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Reduced predator species richness drives the body gigantism of a frog species on the Zhoushan Archipelago in China

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Summary

1. Shifts in the body size of insular vertebrates have been an interesting theme in ecological and evolutionary studies. Four primary factors, including predation pressures, resource availability, inter-species competition and immigrant selection, have been proposed to explain the trend in insular body size. Life-history theory predicts that body size, average age, the proportion of old-aged members and the density of insular populations are negatively correlated with predator species richness, and that body size and population density are positively related to resource availability. The niche expansion hypothesis argues that a positive relationship is expected to exist between insular body size and prey size, which varies in response to extinction due to small or large competitors. The immigrant hypothesis predicts that insular body size is positively correlated with distance to the mainland.

2. We tested these hypotheses by using populations of rice frogs *Rana limnocharis* on 20 islands in the Zhoushan Archipelago and two sites of nearby mainland China.

3. The body size (snout-vent length) of rice frogs on half of the islands was larger before and after the variable of age was controlled for; rice frog density and prey availability was higher and prey size was larger on most of the islands as compared to the two mainland sites. On the islands, the body size and other features [e.g. average age, the proportion of old-aged frogs (ages 3 and 4) and density] of the rice frogs were negatively associated with predator species richness; female body size and other features were positively associated with prey availability. The inference of multivariate linear models based on corrected Akaike Information Criterion (AIC_c) showed that the relative importance of predator species richness on body size and each of the other features was larger than that of prey availability, prey size and distance to the mainland. In addition, the parameters for predator species richness were all negative.

4. The results provided strong support for the life-history theory of predation pressures, but weak evidence for the life-history theory of prey availability, the niche expansion or the immigrant hypothesis. The reduced predator species richness was a dominant factor contributing to the body gigantism of rice frogs on the islands.

Key-words: age structure, insular body size, insular population, number of predator species, sexual size dimorphism

Introduction

Shifts in the body size of insular populations of vertebrate species, as compared with mainland populations, have been observed in a range of taxa, and such observations have played an important role in the development of ecological and evolutionary theory (Foster 1964; Grant 1968; Lomolino 1985, 2005; Meiri, Cooper & Purvis 2008; Palkovacs 2003; White & Searle 2006; Wu, Li & Murray 2006; Case 1978; Adler & Levins 1994; Boback & Guyer 2003; Clegg & Owens 2002). A well-known but still controversial pattern (mainly from mammals) is that small species tend toward gigantism

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on islands, whereas large species evolve a smaller size (Lomolino 1985, 2005; Meiri, Cooper & Purvis 2008; Meiri, Dayan & Simberloff 2006; Bromham & Cardillo 2007; Welch 2009). Four primary factors that may differ between mainland and island environments – predation pressures, resource availability, inter-species competition and immigrant selection – have been proposed to explain the trend in insular body size. These factors may not be mutually exclusive: several factors may affect body size evolution on different islands or even on the same island. As far as we are aware, there have been no studies examining the relative importance of these factors analysed together with changes in insular body size.

Life-history theory concerns predation pressures and resource availability as general causal mechanisms for changes in the insular body size of vertebrates (Adler & Levins 1994; Palkovacs 2003). According to this theory (Palkovacs 2003), an increased or decreased body size of a vertebrate species on islands, relative to the mainland, depends on whether the effects of decreased extrinsic mortality by reduced predation pressures or changed resource availability predominate. Predation pressures have been generally known to be weaker on islands than on the mainland because islands usually support fewer predator species. Decreased predation pressures would result in a decrease in the extrinsic mortality of insular populations (Adler & Levins 1994; Palkovacs 2003), leading to the potential for increased body size and density on islands. The extrinsic mortality in the field is difficult to measure (Adler & Levins 1994; Palkovacs 2003). A direct inference of the reduced extrinsic mortality is that individuals in insular populations may be more likely to survive longer than mainland populations, everything else being held equal. As a result, insular populations should be older in their average age and should have a higher proportion of individuals that have reached older ages than mainland populations do. Reduced or increased resource availability on islands as compared with the mainland may also decrease or increase the body size and the population density (Palkovacs 2003). Therefore, the theory predicts that body size, average age, the proportion of aged individuals and the density of insular populations are negatively correlated with predator species richness if the effects of reduced extrinsic mortality resulting from reduced predation pressures predominate and that body size and population density are positively related to resource availability if the effects of changed resource availability predominate. By contrast, an alternative hypothesis argues that the decreased predation pressures on islands permit large species to evolve to small sizes because large sizes may be a way to offset predation (Lomolino 2005; Meiri 2006; Sinclair, Mduma & Brashares 2003). This hypothesis predicts a positive relationship between insular body size and predation pressures.

