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ORIGINAL PAPER

Geographical variation in body size and sexual size dimorphism of introduced American bullfrogs in southwestern China

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Abstract Invasive species often exhibit geographical variations in life history traits that may allow them to successfully invade different environments. We investigated geographical variation in body size and sexual size dimorphism (SSD) of invasive bullfrogs in southwestern China, by sampling two breeding populations (descendants of a single source population) inhabiting sites at low (1,412 m, Shiping) and high (2,692 m, Luguhu) altitudes. Both populations exhibited significant SSD, with females larger than males. At high altitude, mean body size of both sexes and the degree of SSD were significantly reduced; the reduction in mean body size with increasing altitude was more pronounced in females, although not significantly so. Female bullfrogs also showed a significant decrease in average age at high altitude that may be a major factor related to this pattern; average age of male bullfrogs did not vary significantly with altitude. Growth rate of both sexes was also lower at high altitude. Our results provide the first evidence that introduced bullfrog's exhibit geographical variation in morphology in invaded areas in response to different environments, likely due to changes in climate. Additional research is required to determine the mechanism of this variation (i.e., physiological or developmental plasticity, mortality rate, selective pressure) and most importantly, to evaluate the potential for variation in the impacts of introduced bullfrogs on native ecosystems in China.

Keywords Invasion ecology · Life history traits · Plasticity · Altitude · *Rana catesbeiana*

Introduction

Biological invasions are the subject of increasing concern, as they pose a major threat to native biodiversity and economics at a global scale (Pimentel et al. 2005; Simberloff et al. 2005; Wilcove and Chen 1998). It has been suggested that the life history plasticity of invasive species is an important factor in promoting invasions (Lee 2002; Lodge 2004). Geographical differentiations in life history traits among populations of invasive species are also particularly interesting because of the relatively short time the

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species has been present in an area (Hänfling and Kollmann 2002; Kollmann and Banuelos 2004). Many successful invaders can be flexible in ecological or evolutionary traits, enabling them to cope with variation in environmental or geographical conditions in the introduced area and establish self sustaining populations (Rosecchi et al. 2001; Sakai et al. 2001).

Successful invaders exhibit a high degree of diversity in their life history traits, a characteristic that has been observed across taxa (Alcaraz and Garcia Berthou 2007; Alexander et al. 2009; Benejam et al. 2008; Bohn et al. 2004; Lockwood 1999). In contrast, the failure of some introduced species to successfully invade has been attributed to their poor ability to adapt to geographical gradients (Becker et al. 2005). In general, nonindigenous species decline as altitude increases, probably due to an intensification of the severity of climatic conditions (e.g., drought, cold, radiation; Daehler 2005). Consequently, collection of life history information across the range of an introduced species is crucial, in order to determine the potential success and degree of establishment (Bohn et al. 2004; Mooney and Hobbs 2000). Furthermore, geographical variation in morphology of an invasive species and the associated implications should also be taken into consideration when evaluating potential impacts on native communities (McGarrity and Johnson 2009).

The American bullfrog (*Rana catesbeiana;* hereafter referred to as the bullfrog) is listed among the 100 worst invasive alien species in the world by the Invasive Species Specialist Group of the IUCN-World Conservation Union (Lowe et al. 2000), and is one of only three amphibians classified as such. Bullfrogs are native to eastern North America, but have been introduced into western North America, the Caribbean, South America, Europe, and Asia, with well-documented ecological impacts on native species and ecosystems (Adams 1999; Boone et al. 2007; Kats and Ferrer 2003; Kiesecker et al. 2001; Kupferberg 1997; Wang et al. 2007; Wu et al. 2005). Although substantial research has focused on these negative impacts and the factors predicting the invasion success of bullfrogs (Ficetola et al. 2007; Li et al. 2006), little information is available on geographical variation in evolutionary and ecological characteristics in invaded areas.

Body size and sexual size dimorphism (SSD) often vary geographically, and are considered to be among the most important evolutionary and ecological characters that can be measured in animals, including amphibians (Ashton 2002; Campbell and Echternacht 2003; Morrison et al. 2004). Variation in these traits in an organism is the product of both evolution and morphological plasticity (Travis 1994), and may be influenced by a wide variety of abiotic and biotic factors. In anurans, including bullfrogs, SSD is related to variation in life-history strategies between sexes, and large size may confer competitive or reproductive advantages (Howard 1978a, b). As a result, variation in body size and SSD of invasive anurans may lead to variation in potential impacts on native species and should be evaluated.

Like most anuran species, bullfrogs show a marked SSD in their native range, with females as the larger sex, due to a difference in population age structure of males and females (Howard 1981; Monnet and Cherry 2002; Shirose et al. 1993). Bullfrogs also exhibit geographical variation in body size in their native range, with body size decreasing with increasing latitude (Bruneau and Magnin 1980). Introduced bullfrogs in western Canada are known to grow more rapidly and reach maturity earlier than individuals from native populations in eastern Canada, likely due to milder climatic conditions (Govindarajulu et al. 2006). However, to our knowledge, similar phenotypic plasticity in body size and SSD among introduced bullfrog populations has not yet been demonstrated.

Following the limited success of several early efforts to introduce bullfrog farming in mainland China around 1960, remnant bullfrog stocks from a single source population were expanded in the 1980s and used to establish additional farms across the country (Zeng 1998; Xu et al. 2006). Escaped bullfrogs from these farms have established feral, breeding populations (Li and Xie 2004; Liu and Li 2009) and have successfully invaded southwestern high-altitude areas (Liu and Li 2009). These complex mountain environments are excellent model systems for studying bullfrog responses to altitudinal variation in climatic conditions. In the present study, we collected data on body size, age, growth, and SSD of adult bullfrogs from low and high-altitude populations, in order to evaluate geographical variation in these life-history characteristics in their introduced range in China.

