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Article in *Ecography* · August 2013

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Body size varies with abundance, not climate, in an amphibian population

David M. Green and Jessica Middleton

D. M. Green (david.m.green@mcgill.ca) and J. Middleton, Redpath Museum, McGill Univ., 859 Sherbrooke St. W., Montreal, QC H3A 0C4, Canada.

Body size variation among animals has many possible correlates, temporal as well as geographic. Adult male body size was analysed over the course of 23 yr (1989–2011) in a population of Fowler's toads *Anaxyrus fowleri* at Long Point, Ontario. We used an information theoretic approach to identify the most likely models to explain body length variation in relation to abundance, age and environmental variables, including temperature. Male toads overall averaged 53.6 ± 0.1 (SE) mm ($n = 1976$) but average body length from year to year varied from 50.9 ± 0.2 to 61.4 ± 1.3 mm ($n = 23$ yr), a difference of 18.7%. Abundance was the only variable significantly correlated with body size variation ($R^2 = 0.713$, $p = < 0.001$). A significant 10-yr trend in increased body size ($R^2 = 0.874$, $p = < 0.001$) was coincident with a previously detected negative trend in abundance. A $0.05^\circ\text{C yr}^{-1}$ increase in environmental temperature over the course of our study was not significantly correlated with the toads' body size. Body size variation in these toads is likely related to density-dependent resource availability for growth in the terrestrial stage. Temporal changes in average body size within populations in relation to density may be a significant component of phenotypic variation.

An animal's body size affects every aspect of its biology and is, in turn, affected by multiple components of its environment and heredity (Peters 1983, White et al. 2007). At the large scales of organization of interest to macroecology, animal body size has been treated standardly as a species or population characteristic (Chown and Gaston 2010) and set as the independent variable in relation to large-scale patterns of abundance, climate or resource availability (Angilletta et al. 2004, Walters and Hassall 2006). Implicitly, the average body size of a species or population is assumed to be, if not precisely constant, then at least consistent (White et al. 2007, Gaston et al. 2008). Thus Bergmann's rule (Bergmann 1847) and James's rule (James 1970) concerning animal adaptation to climate at the species or population level, respectively, or the 'abundance–size rule' (Damuth 1981), for example, are all observations cast in terms of some estimated standard species- or population-specific body size, often with data sets consisting of single samples as exemplars (Damuth 1987, Atkinson 1994, Olalla-Tárraga and Rodríguez 2007).

But what, actually, is the standard or average body size of a species or a population? At the level of the individual, it is abundantly evident that adult animal body size is both phenotypically plastic and evolutionary malleable (Millien et al. 2006, Ozgul et al. 2010, Yom-Tov and Geffen 2011). An individual's eventual adult body size is influenced by many contingent factors during its growth and development, including density, temperature, age structure and food availability (Teder et al. 2008, McNab 2010, Huston and Wolverson 2011). Thus significant variability in body

size within and between populations should be expected. Macroecological correlates to the body sizes of species are likely to find explanations only insofar as they relate to the microecological processes of somatic growth, density and selection that affect the body sizes of individuals (Hayward et al. 2009, Chown and Gaston 2010, Liao and Lu 2012).

Variation in animal body size is both geographic and temporal. Geographic body size variation among populations within species is common (Yom-Tov and Geffen 2006, Gaston et al. 2008). Temporal body size variation within populations may occur both over long temporal scales, during which evolutionary change may become evident (Millien et al. 2006), and over short time frames characterized largely by phenotypic plasticity (Yom-Tov and Geffen 2011). Significant changes in average body size over periods of many years have been found within populations of animals as diverse as beetles (Braun et al. 2004), rodents (Smith et al. 1998) and fishes (Bjørnstad et al. 1999, Martinson et al. 2008, Ohshimo et al. 2009). In some cases, body size within populations may change fairly rapidly. Teplitsky et al. (2008) found a significant decrease in body mass in red-billed gulls *Larus novaehollandiae* over a 47-yr period. Ozgul et al. (2009) found a significant decrease in body mass in Soay sheep *Ovis aries* over a 20-yr period. Smith et al. (1998) found a significant decrease in body mass in wood rats (*Neotoma* spp.) in less than eight years. Loehr et al. (2007) showed that tortoises *Homopus signatus* increased and decreased individual growth and body length in relation to rainfall amount over a span of 5 yr. These four studies all implicated environmental

conditions, especially climate change, in inducing body size changes. Buckley et al. (2008), though, found no evidence that environmental temperature varied with abundance, and thus with body size, in lizards of many species and Tryjanowski et al. (2006) found that the correlation between changes in body size and changes in climate varied among closely related, sympatric European water frogs.