The niche expansion hypothesis considers inter-species competition as a cause of shifts in insular body size (Schoener 1970; Van Valen 1965; Grant 1968; Heaney 1978; Dayan & Simberloff 1994; Meiri 2006). This hypothesis is based on assumptions that the niche of insular species will expand due to reduced competitors on islands as compared to the mainland (Diamond 1970; Lack 1976). Body sizes will evolve to be smaller or larger on islands in response to changes in prey size left from the extinction of smaller or larger competitor species on islands. Therefore, a positive relationship is expected between insular body size and prey size.

In addition to these hypotheses, immigrant selection is proposed to explain the large size of species on islands (Lomolino 1985, 2005; White & Searle 2006). This hypothesis (referred as the immigrant hypothesis) assumes that larger migrants with greater energy reserves may be more likely to migrate to remote islands than smaller ones. As a result, the large sizes of small species on islands may be due to the selection of better immigrants from the mainland. A positive relationship between body size on islands and the distance to the mainland is expected by the hypothesis.

There might be differences in the shifts in the body size evolution between males and females for an insular vertebrate species, which might cause a difference in the sexual size dimorphism (SSD) between island and mainland populations. Both the niche polymorphism hypothesis and SSD hypothesis predict a greater degree of insular SSD on an island than on the mainland (Rothstein 1973; Patterson 1983; Meiri 2006). The niche polymorphism hypothesis attributes the increasing insular SSD to an expanding ecological niche of insular species (Rothstein 1973; Patterson 1983), while the SSD hypothesis suggests that a difference in reproduction investment between males and females contributes to an increase in the insular SSD (Meiri 2006). To date, there has been no evidence for a difference in SSD between islands and the mainland (Patterson 1983; Meiri 2006). The factors that potentially influence the shifts in insular body size might have effects on insular SSD, and possibly cause a difference in SSD between islands and the mainland. Therefore, if predation pressures, resource availability, inter-species competition and immigrant selection influence the SSD on islands, then there will be positive or negative relationships between insular SSD and such factors.

We tested these hypotheses by using populations of rice frogs *Rana limnocharis* on 20 islands in the Zhoushan Archipelago and in two sites of nearby mainland China. This archipelago consists of land-bridge islands (Jinling 1987), each of which varies in size from less than 1 km^2 to hundreds of km^2, with isolation distances of several hundreds of metres to about 100 km from the mainland. The rice frog is the most abundant amphibian species on many islands of the archipelago. The frogs have a short life span (Deng 1992), which allows us to identify the age of individual frogs by skeletochronology accurately (Redmer 2002; Leary *et al.* 2005) and to estimate changes in the average age and proportion of old-aged individuals. The predators of the frogs on the islands and mainland are well-documented (Zhu 1990; Zhuge 1990; Zhuge & Gu 1990; Li 1993; Pan, Wang & Yan 2007). As the diet of the rice frog is mainly composed of arthropods (Zhang *et al.* 1966), both prey availability and prey size are easily measured (Wu, Li & Murray 2006). Shifts in the body size of rice frogs have been investigated on a very limited number of islands on the archipelago and compared with the mainland (Wu, Li & Murray 2006).