Materials and methods

Study area and field sampling

Our study area is situated in Yunnan province in the plateau region of southwestern China, in an area with a complex climate including tropical, subtropical, temperate and boreal climates. Based on information gleaned from local bullfrog farmers and local Aquatic Culture Departments, we determined that introduced bullfrogs have been established in the study area for approximately 20 years, and descended from a single source population which was introduced from Cuba. The history of bullfrog farming in China (Fig. 2) is comprised of three small-scale trials during the late 1950s and early 1960s, followed by a nationwide expanded farming effort during the 1980s. The earliest trials (1950s) failed due to limited supply of food for the bullfrogs, and a subsequent successful trial (1960s) was limited to government and university aquaculture facilities in a few provinces due to the limits of the planned economy in China at that time (Chen 1993; Zeng 1998; Wu et al. 2004). By the early 1980s, economic reforms in China resulted in transition toward a market economy, promotion of the aquaculture industry, and improved food supply for bullfrog farming. At this time, bullfrogs descended from the 1960s introduction from Cuba (Fig. 2) were found in Hanshou county of Hunan (Institute of Special Aquaculture Species of Hanshou County Hunan Province, Departmant of Biology, Hunan Normal University 1986; Ministry of Agriculture of the P.R.C. 1996; Sun 1990; Zeng 1998). These remnant stocks have since been expanded throughout China for household farming, resulting in the successful establishment of many feral populations founded by individuals that escaped from holding enclosures (Jiang 2008; Wu et al. 2004; Zeng 1998).

We sampled two introduced populations of bullfrogs in Yunnan province (Fig. 1), from sites located at low (Shiping) and high altitude (Luguhu) sites, collecting a total of 147 adult frogs (Shiping: $n = 72$–37 male, 35 female; Luguhu: $n = 75$–39 male, 36 female) from both sites during the summer of 2008, by hand collecting, dip-netting, and electro fishing at night (1,900–2,230 h). In order to describe the degree of climatic variation between sites, we compared historical monthly average data on minimum and maximum temperatures (Fig. 3), collected from the WorldClim database (1950–2000, spatial resolution: 2.5 arc-minutes, available at http://www.worldclim.org). We found a significant degree of variation in temperature between sites; the high altitude site (Luguhu) experiences much lower minimum (paired samples t tests; $t = 20.443$, $df = 11$, $P = 0.000$) and maximum ($t = 24.641$, $df = 11$, $P = 0.000$) temperatures. Due to the topography of the area, our low and high-altitude sites were also latitudinal separated; thus, climatic variation between sites is likely due to the combined effects of altitude and latitude.

Sex determination and morphometrics

We identified the gender of bullfrogs according to the development of secondary sexual characters. We identified males by the presence of yellow throat pigment and swollen nuptial pads, or by observation of reproductive behaviors such as defense of territories (Howard 1978a, b). If these characteristics were lacking, we classified frogs as females. We measured snout to vent length (SVL) of live specimens to the nearest 0.02 mm with a vernier calliper and weighed them to the nearest 0.01 g with an electronic balance.

Laboratory age estimation

We used skeletochronology to estimate the age of the frogs. This technique has proven to be a reliable tool for determining age of bullfrogs (Spear et al. 2009) and a variety of other amphibian species (Castanet et al. 1988; Halliday and Verrell 1988; Smirina 1994). We clipped the third phalanx of the fourth toe of the hind foot of each frog for skeletochronological age estimation. We embedded phalanx specimens in paraffin for sectioning and stained sections with Ehrlich's haematoxylin to facilitate observation of growth rings or lines of arrested growth (LAGs) under the microscope. We determined the age of each frog by counting the number of LAGs in multiple phalanx sections; we took each LAG to represent 1 year of life. Although we were unable to validate the skeletochronological method using specimens of known age from the study area, this technique was