Amphibians, being small, widespread and prone to congregate in seasonal breeding assemblages, should be amenable subjects for the study of body size variation. Geographic variation in body size has been identified within numerous amphibian species (Olalla-Tárraga and Rodríguez 2007) though there is no consistent correlation to any particular environmental factor. For example, body size in amphibians has been found to vary geographically in apparent conformity to Bergmann's (or, rather, James's) rule in many species (Ashton 2002), opposite to Bergmann's rule in other species (Cvetković et al. 2009, Sinsch et al. 2010) and without evident regard to Bergmann's rule in still other species (Adams and Church 2008). Variable rates of growth within populations are known (Galatti 1992) and the presence of density dependent growth in amphibians, particularly larvae and recently metamorphosed juveniles, is well established (Cohen and Alford 1993, Petranks and Sih 1993, Altwegg 2003, Altwegg and Reyer 2003, Boone 2005, Harper and Semlitsch 2007). Denton and Beebee (1993), showed that adult body size was negatively correlated with density among populations of natterjack toads *Epidalea* (= *Bufo*) *calamita*. However, there is only modest documentation of temporal variation in body size in amphibian populations (Yom-Tov and Geffen 2011) as there are very few longitudinal studies of amphibian populations that present data on body size (Sullivan 1983, Elmberg 1987, Neveu 2009). This is despite the many recent long-term studies of changes in their abundance (Houlahan et al. 2000, Green 2003, Lowe 2012). If adult body size in amphibians may be strongly affected by density-dependent somatic growth rates (Harper and Semlitsch 2007) and the abundances of amphibians may be highly changeable (Green 2003), then temporal variation in body size within populations may be considerable. It might even be enough to confound, or be confused with, evidence of variation in relation to geography, temperature, resources or climate.

We therefore addressed temporal variation in body size in the wild within a single amphibian population in relationship to abundance, age and environmental factors. Body length of adult Fowler's toads *Anaxyrus* (= *Bufo*) *fowleri* has been reported to range from 51 to 63.5 mm in males, and up to 82 mm in females (Dickerson 1907, Wright and Wright 1949, Conant 1958, Klemens 1993, Hulse et al. 2001). The population at Long Point, Ontario, on Lake Erie is known to vary from year to year in abundance and population age structure to a considerable degree (Green 1997, 2005, Greenberg and Green in press). As we shall demonstrate with 23 yr of continuous data, they also vary considerably in body size. If somatic growth rate of individuals is negatively correlated with abundance (Denton and Beebee 1993), then average body size in this population of toads should vary in concert with abundance over time as an inverse power or lognormal relationship (DeLong and Vasseur 2012). Alternatively, if average body size is

simply a function of age in animals with indeterminate growth (Hemelaar 1988, Liao and Lu 2012), there should be a significant correlation between age and body size. Finally, if there exists an energetic relationship between average body size and abundance (Arendt 2011), then both should be correlated in these ectothermic animals with mean environmental temperature during their active growing season (Sinsch et al. 2010).

Methods

Study area and sampling

Intensive mark–recapture study of Fowler's toad was conducted annually from 1989 through 2011, inclusive, along 8.4 km of the Lake Erie north shore at the western base of Long Point, Ontario (between 42°34'33"–42°35'3"N and 80°22'15"–80°28'24"W). In general aspect, the study area is a system of sand dunes running parallel to sandy beach along the shore of the lake. North of the dunes are shallow marshes where the toads breed. In this study area, there are few discrete breeding sites where the animals chorus consistently from year to year. Long Point is a highly dynamic environment and the animals are opportunistic in selecting breeding sites, which often are ephemeral. Surveys of male Fowler's toads were conducted at breeding sites and on the Lake Erie beaches where non-breeding animals can easily be located as they forage at night (Green 2005). All procedures with the animals were conducted under the auspices of research permits and letters of authorization issued by the Ontario Ministry of Natural Resources and Environment Canada in accordance with the Ontario Endangered Species Act and Canadian Species at Risk Act, as well McGill Univ. Animal Use Protocol no. 4569.

Body size determination

The snout-vent length (SVL) of every toad encountered was measured with dial callipers accurate to 0.1 mm. Toads were held firmly in hand and pressed flat with a thumb in order to measure them from the back of the vent to the tip of the snout in a consistent way. We limited the present study to adult males, which were readily identifiable from both adult females and juveniles by their dark throats and by the release calls they made when handled. Adult females tend to be larger than adult males but have no obvious morphological characteristics to distinguish them from juveniles other than relative size.

Abundance estimates

We used the abundance estimates of adult male toads determined by Greenberg and Green (in press). These were derived from intensive mark–recapture studies that yielded an estimated abundance, \hat{N} , for each breeding season based on probability of first capture, p , and probability of recapture, c , using the closed capture model, $\{\hat{N}, p(t) = c(t)\}$, embodied in the program MARK (White and Burnham 1999). All estimates of \hat{N} were normalized via log-transformation for analysis.