We first compared the differences in body size, SSD and the other features of rice frog populations (average age, proportion of old-aged frogs, and density) and the number of predator species, prey availability and prey size between the sampled islands of the Zhoushan Archipelago and the nearby mainland. We then determined the relationships among the body size, SSD and other features of rice frog populations, the island area and four primary factors on the islands. Finally, we estimated the relative importance and parameters of the four primary factors together on the frogs' body sizes, SSD and other features of the rice frog populations on the islands using the information-theoretic approach.

Materials and methods

STUDY SITES

The study was conducted on 20 islands of the Zhoushan Archipelago (29°31′–31°04′N, 121°30′–123°25′E): Zhoushan, Daishan, Liuheng, Jintang, Qushan, Dachangtu, Taohua, Daxie, Xiushan, Meishan, Sijiao, Xiashi, Dengbu, Cezi, Xiaochangtu, Changbai, Dayushan, Fodu, Damao and Huni, and on the nearby mainland called the Guoju of Beilun region and the Sanhecun of Zhenhai region in the Zhejiang Province, China (Fig. 1). The Zhoushan Archipelago was connected to the mainland by a land-bridge in the Pleistocene era, but was isolated from the mainland by rising sea levels some 7000–9000 years ago (Wang & Wang 1980; Jinling 1987). The total area of the archipelago is about 1371 km^2. It contains 1339 islands ranging in size from small rocks to the largest island (Zhoushan), which covers an area of 468·7 km^2. The topography, climate, vegetation and fauna of the islands are very similar to those found on the mainland (Jinling 1987; Zhuge & Gu 1990; Huang, Jin & Cai 1990). Both the archipelago and the nearby mainland are in the coastal hill-plain zone of the Zhejiang Province, covered with hills (70% of the total area) and plains (30% of the total area). The highest peak on the mainland is 657 m tall, as compared to 544 m on the Zhoushan archipelago. Natural vegetation is dominated by a sub-tropical evergreen broadleaf forest. The climate is typical of the sub-tropical ocean monsoon zone and is highly seasonal, with a mean temperature range from 5·7 °C in January to 26·7 °C in July. The islands and the mainland receive about 1200–1400 mm of annual rainfall. People inhabit 98 of the islands, and fishing is the primary occupation (Jinling 1987). Species richness on the islands is poorer than it is on the mainland, with zero to ten amphibian species per island found in the archipelago (no amphibian species on most of the islands that are less than 0·3 km^2) as compared with 17 species in the Beilun region and 14 species in the Zhenhai region on the mainland (Yiming, Niemel & Dianmo 1998; Wu, Li & Murray 2006; Huang, Jin & Cai 1990).

STUDY SPECIES

Rice frogs are middle-sized [35·9 mm in snout-vent length (SVL) for males and 43 mm for females] and are distributed throughout most provinces in southern and central China (Huang, Jin & Cai 1990; Fei *et al.* 1999). The frogs live in grass, crops and stones around rice fields,