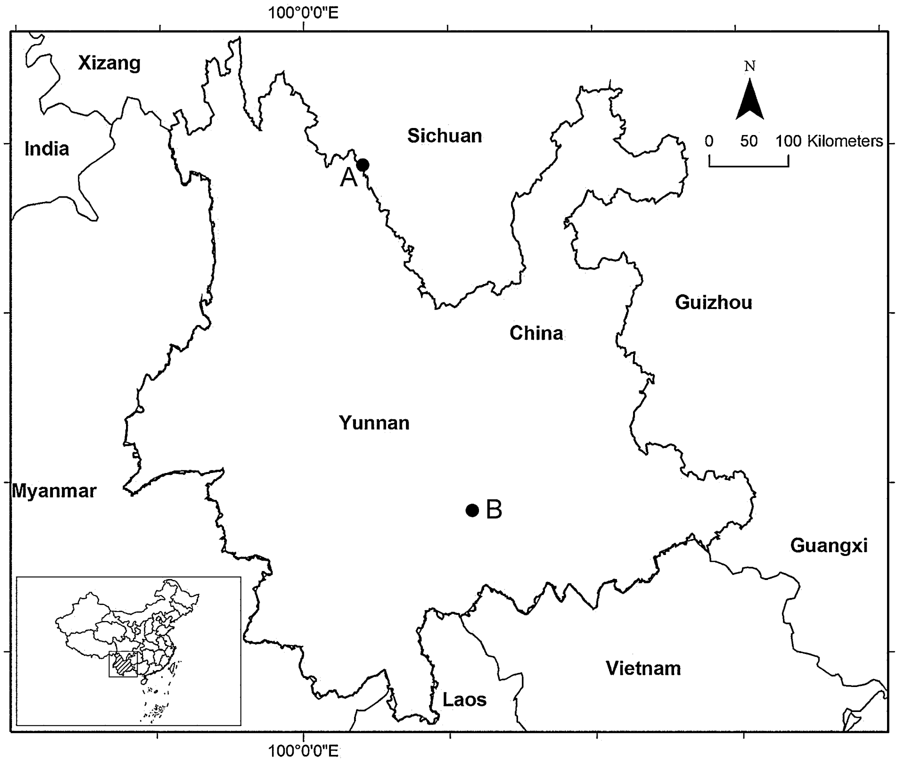

Fig. 1 Location of American bullfrog (*Rana catesbeiana*) populations sampled at **a** low (Shiping, N 23°42′ E102°28′ 1,412 m) and **b** high (Luguhu, N 27°42′ E 100°51′ 2,692 m) altitude sites in southwestern China

first validated using bullfrogs (Schroeder and Baskett 1968), and has been used successfully to study other ranids living at various elevations in mainland China and Taiwan (Lai et al. 2005; Ma et al. 2009). However, in older individuals, endosteal resorption can obscure the innermost LAG and lead to misinterpretation of skeletochronological age. In order to minimize the problem of LAG resorption, we analyzed sections taken from a point just proximal to the midpoint of the bone (intermediate phalanx). To identify cases of LAG resorption, we calculated the diameters of the innermost and the other visible LAGs; LAG resorption was indicated when the diameter of innermost visible LAG was >2 SD greater than the group mean (Sagor et al. 1998). Although LAG resorption is believed to only minimally influence age determination (Gibbons and McCarthy 1983; Miaud et al. 1999), we corrected two specimens which were suspected to have resorption phenomena. Furthermore, the sharpness of LAGs may also influence the estimation of frog age; we thus removed three specimens which had faint LAGs. Hence, we believe our age estimation based on skeletochronology accurately portrays the true age structure of these populations. We established the age of each frog based on independent counts by two observers of the number of LAGs in phalanx sections.

Statistical analysis

Skeletochronological age data were not normally distributed (strong negative skew), and mathematical transformations (e.g., logarithmic) failed to normalize data. Therefore, we rank transformed age data and used ANOVA to analyze the rank-transformed data; this nonparametric equivalent of a two-way ANOVA allowed us to compare average age between sexes and altitudes and evaluate potential interactive effects of these two factors.

Before comparing body size (SVL) between sexes and altitudes, we used partial correlation analysis to evaluate the relationship between body size and age after controlling for site and sex, and found a significant positive correlation between body size and age ($r = 0.848$, $df = 143$, $P = 0.000$). Therefore, we used ANCOVA with age as the covariate to evaluate variation in SVL between sexes and altitudes after controlling for the effects of age.

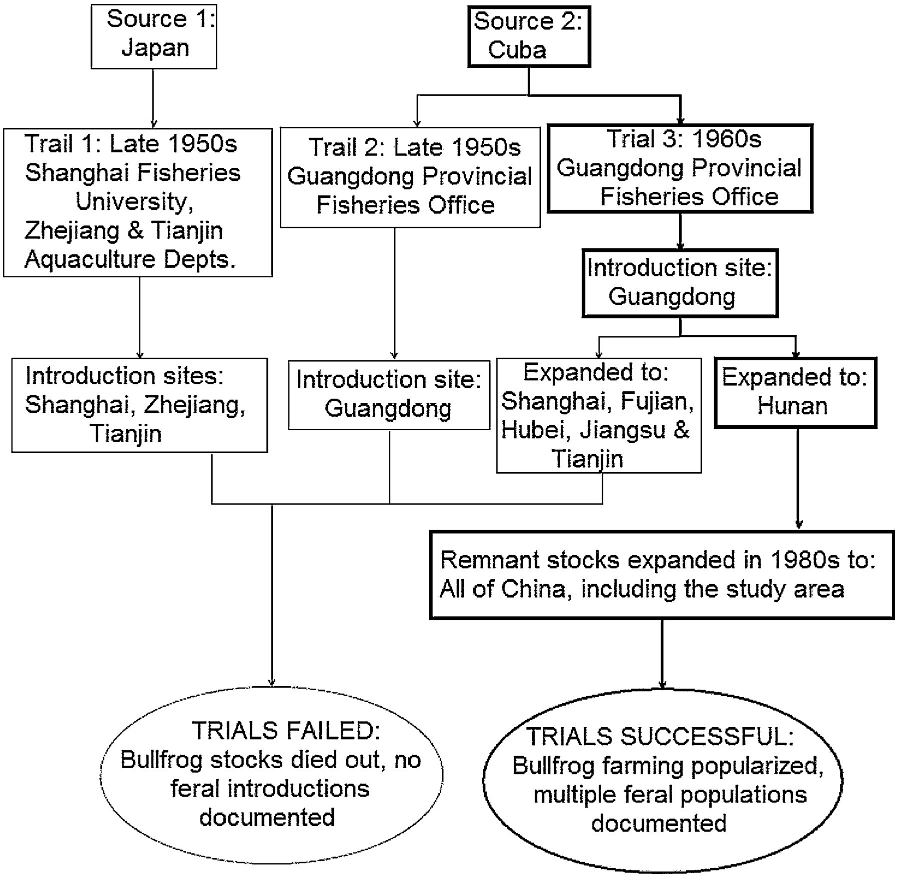

Fig. 2 History of American bullfrog (*Rana catesbeiana*) farming trials (history of extant populations shown by *bold lines*) in China, showing source and timing of introductions to the study area in Yunnan province