Temperature and lake level records

Daily air temperature and rainfall records from 1988 to 2010 were obtained from the National Climate Data and Information Archive of Environment Canada (<http://climate.weatheroffice.gc.ca/climateData/canada_e.html>) for the Port Colborne weather station, located near the north shore of Lake Erie approximately 100 km ENE of Long Point. Port Colborne and Long Point are both in the eastern Lake Erie Basin climatic regime (Sly 1976) and weather patterns at the two stations can be considered comparable. Port Colborne is the closest weather station to Long Point with continuous records from 1989 to the present.

Based on observations of spring emergence of adult toads over the years of study and the minimum temperature, about 14°C, at which the toads are active, we defined the active season for the toads as commencing 41 d after the vernal equinox, i.e. about 1 May, and continuing for 154 d to about 1 October. We used maximum daily air temperature in our analyses as it tends to vary over a greater range than mean or minimum temperature.

We compiled records of Lake Erie water levels, in meters, for May through August from 1988 to 2011 using data available from the Canadian Hydrographic Service (<www.waterlevels.gc.ca/>). Lake levels were measured relative to the International Great Lakes Datum 1985 for Lake Erie, set at 173.5 m above mean sea level.

Age of adult toads

From 1992 onwards, chronological ages of adult toads were determined using skeletochronology as described by Kellner and Green (1995), following the methods of Leclair and Castanet (1987). For any one year, we used a random sampling of newly marked toads, as well as recaptured toads marked and aged in the previous year. Because the toads were captured shortly after emergence from hibernation, lines of arrested growth (LAGs) deposited in the bone during the previous winter's hibernation were not discernible from the outer edge of the bone, which was therefore counted in all cases as a LAG.

The average age of adult males in any given year was determined from the skeletochronology results of that year plus known-aged animals recaptured from previous years. Because of differing sampling sizes each year, the contributions of recaptured animals to estimations of age structure were adjusted so that the ratio of aged new animals to aged recaptured animals matched the ratio of new to recaptured animals overall. Skeletochronological results were not available for the years 1993 and 2001. In 1994, one toad was recaptured from the previous year. Though its age had not been determined, rather than discount it from the 1994 results, we made the assumption that it was 3 yr old.

Data analysis

We used Akaike's (1974) information criterion adjusted for small sample sizes, AIC_C , and Akaike weights to evaluate models related to annual variation in body size among male

Fowler's toads in this population. The dependent variable was SVL (snout-vent length), the average body size of males in each year. Since 2-yr olds are the most abundant age class among the toads (Kellner and Green 1995, Middleton and Green unpubl.), we also used the average body length of the 2-yr olds only as a dependent variable (SVL_{age2}) to control for age in relation to the environmental variables.

We considered the following independent variables for analysis in our models.

Year: years from 1989 to 2011, inclusive, to investigate evidence of a temporal trend. Because of the change in population dynamics in this population from a regulated state during the period 1989–2001 incl. to a declining trend during the period 2002–2011 incl. (Greenberg and Green in press), we also considered each of these time periods separately.

Age: the average age, per year, of known-aged adult individuals.

N : the log-transformed estimate of abundance, i.e. $\ln(\hat{N})$, each year. We used either estimated abundance of the year (N_{yr}), the previous year (N_{yr-1}) or the year before that (N_{yr-2}). For 2-yr old individuals, we considered either N_0 , N_1 , or N_2 , which were $\ln(\hat{N})$ of all adults in their first year and in the years when they were 1- and 2-yr old, respectively.

Temp: the average daily maximum air temperature of the 154-d active season during the previous year ($Temp_{yr-1}$) or the year before that ($Temp_{yr-2}$). **TempLate**, with variants as for Temp, was the average daily maximum air temperature during the latter half of the active season when young-of-year juveniles would experience greatest growth following metamorphosis (Hota 1994). For 2-yr olds, $Temp_0$ was average daily maximum air temperature in the year when the animals would have been tadpoles and $Temp_1$ was when they were 1-yr of age and may be expected to have done most of their post-metamorphic growth.

Rain: total precipitation, in mm, during the toads' 154-d active season during the previous year ($Rain_{yr-1}$) or the year before that ($Rain_{yr-2}$). For 2-yr olds, $Rain_0$ was the total precipitation in the animals' first year of life and $Rain_1$ when they were 1 yr of age.

Lake: water level of Lake Erie of the year ($Lake_{yr}$), one year ($Lake_{yr-1}$) or two years ($Lake_{yr-2}$) previous. For 2-yr olds, $Lake_0$ was lake level in the animals' first year of life whereas $Lake_1$ was lake level the year after.