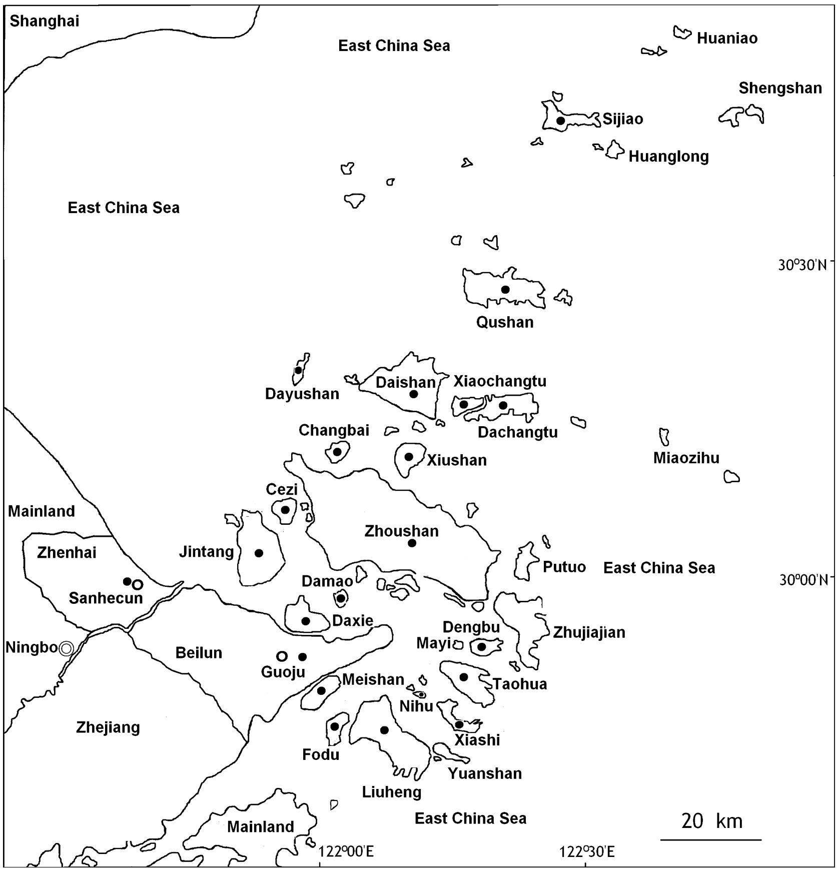

Fig. 1. Study sites on the Zhoushan Archipelago and neighbouring mainland China. ● indicates a sample location.

dry land, ponds, bogs and ditches (Wu, Li & Murray 2006; Huang, Jin & Cai 1990). They emerge from hibernation at the end of March to early April on the mainland and the archipelago. Males mature in less than 1 year and are characterized by a black pigment on the throat (Deng 1992). Females become mature after 1 year. The maximal life span is about 3·5 years for males and 4·5 years for females (Deng 1992). The frogs breed between the end of April and late August. New juvenile frogs after metamorphosis can be found as early as July. Hibernation usually begins in early November (Huang, Jin & Cai 1990). There are no hunting activities carried out by humans on this frog in our study areas (Yiming, Zhengjun & Duncan 2006).

METHODS

Body size, density, prey availability and prey size of rice frogs

We collected field data on the mainland Guoju twice and on Sanhecun once, and once on each sampled island in a randomly determined order during the breeding season between early June and late August in 2008 (11 islands and Guoju) and 2009 (nine islands and Guoju and Sanhecun). We used line transects (Wu, Li & Murray 2006; Jaeger 1994) to survey the rice frog density. We spent three to five nights to set up three to six line transects (five transects for Guoju each year) having a width of 2 m and a length of 100–150 m along the accessible edges of the rice fields, the shorelines of ponds, ditches, and dry land on each island and on Guoju and Sanhecun; these were paralleled at an interval of about 15–20 m. We searched for rice frogs in transects with a 12-V DC lamp (Qingtianzhu 201, Northwestern light Industry Company, Xian, China) between 19:00 and 21:30 and counted each frog that we encountered. We collected frogs along each transect by hand or by using nets. The frogs were labelled with a toe-tag and placed in separate plastic bags with holes (for air flow) and returned to the laboratory.

We measured the SVL of each frog (to the nearest 0·02 mm) with callipers. The body mass of each frog was weighted to be approximately 0·1 g. We used SVL rather than body mass to represent the body size because SVL is correlated with body mass in amphibians (Duellman & Trueb 1986) and it is less sensitive than body mass for short-term changes in body conditions, such as prey consumption, reproductive status and the amount of urine in the bladder (Ryser 1989; Pough 2007). Males were identified based on the secondary sexual characteristics of their black pigment on the throat (Huang, Jin & Cai 1990). Frogs lacking male characteristics and being greater than or equal to 1 year in age were considered to be females (Werner, Wellborn & McPeek 1995). The fourth digit of the right hind limb was clipped and kept in buffered formalin (of 10%) for further age estimation. The captured frogs were released at their capture site the following morning.