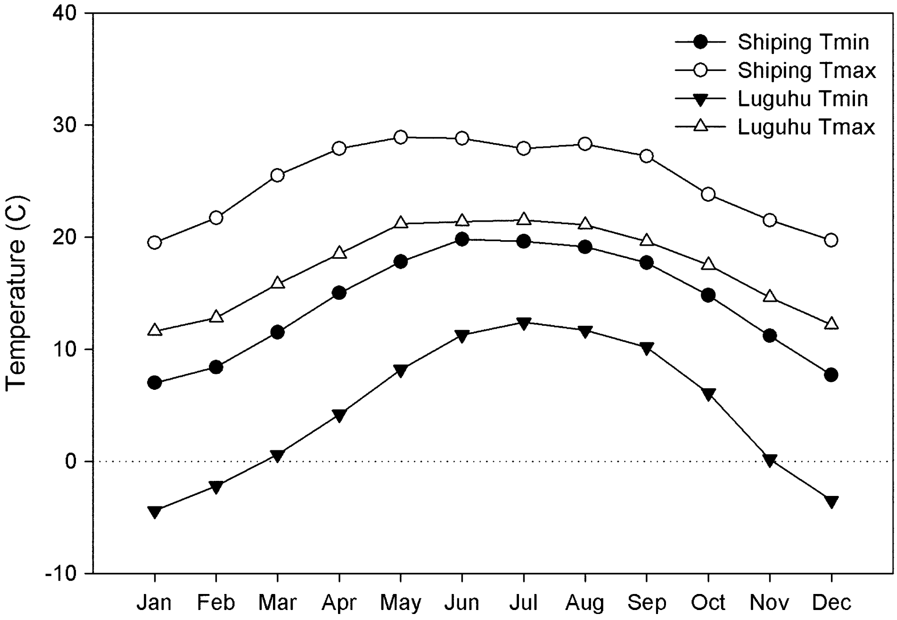

Fig. 3 Comparison of monthly minimum and maximum temperatures at low (Shiping, 1,412 m) and high (Luguhu, 2,692 m) altitude study sites in southwestern China. (Historical monthly average data from 1950 to 2000)

We estimated SSD of each age group (year) for each population using the SDI index (Lovich and Gibbons 1992), where SDI = [mean size of the larger sex/(mean size of the smaller sex-1)]. This index has the best statistical properties of all dimorphism indexes that have been proposed (Smith 1999; Stillwell et al. 2007). We also calculated sex ratios (male:female) of each age group for each population. We compared SDI and sex ratios between low and high altitude sites using ANOVA. We did not include age as a factor in the analyses due to the nature of the data; there was only one SDI or sex ratio value per age group per population (thus only $n = 2$ for each age × altitude combination). In order to explore the potential for interactive effects of age and altitude, we followed ANOVA with nonparametric correlation analyses and graphing.

We described and compared growth rates between populations from low and high altitudes by fitting growth equations with von Bertalanffy's model (von Bertalanffy 1957) using the equation $\mathrm{SVL}_t = [\mathrm{SVL}_\infty (1-\mathrm{b} \times \mathrm{e}^{-\mathrm{kt}})^3]$, where SVL_t is SVL at age t, SVL_∞ is the estimated asymptotic SVL, k is a growth coefficient relating to how quickly SVL_∞ is reached, and b is a constant. We estimated asymptotic size (SVL_∞), growth coefficients (k), and constants (b) based on nonlinear regression of size-at-age data for each sex at each site.

We performed all statistical analyses using SPSS 17.0 (SPSS Inc., 2008), and determined statistical significance at the level of $\alpha = 0.05$.

Results

Age and body size

Average age (Fig. 4) of female bullfrogs at our study sites was significantly greater than that of males (ANOVA; $F_{[1,146]} = 8.367$, $P = 0.004$). Average age of frogs from the low-altitude population was significantly greater than that of frogs from the high-altitude population ($F_{[1,146]} = 7.328$, $P = 0.008$), but there was not a significant interactive effect of sex and altitude ($F_{[1,146]} = 0.565$, $P = 0.453$). Bullfrog age was positively correlated with body size (SVL), even after controlling for the effects of sex and altitude (Pearson partial correlation = 8.387, $df = 6$, $P = 0.211$). After controlling for the effect of age, bullfrogs exhibited significant SSD (Fig. 4), with females as the larger sex (ANCOVA; $F_{[1,146]} = 20.878$, $P = 0.000$), and significant geographical variation in body size, with frogs at the low-altitude site attaining greater average body size ($F_{[1,146]} = 321.254$, $P = 0.000$); however, there was not a significant interactive effect of sex and altitude on body size ($F_{[1,146]} = 3.640$, $P = 0.058$).