The several variants of N , Temp, Rain or Lake were obtained simply shifting the data a year at a time relative to SVL. They are thus not independent and we first considered all the variants of each of these four variables as alternative models for explaining variation in SVL or SVL_{age2} to identify the variant to be used for subsequent analyses according to AIC_C score and AIC_C weight. If none of the variants had a lower value of AIC_C than the null model, the variable was not used further.

We considered all possible models for SVL or SVL_{age2} vs Year, Age and informative variants of N , Temp, Rain and Lake and calculated AIC_C and Akaike weights to identify the most informative among them with regards to their ability to explain observed variation in body size. We retained the model with the lowest AIC_C value and other models with $\Delta AIC_C < 2$. For models incorporating more than one independent variable, we ran multiple regressions to identify the relative contribution of each variable to the over-

all regression. Model selection and subsequent regression analyses were performed using JMP-8 software.

Results

In total, 1741 individual adult male Fowler's toads were captured and measured over 23 yr. Although the life span of Fowler's toad in the wild is short (Kellner and Green 1995), 235 captures were made in one or more consecutive years, resulting in a total of 1976 body length measurements. Of these, the smallest adult males we found were 43 mm SVL whereas the largest was 70 mm (Table 1), a considerably greater range in body size than has been previously reported for the species.

The overall average SVL (1989–2011, incl.) was 53.6 ± 0.1 mm (SE) mm for all males ($n = 1976$). However, the average annual SVL over all 23 yr was 55.1 ± 0.7 mm (SD) since average body lengths varied considerably from year to year (Table 1, Fig. 1). Average SVL was greatest in 2011, when males were 61.4 ± 1.3 mm (SE), and least in 1993, when males were 50.9 ± 0.2 mm (SE), a difference of 18.7%. There were also a significant trend towards larger average SVL over the course of the study ($p = 0.001$, $R^2 = 0.321$, $n = 23$ yr), due largely to the years 2002–2011 ($p < 0.001$, $R^2 = 0.874$, $n = 10$ yr). There was

Table 1. Body size averages for male Fowler's toads at Long Point, Ontario, 1989–2011.

Year	Snout-vent length (mm)			n
	average (\pm SE)	min	max	
1989	56.1 ± 0.58	51	65	37
1990	51.2 ± 0.42	44	62	58
1991	51.4 ± 0.18	43	60	249
1992	52.4 ± 0.18	44	60	219
1993	50.9 ± 0.19	43	61	255
1994	54.2 ± 0.24	49	59	83
1995	55.4 ± 0.53	47	64	43
1996	55.9 ± 0.38	49	60	37
1997	57.1 ± 0.61	49	62	31
1998	55.3 ± 0.21	48	62	180
1999	56.1 ± 0.40	50	65	65
2000	54.5 ± 0.58	44	64	50
2001	54.4 ± 0.44	47	62	57
2002	54.7 ± 0.31	43	67	133
2003	53.5 ± 0.44	44	62	85
2004	52.8 ± 0.30	46	65	151
2005	54.2 ± 0.30	50	63	76
2006	54.7 ± 0.61	47	64	33
2007	54.7 ± 0.58	48	63	37
2008	58.5 ± 0.67	50	66	32
2009	59.1 ± 0.60	53	70	34
2010	58.2 ± 0.83	53	64	16
2011	61.4 ± 1.27	52	69	15