We surveyed prey availability immediately using a sweeping method (McCoy 1990; Wu, Li & Murray 2006) along the line transects where we captured the frogs. We conducted 100 sweeps through air and vegetation (0–0·5 m above the ground) with an insect sweep net along each line transect. We placed animals in the sweep net into plastic cups with ethyl acetate. We identified all of the prey specimens that were captured to the lowest possible taxonomic level (usually the Family) and measured the maximum length and width of each prey specimen individually. We used the volume of the prey specimens as an indicator of the prey's size (Werner, Wellborn & McPeek 1995; Hirai & Matsui 1999). The volume of each prey specimen was calculated using the formula for an ellipsoid: food volume $= 4/3\pi \times$ (maximum length$/2) \times ($maximum width$/2)^2$. The largest prey specimen that was captured on each island was smaller than the maximum prey specimen found in the stomach content analysis of rice frogs in Guoju (the maximum arthropod prey in the stomach contents is a mole cricket that is 24·46 mm length and 7·9 mm wide) (Wu, Li & Murray 2006), suggesting that the prey specimens that were captured on each island are potential food items that can be consumed by rice frogs. We defined the total volume of prey specimens in a line transect as the measure of the prey availability in that transect (Wu, Li & Murray 2006).

Age estimation

Following the skeletochronology procedure of Redmer (2002) and Leary *et al.* (2005), we removed the toe's surrounding soft tissue from the bone, dehydrated the bone, embedded the phalanges in paraffin and sectioned them at 15–20 mm into 30 sections for each toe; we stained them for microscope observation. Each year of life was marked by a line of arrested growth (LAG) deposited in the periosteal bone during hibernation. Age was equal to the number of hibernations (e.g. a 3 year-old frog experienced three hibernations and presented three LAGs). These lines appeared as red dark-stained rings in the sections. We took a photo of each section. Age estimates were assessed independently by two observers with no prior knowledge of the body size measurements (Leary *et al.* 2005; Redmer 2002). Age estimates that were justified by the two scorers were identical for all of the cases. Because the oldest age identified was 4 years, we defined ages 3 and 4 as 'old ages'. We calculated the proportion of old-aged frogs for each island and for the mainland.

Predators, island area and distance to the mainland

We considered a species to be a predator of rice frogs if the diet of the species was reported to contain frogs and the species shared similar habitats with rice frogs (Huang, Jin & Cai 1990; Zhuge 1990; Zhuge & Gu 1990; Pan, Wang & Yan 2007). We only considered those resident birds and migratory birds that inhabit the study areas between late spring or summer and mid-autumn and that can predate frogs as bird predators on rice frogs because they consume the frogs as they forage during these periods.

Predator species of rice frogs include most small carnivorous mammals, some snakes and wading and predatory birds in the Beilun and Zhenhai regions as well as on the Zhoushan Archipelago of the Zhejiang province (Appendix S1, Supporting Information). There are no specialist predator species of rice frogs (Huang, Jin & Cai 1990). We used the number of predator species in Beilun (535 km^2) where Guoju is located and in Zhenghai (266·9 km^2) where Sanhecun is located as the number of predator species in Guoju and in Sanhecun on the mainland. We obtained the number of predator species of the frogs from two sources: published and unpublished data. We collected data on the number of predator bird species, small carnivorous mammal species, and predator snake species on a larger part of the islands and the mainland from certain publications (Li 1993; Yuan 1985; Jinling 1987; Zhuge & Gu 1990; Zhuge 1990; Zhu 1990; Huang, Jin & Cai 1990; Committee 1993, 1989; Wang 2006). There are no published data on the number of snake predator species for a large part of the islands and the number of mammal and bird predator species on some small islands. We obtained these data by visiting the forestry and environmental departments of local governments on the islands that conducted surveys on vertebrate resources between 1989 and 2000 (unpublished data).

The distances to the mainland were measured on a map (scale 1 : 400 000). Island areas were obtained from the work of Chen (1989).