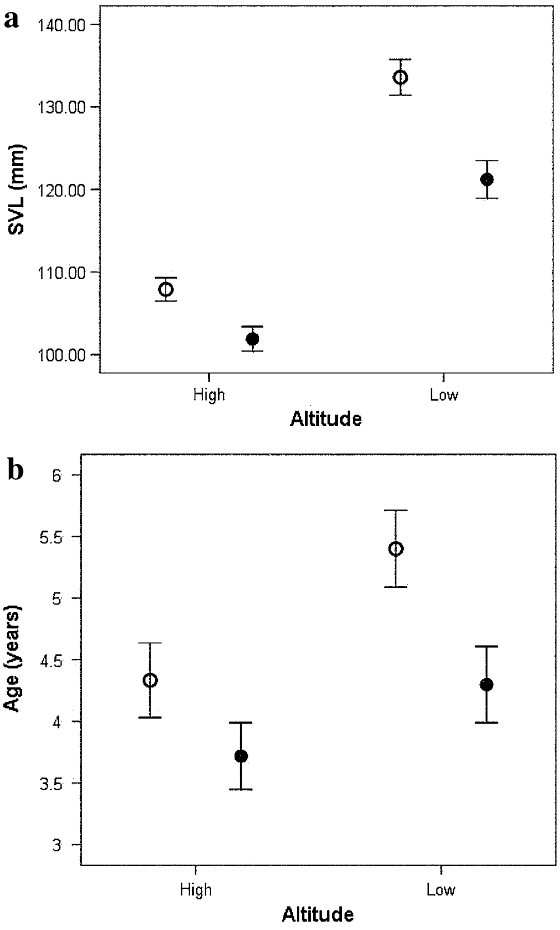

Fig. 4 Sex-specific variation in body size (**a**) and average age (**b**) and of American bullfrog (*Rana catesbeiana*) populations sampled at low (Shiping, 1,412 m) and high-altitude (Luguhu, 2,692 m) sites in southwestern China. *Closed* and *open circles* represent males and females, respectively; *vertical bars* indicate standard error (±1 SE)

Sex ratio and degree of SSD

Sex ratio (Fig. 5a) of bullfrogs did not vary significantly between low and high-altitude populations (ANOVA; $F_{[1,13]} = 0.515$, $P = 0.487$). Sex ratio of

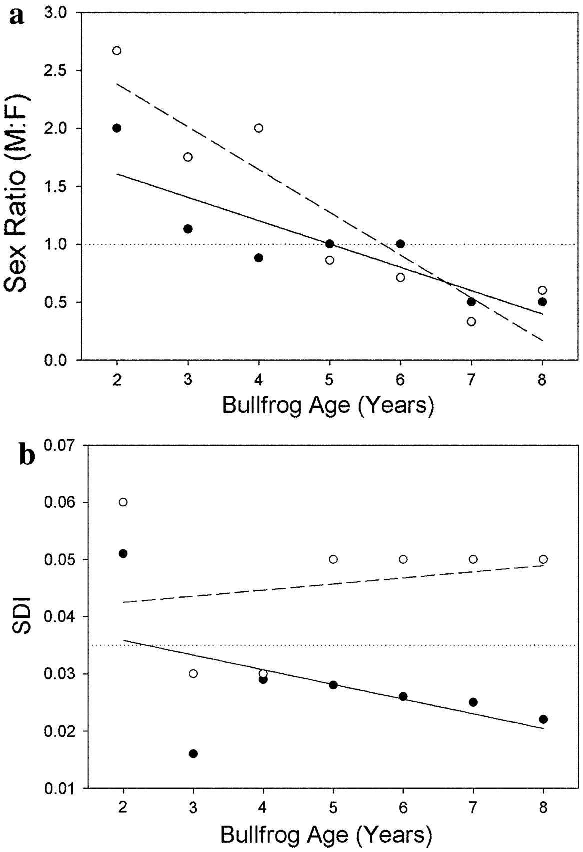

Fig. 5 Age-specific sex ratio (**a**) and degree of SSD (**b**; SDI index) of American bullfrog (*Rana catesbeiana*) populations sampled at low (Shiping, 1,412 m, *open circles*) and high (Luguhu, 2,692 m, *filled circles*) altitude sites in southwestern China. The *horizontal lines* in the figures represent **a** equal abundance of both sexes (1:1) in the population sample, or **b** the median degree of SSD (median SDI value)

bullfrogs was negatively correlated with age in both low and high-altitude populations (Spearman rho; Low = −0.849, $P = 0.003$; High = −0.873, $P = 0.010$), with the predominant sex shifting from male to female, and graphical analysis did not suggest an apparent interactive effect of age and altitude (Fig. 5a).

The degree of SSD (SDI; Fig. 5b) of bullfrogs was significantly greater in the low-altitude population (ANOVA; $F_{[1,13]} = 9.473$, $P = 0.010$), consistent with the higher average female age seen in this population. We found no significant correlation between SDI and age at either site (Spearman rho; Low = −0.179, $P = 0.702$; High = 0.327, $P = 0.474$), suggesting that interactive effects suggested by graphing (Fig. 5b) are likely not significant.

Growth

We calculated the relationship between body size and age for each sex in each population using von Bertalanffy's model (Table 1). Growth coefficients (k), which describe how quickly the asymptotic size (SVL_∞) is reached, had a higher value at lower than at higher altitudes both for females and males. Also, females had a larger asymptotic size than males at both altitudes. For both sexes at both low and high altitudes, the predicted asymptotic body sizes were higher than the maximum observed SVLs, suggesting that frogs could potentially grow even larger.