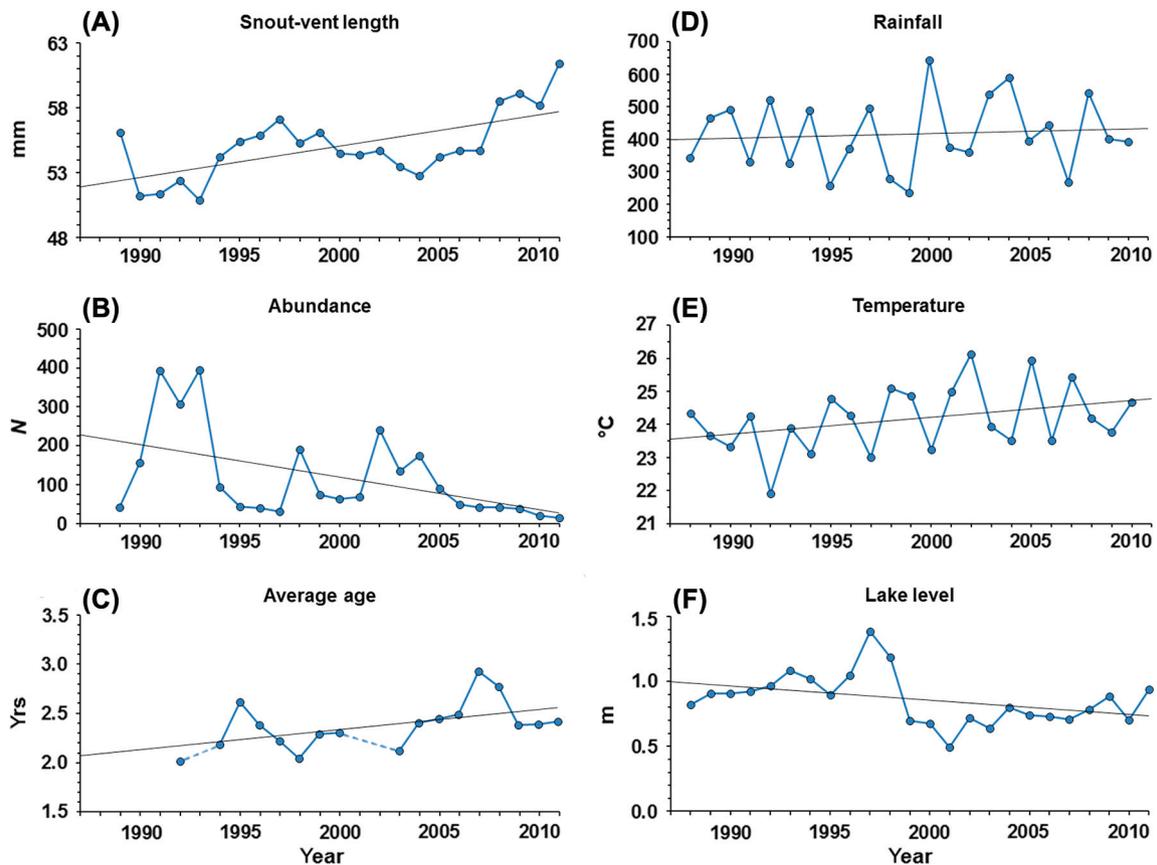


Figure 1. Variation in adult male Fowler's toads *Anaxyrus fowleri* from 1989 to 2011 (A–C) and environmental variables (May through September) from 1988 to 2011 (D–F) at Long Point Ontario. (A) Average body size measured as snout-vent length (SVL) of toads. (B) Estimated abundance of toads. (C) Average age of adult toads. (D) Total rainfall. (E) Average daily maximum air temperature. (F) Lake Erie water level relative to Lake Erie IGLD 1985 datum.

no significant trend in SVL over the years 1989–2001 ($p = < 0.088$, $R^2 = 0.328$, $n = 13$ yr)

Adult male toads averaged 2.33 ± 0.05 (SE) years of age ($n = 539$). The majority of adult males (62.4%) were 2 yr old. No toads were older than 5-yr of age. The average annual age was 2.39 ± 0.06 (SE) ($n = 17$ yr). The average age of the toads tended to increase over the years of study ($p = 0.036$, $R^2 = 0.261$, $n = 17$ yr (Fig. 1)). There was no trend discernible relationship between SVL in relation to Age ($p = 0.324$, $R^2 = 0.065$, $n = 17$ yr).

There were 15 yr in which 5 or more known 2-yr olds were sampled. SVL_{age2} among these 2-yr olds was highly correlated with SVL in the population as a whole ($p < 0.001$, $R^2 = 0.915$). There was likewise a significant trend over time in SVL_{age2} ($p = 0.028$, $R^2 = 0.284$, $n = 15$ yr).

The average daily maximum air temperature, variable Temp, during the 154-d active season for the toads was 22.9 ± 1.4 (SE) $^{\circ}\text{C}$ over the span of 23 yr from 1988 through 2010. A trend of increasing average temperature by 0.05°C yr^{-1} was not statistically significant ($p = 0.151$, $R^2 = 0.101$) owing to considerable variation from year to year (Fig. 1). There was no significant relationship between $\text{Temp}_{\text{yr}-1}$ and SVL in the toads (Fig. 2).

Average rainfall, variable Rain, over the 23 yr during the 154-d active season for the toads was 419.6 ± 23.0 (SE) mm. Although the amount of rain varied from a high of 643 mm to a low of 235 mm (Fig. 1), no trend in Rain was detectable

