series, and model selection, which may be overly liberal in detecting density dependence. Nevertheless, it is not entirely necessary to prove that the population of Fowler's toads at Long Point, Ontario, is density regulated for our results to show quite strongly that the population shifted at about the year 2002 from a dynamic regime of fluctuating abundance to a condition of uncompensated decline.

The change in the dynamics of the toad population appears strongly linked to the uncontrolled spread of common reeds and the corresponding decline in the extent of open water in the Long Point marshes (Wilcox et al. 2003; Badzinski et al. 2008). The change point in our data in the year 2002 corresponds to a transition between an earlier period before common reeds dominated the marsh and a later period when common reeds effectively eliminated all shallow, sparsely vegetated, aquatic breeding habitat used by the toads. Common reeds proliferate especially during periods of low water (Whyte et al. 2008); thus, Lake Erie water levels also played a substantial role in this process. Once toads' breeding habitat had all but disappeared, any further expansion of common reeds may have been largely irrelevant for the toads, whose subsequent downward trend in abundance can be interpreted as regulation toward the new, lower carrying capacity of the altered environment. This would explain the strong effect of common reed and ln(N) on toad abundance over the full data set but the lack of significant effect of either variable when only abundance of the toads from 2002 on was considered.

Although the current outlook for this population of Fowler's toad may appear bleak, there is the potential for a successful recovery. The toads appear to be well adapted to the dynamic nature of their marshland and sand dune environment (Breden 1988) and have high reproductive potential; adult female Fowler's toads can lay clutches of 2,000–10,000 eggs (Green 2005). Their natural resilience to environmental perturbations indicates that mitigation of breeding habitat loss through control of common reeds should result in a fairly rapid, positive response by the population. Although no effective method for controlling the invasive common reed has yet been devised (Tewksbury et al. 2002), temporary artificial breeding ponds could rescue this population of toads until effective strategies can be implemented to limit the extent of common reeds and restore breeding sites in wetland complexes.

Our results underscore the importance of long-term time series of data for identifying declines in vertebrate populations and their causes. Understanding of the natural dynamics of species, particularly those of conservation concern, is a necessity for identifying patterns consistent with changes to those dynamics (Pechmann & Wilbur 1994) and the onset of population decline (Lande et al. 2003). The establishment and maintenance of long-term monitoring projects are therefore crucial for accurate assessment of population status, recovery of populations in decline, and mitigation of the causes of population loss.

Acknowledgments

Supporting Information

Environmental data for the study area at Long Point, Ontario, and extent of area occupied by invasive common reeds in the Crown Marsh, 1989–2011 (Appendix S1) and full results of model selection (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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