Table 1 Growth parameters of von Bertalanffy's model for American bullfrog (*Rana catesbeiana*) populations sampled at low (Shiping, 1,412 m) and high (Luguhu, 2,692 m) altitude sites in southwestern China

Altitude	Sex	SVL_∞^a	95% CI	k^b	95% CI
High	Male	121.87	106.00–137.73	0.305	0.032–0.578
	Female	136.13	105.63–166.63	0.175	0.014–0.365
Low	Male	142.62	128.88–156.36	0.378	0.113–0.642
	Female	154.04	135.41–172.67	0.294	0.055–0.533

[a] Asymptotic body size (SVL)

[b] Growth coefficient

Discussion

Vertebrates often exhibit a geographical pattern of variation in body size; body size may increase or decrease with increasing latitude or altitude, and the type and degree of variation can vary within a species (Bergmann 1847; Ashton 2002; Ashton and Feldman 2003; Blanckenhorn and Demont 2004). Temperature is generally accepted as one of the main selective factors accounting for this pattern, particularly in endotherms (Ashton 2002; Blackburn et al. 1999). Geographical variation in SSD has also been documented in ectotherms, including anurans; however, the mechanism of this variation is likely complex and highly variable (Ashton 2002; McGarrity and Johnson 2009; Monnet and Cherry 2002; Morrison and Hero 2003; Rosso et al. 2005; Schauble 2004). Geographical variation in body size is of particular interest because it is an important measure of an organism's fitness and can affect many other physiological and life-history traits (Stearns 1992; Gaston and Blackburn 2000; Brown et al. 2004). It is critical to understand how introduced species respond to the novel environments they invade, and especially geographical trends associated with their response, if we are to predict and manage the impacts of invasive species.

This study provides the first report of geographical variation in body size and SSD of invasive bullfrog populations, and confirms that bullfrogs exhibit plasticity of life-history traits in response to novel environments, as reported for other successful introduced species (Alcaraz and Garcia-Berthou 2007; Bohn et al. 2004; Lockwood 1999). Our results indicate that invasive bullfrogs in China have responded rapidly to a high altitude environment with a decrease in the female-dominated SSD, driven by a decrease in average female body size with increasing altitude. We suggest that this trend of decreasing SSD and female body size of introduced bullfrogs is largely driven by an accompanying decrease in female age distribution.

Variation in body size among populations (or between sexes) can often be attributed to differences in population age structure. In the present study, both average body size and average age of females were greater at low altitude, suggesting that the geographical variation seen in female body size and SSD may be the result of differences in age distribution between the two populations. However, the geographical difference in average body size of females remained significant even after controlling for the effects of age, suggesting that factors other than age also contribute to this variation. Although average body size of males was also greater at low altitude, male age distribution did not differ significantly between populations; this also suggests that other possible factors such as growth or mortality rate may influence variation in body size.

Differences in growth rate between our study populations may also have been instrumental in driving geographical variation in average body size. Von Bertalanffy's model showed that bullfrogs at low altitude exhibit relatively high growth rates compared with frogs from higher altitude (Table 1). Consequently, the decrease in average bullfrog body size with increasing altitude is probably the combined result of reductions in both age (females) and growth rate (both sexes). Geographical variation in growth rate is likely attributable in large part to climatic variation. Sites at lower altitudes experience a mild climate and comparatively longer summers, which allows for an extended period of activity, feeding, and growth. In contrast, frogs inhabiting ponds at higher altitudes are subjected to longer periods of low temperature when water bodies are frozen and frogs must remain in torpor; thus they have a shorter activity period which results in reduced growth rates (Hemelaar 1988; Ryser 1996). In addition, the harsher climate (i.e., lower minimum temperature) may be responsible for the reduction in average age at higher altitudes, due to an associated increase in the prevalence of cold-induced mortality.

Colonization history of an introduced species is often an important driving force behind life-history variation; traits are often the result of events during an organism's ancestry, rather than adaptations to current conditions (Pearson et al. 2002). Observed variation in ecological traits among populations that have resulted from discrete introductions may merely be the by-product of differences among source populations, rather than a response to environment or selective pressure. Introduced bullfrogs in China (including our study populations) have descended from a single source population; therefore the significant morphological variation among invasive bullfrogs observed in the current study cannot be attributed to colonization history.

It has been suggested that evaluation of variation in the demographics of introduced species among regions, and the resultant variation in their impacts, is critical to maximizing the effectiveness of control efforts (Adams and Pearl 2007). Female bullfrogs are highly fecund, producing large clutches of eggs that increase in number exponentially with increasing female body size (Howard 1978a). Our results identify a geographical trend of decreasing SSD with increasing altitude, driven by a pronounced decrease in female size of invasive bullfrogs at high altitude. Undoubtedly, this finding has important implications for impacts of bullfrog invasion of southwestern China, an amphibian conservation hotspot (Chen and Bi 2007). Smaller female bullfrog size at high altitude could result in lower reproductive output, which could slow the rate of population increase and reduce the impact on native species. A significant decrease in mean body size might also reduce competition and predation of native species by the invader. However, the climate at higher elevations is harsher and there are likely fewer resources; thus, successful establishment of bullfrogs could have a greater impact on native species at these sites. Additionally, the rapid reduction in average mature body size of introduced bullfrogs in response to the novel, harsher climate might be accompanied by a tendency to allocate resources to reproduction at a younger age (rather than growth), thus enhancing their ability to establish breeding populations at these potentially sensitive sites. Therefore, we recommend these topics for future research.

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References

Adams MJ (1999) Correlated factors in amphibian decline: exotic species and habitat change in western Washington. J Wildl Manage 63:1162–1171

Adams MJ, Pearl CA (2007) Problems and opportunities managing invasive bullfrogs—is there any hope? In: Gherardi F (ed) Biological invaders in inland waters—profiles distribution and threats. Springer, The Netherlands, pp 679–693

Alcaraz C, Garcia-Berthou E (2007) Life history variation of invasive mosquitofish (*Gambusia holbrooki*) along a salinity gradient. Biol Conserv 139:83–92

Alexander JM, Edwards PJ, Poll M, Parks CG, Dietz H (2009) Establishment of parallel altitudinal clines in traits of native and introduced forbs. Ecol 90:612–622

Ashton KG (2002) Do amphibians follow Bergmann's rule? Can J Zool 80:708–716

Ashton KG, Feldman CR (2003) Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. Evolution 57:1151–1163