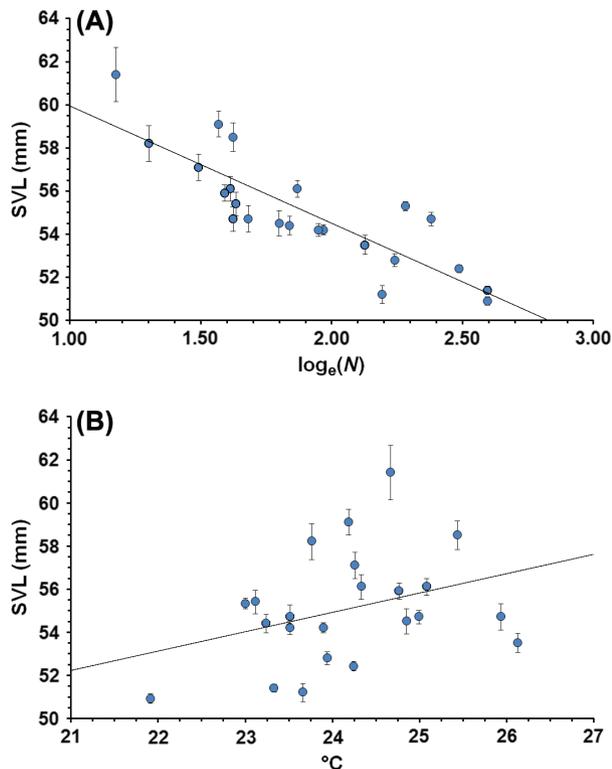


Figure 2. Relationships between average body size (snout-vent length [SVL], with standard errors) vs (A) \log_e -transformed estimated annual abundance and (B) average late summer temperature for adult male Fowler's toads over 23 yr from 1989 through 2011 at Long Point, Ontario. The relationship of SVL to abundance is significant ($p = < 0.001$, $R^2 = 0.713$), the relationship of SVL to temperature is not ($p = 0.097$, $R^2 = 0.125$).

Table 2. Evaluation of alternative models for Fowler's toad average snout-vent length (SVL) relative to log abundance (N), year and average adult age at Long Point, Ontario, Canada.

Model	Parameters	AICc	ΔAICc	Akaike weight	R^2	p
1	N	66.110	0.000	0.397	0.669	<0.001
2	N, Age	67.411	1.301	0.207	0.709	<0.001
3	N, Age, Year	68.222	2.112	0.138	0.760	<0.001
4	N, Year	68.390	2.279	0.127	0.692	<0.001
5	N, $\text{Temp}_{\text{yr}-1}$	69.597	3.487	0.070	0.669	<0.001
6	N, Age, $\text{Temp}_{\text{yr}-1}$	71.482	5.372	0.027	0.710	0.001
7	N, Year, $\text{Temp}_{\text{yr}-1}$	72.461	6.351	0.017	0.692	<0.001
8	N, Age, Year, $\text{Temp}_{\text{yr}-1}$	72.670	6.560	0.015	0.767	0.001
9	Year	78.327	12.216	0.001	0.321	0.001
10	Year, Age	81.773	15.663	0.000	0.322	0.066
11	Year, $\text{Temp}_{\text{yr}-1}$	81.785	15.675	0.000	0.322	0.005
12	null	81.910	15.800	0.000	–	–

over the 23 yr of study ($p = 0.799$, $R^2 = 0.003$). No model of Rain had an AICc value lower than a null model. The variable Rain was therefore discarded in subsequent analyses.

Lake Erie water levels, variable Lake, averaged 0.86 ± 0.04 (SE) m above the IGL datum 1985, i.e. 174.36 m above mean sea level (Fig. 1). Water levels were all above this average from 1989 through 1998 and below this average from 1999 to 2010 except for 2009. Water level rose above average in 2011. This long-term fluctuation rendered a significant negative trend in lake level over the course of the study ($p = 0.034$, $R^2 = 0.197$). Lake Erie water level (variable Lake) was likewise uninformative except for Lake_{yr} compared to SVL over the latter 10 yr of the study (AICc weight = 0.498).

The best model to explain variation in SVL was N_{yr} , which returned a strong, negative correlation ($p < 0.001$, $R^2 = 0.713$, $n = 23$ yr (Fig. 2)). The seven next best models also incorporated N_{yr} but only $N_{\text{yr}} + \text{Age}$ had a $\Delta\text{AICc} < 2$ (Table 2). The multiple regression using $N_{\text{yr}} + \text{Age}$ was also significant ($p < 0.001$, $R^2 = 0.709$, $n = 17$ yr) but this was due wholly to the contribution of N_{yr} ($p = < 0.001$) and not Age ($p = 0.187$).

Using only 2-yr old animals, the best model to account for variation in SVL_{age2} was N_2 , i.e. abundance in the same year ($p < 0.001$, $R^2 = 0.702$, $n = 15$ yr). The next best was $N_2 + \text{Year}$ ($\Delta\text{AICc} = 0.591$, $p < 0.001$, $R^2 = 0.760$, $n = 15$ yr) the significance of this relationship was only to the contribution of N_2 ($p = < 0.001$), not Year ($p = 0.115$). Neither N_0 nor N_1 returned informative models compared to N_2 ($\Delta\text{AICc} > 2$). SVL_{age2} did not correlate with any environmental variables.