STATISTICAL ANALYSIS

The SVL of each frog, the number of predator species, the island area, distance to the mainland and the volume of prey were $\log_{10}(x)$-transformed, and the density of the rice frogs and prey availability in a line transect was $\log_{10}(x + 1)$-transformed to meet the assumptions of a normal distribution. A preliminary analysis showed that SVL, the average age and proportion of old-aged frogs of both sexes, the prey availability and prey size did not differ significantly between the years 2008 and 2009 in the nearby mainland of Guoju (e.g. $t = 0{\cdot}398$, d.f. = 118, $P = 0{\cdot}692$ for male SVL; $t = 0{\cdot}374$, d.f. = 8, $P = 0{\cdot}718$ for the rice frog density; $t = 0{\cdot}411$, d.f. = 8, $P = 0{\cdot}692$ for prey availability). We therefore combined the data from the 2 years in Guoju into one data set. We examined the differences in the mean SVL for males and females, the frog density, prey availability and prey size among two sites on the mainland and the islands using one-way ANOVA. Then, we used the least significance difference test to perform multiple comparisons. We calculated the SSD as the mean female body size divided by the mean male body size (Fairbairn 1997) for each island and mainland population. We examined the difference in the SSD between the mainland and island populations using a *t*-test. We tested the difference in the proportion of old-aged male and female frogs between each site of the mainland and each island using a Chi-squared test. Because the age estimated using skeletochronology is a discrete variable, we used the Kruskal–Wallis test to examine the difference in the average age of rice frogs between two sites of the mainland and islands. Amphibians can continue to grow after sex maturation (Duellman & Trueb 1986). Therefore, the age structure of an amphibian population might influence its mean body size. To control for the effect of age on body size, we performed an analysis of covariance (ANCOVA), with age as a covariate, to examine the difference in the body sizes between the frogs at two sites of the mainland and on the islands.

We determined the relationships among body size, SSD and other features (e.g. average age, the proportion of old-aged frogs, and density) of the rice frog populations on the islands and island areas, the number of predator species, prey availability, prey size and distance to the mainland using a Pearson correlation analysis.

We used the information-theoretic approach (Burnham & Anderson 2002) to estimate the effect of predator species richness, prey availability, prey size and distance to the mainland on body size, SSD and other features of rice frogs on the islands (Appendix S2, Supporting Information). This approach can make a more reliable inference from an entire set of models than selecting a single best model (Whittingham *et al.* 2006; Johnson & Omland 2004; Burnham & Anderson 2002). We fit the body size, average age, proportion of old-aged frogs for males and females, the density and SSD as a response variable by employing multivariate linear models with predator species richness, prey availability, prey size and the distance to the mainland as the predictor variables. Because we were interested in the relative importance of an individual variable, we excluded models with interaction terms from the calculation of relative variable importance. We created 15 linear regression models (2^4–1) for each response variable, which included all of the combinations of the four predictor variables. We compared alternative models using the second-order corrected Akaike Information Criterion ($\mathrm{AIC_c}$) (Burnham & Anderson 2002; Johnson & Omland 2004). The smallest $\mathrm{AIC_c}$ value identified the model with the best fit. We calculated the differences in $\mathrm{AIC_c}$ values between each model and the best model by following the formula:

$$\Delta_\mathrm{j} = \mathrm{AIC_j} - \mathrm{AIC_{min}}$$

Here, AIC_j is the $\mathrm{AIC_c}$ value of model j and $\mathrm{AIC_{min}}$ is the $\mathrm{AIC_c}$ value of the best model. We calculated the Akaike weight (W_j) of each model as (Burnham & Anderson 2002; Johnson & Omland 2004):

$$\mathrm{W}_j = \exp(-1/2\Delta_j)/\sum_{j=1}^{R}\exp(-1/2\Delta_j)$$

$\mathrm{W_j}$ provides a relative weight of evidence of the model j ($\mathrm{R} = 15$). To provide a relative ranking of the four primary factors on each of the features of rice frogs, we calculated the relative importance of a variable by summing the Akaike weights across all of the models in which the variable appeared; this measured the overall strength of evidence for each predictor on a scale from zero to one. We used the Akaike weights to calculate model-averaged parameter estimates as (Burnham & Anderson 2002; Johnson & Omland 2004):

$$\hat{\bar{\theta}}_j = \sum_{j=1}^{R} W_j\hat{\theta}$$

where $\hat{\bar{\theta}}_j$ is the estimate of parameter $\hat{\theta}$ from the jth model across all R models. We also calculated the variance of these parameters according to the Burnham and Anderson formula (Burnham & Anderson 2002).