Becker T, Dietz H, Billeter R, Buschmann H, Edwards PJ (2005) Altitudinal distribution of alien plant species in the Swiss Alps. Perspect Plant Ecol 7:173–183

Benejam L, Alcaraz C, Sasal P, Simon-Levert G (2008) Life history and parasites of the invasive mosquitofish (*Gambusia holbrooki*) along a latitudinal gradient. Biol Inv Online First. Available at: http://www.springerlink.com/content/a8927140mhrh7171/. Accessed 12 Aug 2009

Bergmann C (1847) Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Göttinger Studien 3:595–708

Blackburn TM, Gaston KJ, Loder N (1999) Geographic gradients in body size: a clarification of Bergmann's rule. Divers Distrib 5:165–174

Blanckenhorn WU, Demont M (2004) Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum? Integr Comp Biol 44:413–424

Bohn T, Sandlund OT, Amundsen PA, Primicerio R (2004) Rapidly changing life history during invasion. Oikos 106:138–150

Boone MD, Semlitsch RD, Little EE, Doyle MC (2007) Multiple stressors in amphibian communities: effects of chemical contamination, bullfrogs, and fish. Ecol Appl 17:291–301

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85:1771–1789

Bruneau M, Magnin E (1980) Croissance, nutrition et reproduction des ouaouarons *Rana catesbeiana* Shaw (Amphibia Anura) des Laurentides au nord de Montreal. Can J Zool 58:175–183

Campbell T, Echternacht A (2003) Introduced species as moving targets: changes in body sizes of introduced lizards following experimental introductions and historical invasions. Biol Inv 5:193–212

Castanet J, Newman DG, Saintgirons H (1988) Skeletochronological data on the growth, age, and population-structure of the Tuatara, *Sphenodon punctatus*, on Stephens island and Lady-Alice island, New Zealand. Herpetologica 44:25–37

Chen SZ (1993) Preliminary study on introduced frogs in China. Chin J zool 28(2):12–14

Chen YH, Bi JF (2007) Biogeography and hotspots of amphibian species of China: implications to reserve selection and conservation. Curr Sci 92:480–489

Daehler CC (2005) Upper-montane plant invasions in the Hawaiian islands: patterns and opportunities. Perspect Plant Ecol 7:203–216

Ficetola GF, Thuiller W, Miaud C (2007) Prediction and validation of the potential global distribution of a problematic alien invasive species—the American bullfrog. Divers Distrib 13:476–485

Gaston KJ, Blackburn TM (2000) Macroecology: pattern and process. Blackwell, Oxford

Gibbons MM, McCarthy TK (1983) Age determination of frogs and toads (Amphibia, Anura) from north-western Europe. Zool Scr 12:145–151

Govindarajulu P, Price WS, Anholt BR (2006) Introduced bullfrogs (*Rana catesbeiana*) in western Canada: has their ecology diverged? J Herpetol 40:249–260

Halliday TR, Verrell PA (1988) Body size and age in amphibians and reptiles. J Herpetol 22:253–265

Hänfling B, Kollmann J (2002) An evolutionary perspective of biological invasions. Trends Ecol Evol 17:545–546

Hemelaar A (1988) Age, growth and other population characteristics of *Bufo bufo* from different latitudes and altitudes. J Herpetol 22:369–388

Howard RD (1978a) Evolution of mating strategies in bullfrogs, *Rana catesbeiana*. Evolution 32:850–871

Howard RD (1978b) Influence of male-defended oviposition sites on early embryo mortality in bullfrogs. Ecology 59:789–798

Howard RD (1981) Sexual dimorphism in bullfrogs. Ecology 62:303–310

Institute of Special Aquaculture Species of Hanshou County Hunan Province, Departmant of Biology, Hunan Normal University (1986) Breeding and farming technology of bullfrogs (Rudin). China Fish 11:21

Jiang GZ (2008) On the development of Chinese freshwater fish culture technology in the 20th century. Dissertation, Nanjing Agricultural University

Kats LB, Ferrer RP (2003) Alien predators and amphibian declines: review of two decades of science and the transition to conservation. Divers Distrib 9:99–110

Kiesecker JM, Blaustein AR, Miller CL (2001) Potential mechanisms underlying the displacement of native red-legged frogs by introduced bullfrogs. Ecology 82:1964–1970

Kollmann J, Banuelos MJ (2004) Latitudinal trends in growth and phenology of the invasive alien plant *Impatiens glandulifera* (Balsaminaceae). Divers Distrib 10:377–385

Kupferberg SJ (1997) Bullfrog (*Rana catesbeiana*) invasion of a California river: the role of larval competition. Ecology 78:1736–1751

Lai YC, Lee TH, Kam YC (2005) A skeletochronological study on a subtropical, riparian ranid (*Rana swinhoana*) from different elevations in Taiwan. Zool Sci 22:653–658

Lee CE (2002) Evolutionary genetics of invasive species. Trends Ecol Evol 17:386–391

Li C, Xie F (2004) Invasion of bullfrog (*Rana catesbeiana*) in China and its management strategies. Chinese J Appl Environ Biol 10:95–99

Li YM, Wu ZJ, Duncan RP (2006) Why islands are easier to invade: human influences on bullfrog invasion in the Zhoushan archipelago and neighboring mainland China. Oecologia 148:129–136

Liu X, Li YM (2009) Aquaculture enclosures relate to the establishment of feral populations of introduced species. PLoS ONE 4(7): e6199. doi:10.1371/journal.pone.0006199. Accessed 12 Aug 2009