Discussion

Clearly, average body size in this population of toads is a function of their changeable abundance. The relationship is virtually immediate, and much faster than seen in previously notable instances of rapid body size change in animal populations (Smith et al. 1998, Loehr et al. 2007). This may be because they are short-lived animals (Kellner and Green 1995) that only breed annually. As we have found, the majority of the breeding population consists of newly adult individuals

that are either one or two years old (Middleton and Green unpubl.). Late season growth rate prior to sexual maturity is the most probable proximate driver of average body size in these toads since anurans commonly grow rapidly prior to sexual maturity and much more slowly thereafter, in conformity to the von Bertalanffy (1938) growth curve (Hota 1994, Iturra-Cid et al. 2010, Sinsch et al. 2010). Our data, collected in early spring, reflect the relationship between size and abundance reached by the toads by the end of the previous summer, immediately prior to their entering into their winter dormancy.

The biphasic life-history of toads readily suggests an environmental link between abundance and density in this population that is not related to climate change. The dune and beach habitat used by the adults (including juveniles) has remained more or less consistently available throughout the period of study. This is not true of larval habitat. Encroachment by the invasive reed, *Phragmites australis* (Badzinski et al. 2008) began to affect the population of toads around 2002 by progressively eliminating larval habitat in the marshes (Greenberg and Green unpubl.). The consequent dwindling of adult abundance without significant loss of adult habitat resulted in lower adult density and thus likely greater relative resource availability. This phenomenon has not been investigated explicitly in amphibians despite evidence of density-driven body size changes within populations, particularly among tadpoles (Semlitsch and Caldwell 1982, Leips and Travis 1994, Stark et al. 2012).

Although there has been a steady increase in environmental temperature over the course of our study, there is no detectable effect on body size in these toads. Quite contrary to Bergmann's rule applied to climate change (Millien et al. 2006) or the temperature-size rule for ectotherms (Atkinson 1994, Walters and Hassall 2006, Gardner et al. 2011), the toads are getting bigger while the temperature increases. This only apparently contradicts studies of amphibian populations that have found correlations between body size and climate change (Tryjanowski et al. 2006, Neveu 2009) since few, if any, simultaneously have considered abundance. It is, in fact, surprising how often abundance has generally been overlooked or discounted in studies of body size variation within animal populations. Alaska sockeye salmon clearly show a negative correlation between body size, or growth rate, and abundance over an approximately 70-yr span from the late 1920s to the late 1990s (Martinson et al. 2008), as do Japanese sardines *Sardinops melanostictus* in the Sea of Japan and the East China Sea from 1953 to 2006 (Ohshimo et al. 2009). Instead of looking to abundance, complex interactions between recruitment, prey biomass and climatic oscillations were proposed by Martinson et al. (2008) and Ohshimo et al. (2009) to explain the observed changes in body size in these fishes. Millien (2004) and Millien and Damuth (2004) found antiparallel latitudinal patterns of body size variation in two species of Japanese field mice, *Apodemus argenteus* and *A. speciosus*, but did not consider density as a factor. Braun et al. (2004) found a decrease in body size and concomitant increase in abundance in 63 species of ground beetles over 16 yr but neither they nor Lövei and Magura (2006), in their reanalysis of the same data, considered the size-abundance relationship so evident in these data. On the other hand, Wilson et al. (2007)

recognized a significant negative correlation between density and body size in Soay sheep inhabiting St Kilda, Scotland, which apparently overrode an expected effect of selection for larger body size.

Nevertheless, long-term correlations between abundance and adult body size have been found in assorted animals, mainly mammals and birds (Yom-Tov and Geffen 2011). Adult body size, at least in mammals, appears to be determined to a great extent by nutrition during early development, when an individual experiences its greatest rate of growth (Geist 1987, Henry and Uliaszek 1996, Lindstrom 1999, Ozgul et al. 2010). Thus variation in food availability may drive systematic variation in somatic growth rate, and resulting adult body mass, in deer (Myserud et al. 2001, Toigo et al. 2006), bears (Zedrosser et al. 2006), lemmings (Krebs 1996), porpoises (Read and Gaskin 1990) and wild dogs (McNutt and Gusset 2012). Among birds, growth rates have been shown to vary in great tits in relation to territory size, and thus both density and food availability (Wilkin et al. 2006). Body size variation over time is known within populations of ectothermic vertebrates as well. Loggerhead turtles *Caretta caretta* (Hatase et al. 2002), Australian water pythons *Liasis fuscus* (Madsen and Shine 2000) and arctic cod *Gadus morhua* (Jørgensen 1992) all exhibit variable growth rates attributable to food availability.

This, then, is the most likely explanation for the negative effect of abundance on body size variation we have observed in Fowler's toads (Teder et al. 2008, McNab 2010, Huston and Wolverton 2011). It may seem unlikely that food availability could be limiting for a small insectivore but at Long Point, the toads tend to forage along the narrow band of damp beach beside the lake and so there is considerable potential for interference competition among individuals for available prey. Furthermore, the toads live solitary and generally asocial lives outside of the breeding season. They may disturb or actively avoid each other during their periods of evening activity. At increasingly higher densities, inter-individual interference, disturbance or avoidance behavior would all tend to decrease an individual's rate of food intake and increase the extent of its foraging even when the abundance of insect prey is unchanged. Denton and Beebe (1993) noted that individual natterjack toads living in high-density populations tended to be in poorer physiological condition, and roamed much more widely, than toads living in low density areas.

Two opposing temporal patterns of size vs abundance have been described in animal populations. Opposite to the negative correlation found among fishes (Martinson et al. 2008, Ohshimo et al. 2009), beetles (Braun et al. 2004) or Fowler's toads, populations of voles and lemmings characteristically undergo simultaneous, positively correlated cycles of abundance and body size (Krebs 1996). This effect is a carry-over result of higher somatic growth rates and survival rates during the phase of population growth such that at peak abundance, the population has a great many larger and older individuals (Oli 1999). Looking to possible effects of climate change rather than mere abundance, Ozgul et al. (2010) attributed a similarly concurrent increase in body size and abundance in yellow-bellied marmots *Marmota flaviventris* in Colorado to longer growing seasons. Teplitsky et al. (2008), though, cast doubt

on climate change as the driving force behind positively correlated declines in both body mass and abundance in red-billed gulls *Larus novaehollandiae*. Oli's (1999) explanation for positively correlated changes in body size and abundance relies on individuals having life spans that overlap several generations. Positive versus negative correlations between size and abundance may reflect the difference between endothermic versus ectothermic physiologies. Nevertheless, salmon, sardines and beetles are semelparous, and our population of Fowler's toads is virtually so since few individuals evidently live to breed more than once (Middleton and Green unpubl.).

The rapidity of the toads' response to changing abundance also implies that it is a purely phenotypic rather evolutionary response. The body size variation we observe in this population of toads, and in other species, in inverse relation to population density appears to be distinct from the effects of selection pressures that may drive rapid evolution in body size. Differential, size-related mortality due to harvesting can produce rapid, evolutionary changes in body size in diverse species of ectothermic vertebrates (Sasaki et al. 2009, Wolak et al. 2010, Carlson et al. 2011). Selection pressure can be strong enough to drive a population to smaller body size at the same time as hunting pressure reduces population density, as seen in the snake, *Gloydius blomhoffii*, in Japan (Sasaki et al. 2009). Such effects may be especially prevalent among harvested fishes in which the pressure of fishing leads to a population-level response towards rapid maturation at smaller size. There is no harvest for Fowler's toads and so the possibility that the changes we see in body size are due to rapid evolutionary response to strong selection appears remote.

The most basic implication of strong temporal body size variability for macroecology is that estimates of average body size for a population or species may need to be treated with caution insofar as they may depend on both where and when the measurements are taken. We found an 18.7% difference between smallest and largest average male body sizes within a single population over 23 yr. By comparison, among six populations of the Chinese toad, *Bufo andrewsi*, ranging in elevation from 676 to 2100 m, average male body length varied from about 73 to 82 mm, a difference of 11.8% (Liao and Lu (2012), among three populations of the Chinese frog, *Rana chensinensis*, from 567 to 1700 m elevation, average male body length differed up to 11.7% (Ma et al. 2009) and among nine populations of natterjack toad in Spain, ranging from 10 to 2270 m elevation, the largest and smallest average male body sizes differed by 29.4% (Leskovar et al. 2006, Oromi et al. 2012). In terms of latitude, largest and smallest average male body size differed among 12 populations of European common frog *Rana temporaria* throughout Sweden by 16.8% (Laugen et al. 2005), among five populations of common toad *Bufo bufo* from Switzerland to Norway by 26.6% (Hemelaar 1988) and among 14 populations of common toad from Serbia to Scandinavia by 32.4% (Cvetković et al. 2009). We conclude, therefore, that whether amphibians do (Ashton 2002) or do not (Adams and Church 2008, 2011) follow Bergmann's or any other ecogeographic rule, temporal changes in body size within populations may also be a significant component of variation.

Acknowledgements – We thank the Canadian Wildlife Service (Aylmer District), Ontario Ministry of Natural Resources (Vineland), Ontario Park (Long Point Provincial Park) and legions of student volunteers over the years for their assistance with this long-term study. Funding for this research was provided through grants from the Natural Sciences and Engineering Research Council (NSERC) of Canada, Canadian Wildlife Service, Ontario Ministry of Natural Resources and World Wildlife Fund Canada to DMG.

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