Lockwood JL (1999) Using taxonomy to predict success among introduced avifauna: relative importance of transport and establishment. Conserv Biol 13:560–567

Lodge DM (2004) Alien species and evolution: the evolutionary ecology of exotic plants, animals, microbes, and interacting native species. Nature 432:276–277

Lovich JE, Gibbons JW (1992) A review of techniques quantifying sexual size dimorphism. Growth Dev Aging 56:269–281

Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the World's worst invasive alien species: a selection from the Global Invasive Species Database. Published by The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN)

Ma X, Tong L, Lu X (2009) Variation of body size, age structure and growth of a temperate frog, *Rana chensinensis*, over an elevational gradient in northern China. Amphib-reptil 30:111–117

McGarrity M, Johnson S (2009) Geographic trend in sexual size dimorphism and body size of *Osteopilus septentrionalis* (Cuban treefrog): implications for invasion of the southeastern United States. Biol Inv 11:1411–1420

Miaud C, Guyetant R, Elmberg J (1999) Variations in life-history traits in the common frog *Rana temporaria* (Amphibia : Anura): a literature review and new data from the French Alps. J Zool 249:61–73

Ministry of Agriculture of the P.R.C. (1996) Brief introduction of aquaculture species in China. J Beij Fish 3:3–11

Monnet JM, Cherry MI (2002) Sexual size dimorphism in anurans. P Roy Soc Lond B Bio 269:2301–2307

Mooney H, Hobbs R (2000) Invasive species in a changing world. Island Press, Washington, DC

Morrison C, Hero JM (2003) Geographic variation in life-history characteristics of amphibians: a review. J Anim Ecol 72:270–279

Morrison C, Hero JM, Browning J (2004) Altitudinal variation in the age at maturity, longevity, and reproductive lifespan of anurans in subtropical Queensland. Herpetologica 60:34–44

Pearson D, Shine R, Williams A (2002) Geographic variation in sexual size dimorphism within a single snake species (*Morelia spilota*, Pythonidae). Oecologia 131:418–426

Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol Econ 52:273–288

Rosecchi E, Thomas F, Crivelli AJ (2001) Can life-history traits predict the fate of introduced species? A case study on two cyprinid fish in southern France. Freshw Biol 46:845–853

Rosso A, Castellano S, Giacoma C (2005) Ecogeographic analysis of morphological and life-history variation in the Italian treefrog. Evol Ecol 18:303–321

Ryser J (1996) Comparative life histories of a low-and a high-elevation population of the common frog *Rana temporaria*. Amphibia-Reptilia 17:183–195

Sagor ES, Ouellet M, Barten E, Green DM (1998) Skeletochronology and geographic variation in age structure in the wood frog, *Rana sylvatica*. J Herpetol 32:469–474

Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. Annu Rev Ecol Syst 32:305–332

Schauble CS (2004) Variation in body size and sexual dimorphism across geographical and environmental space in the frogs *Limnodynastes tasmaniensis* and *L.* peronii. Biol J Linn Soc 82:39–56

Schroeder EE, Baskett TS (1968) Age estimation, growth rates, and population structure in Missouri bullfrogs. Copeia 3:583–592

Shirose LJ, Brooks RJ, Barta JR, Desser SS (1993) Intersexual differences in growth, mortality, and size at maturity in bullfrogs in central Ontario. Can J Zool 71:2363–2369

Simberloff D, Parker IM, Windle PN (2005) Introduced species policy, management, and future research needs. Front Ecol Environ 3:12–20

Smirina E (1994) Age determination and longevity in amphibians. Gerontol 40:133–146

Smith RJ (1999) Statistics of sexual size dimorphism. J Hum Evol 36:423–458

Spear P, Boily M, Giroux I, DeBlois C, Leclair M, Levasseur M, Leclair R (2009) Study design, water quality, morphometrics and age of the bullfrog, *Rana catesbeiana*, in sub-watersheds of the Yamaska river drainage basin, Québec, Canada. Aquat Toxicol 91:110–117

Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford

Stillwell RC, Morse GE, Fox CW (2007) Geographic variation in body size and sexual size dimorphism of a seed-feeding beetle. Am Nat 170:358–369

Sun DJ (1990) The artificial breeding technology of bullfrogs. J Heilongjiang For 1:23–24

Travis J (1994) Evaluating the adaptive role of morphological plasticity. In: Wainright PC, Reilly SM (eds) Ecological morphology: integrative organismal biology. University of Chicago Press, Chicago

von Bertalanffy L (1957) Quantitative laws in metabolism and growth. Q Rev Biol 32:217–231

Wang YP, Guo ZW, Pearl CA, Li YM (2007) Body size affects the predatory interactions between introduced American bullfrogs (*Rana catesbeiana*) and native anurans in China: an experimental study. J Herpetol 41:514–520

Wilcove DS, Chen LY (1998) Management costs for endangered species. Conserv Biol 12:1405–1407

Wu ZJ, Wang YP, Li YM (2004) Natural populations of bullfrogs (*Rana catesbeiana*) and their potential threat in the east of Zhejiang province. Biodivers Sci 12:441–446

Wu ZJ, Li YM, Wang YP, Adams MJ (2005) Diet of introduced Bullfrogs (*Rana catesbeiana*): predation on and diet overlap with native frogs on Daishan island, China. J Herpetol 39:668–674

Xu H, Qiang S, Han Z, Gu J, Huang Z, Sun H, He S, Ding H, Wu H, Wan F (2006) The status and causes of alien species invasion in China. Biodivers Conserv 15:2893–2904

Zeng XJ (1998) Prospect and strategy of bullfrog farming. Inland Fish 10:4–5