All of the analyses were conducted with R version 2·8·1 (Venables, Smith and the R Development Core Team 2008). All tests were two-tailed, and statistical significance was set at $P < 0{\cdot}05$.

Results

COMPARISONS OF BODY SIZE, SSD AND OTHER FEATURES OF RICE FROGS AND ENVIRONMENTAL CHARACTERISTICS BETWEEN ISLANDS AND THE MAINLAND

The body size for both sexes of rice frogs differed among the two sites of the mainland and the 20 islands (one-way ANOVA, $F = 41{\cdot}694$, d.f. = 21, $P < 0{\cdot}001$ for males; $F = 8{\cdot}542$, $P < 0{\cdot}001$ for females). Males in Guoju were larger than males in Sanhecun, but females were not larger (Table 1). The body size of the two sexes was larger on nine islands as compared to both sites of the mainland. Furthermore, the body size of males on Liuheng and Daxie was larger and on Jintang and Meishan and the body size of females on Zhoushan was smaller than it was in the Guoju region. The body size of males on Zhoushan, Daishan, Liuheng, Qushan, Dachangtu, Daxie and Xiushan, and females on Xiushan and Xiashi, was larger, but females on Zhoushan were smaller than were females in the Sanhecun region.

The *t*-test showed that the SSD of two sites on the mainland did not differ from that of the 20 islands ($t = 0{\cdot}089$, d.f. = 20, $P = 0{\cdot}9301$).

Table 1. The body size, SSD, average age and proportion of old-aged (ages 3 and 4) frogs for rice frogs on 20 islands of the Zhoushan Archipelago and in two regions of nearby mainland China. The least significance difference test was used for comparisons on body size between an island and a region of the mainland before controlling for age (see text), and P_a is the probability. The Chi-squared test was used for the comparison of the proportion of old-aged frogs between an island and a region of the mainland, and P_b is the probability. P_c is the probability for comparisons of body size after controlling for age by ANCOVA. Bn (or Zn) = no significance between an island (or a region) and Beilun (or Zhenghai); Ba, Bb and Bc (or Za, Zb and Zc) = significant at 0·05, 0·01 and 0·001, respectively (in bold type)

	Males						Females						
Locations	N	SVL ± SD (mm)	P_a	Average age ± SD	Old ages (%) (P_b)	P_c	N	SVL ± SD (mm)	P_a	Average age ± SD	Old ages (%) (P_b)	P_c	SSD
Beilun mainland	120	36·8 ± 4		2 ± 0·8	22·5		79	38·8 ± 3·9		2·2 ± 0·9	34·2		1·055
Zhenhai mainland	54	35·4 ± 2·4	**Bb**	2 ± 1	27·8(Bn)	**Bb**	46	38·1 ± 2·9	Bn	2 ± 0·8	28·3(Bn)	Bn	1·079
Zhoushan	71	36·9 ± 1·9	Bn,**Zb**	1·9 ± 1	26·8(Bn,Zn)	Bn,**Zc**	26	36·8 ± 5·8	**Bb**,**Za**	2 ± 0·7	15·4(**Bc,Za**)	Bn,**Za**	0·996
Daishan	64	36·5 ± 2·5	Bn,**Za**	2 ± 0·9	26·6(Bn,Zn)	Bn,**Za**	34	38·5 ± 3·9	Bn,Zn	2·1 ± 0·9	32·4(Bn,Zn)	Bn,Zn	1·055
Liuheng	62	37·8 ± 2·1	**Bb,Zc**	2 ± 0·9	27·4(Bn,Zn)	**Bb,Zc**	36	38·3 ± 3·4	Bn,Zn	2·2 ± 0·9	36·1(Bn,Zn)	Bn,Zn	1·015
Jintang	56	35·8 ± 3·1	**Ba**,Zn	1·9 ± 1	26·8(Bn,Zn)	Bn,Zn	40	38·9 ± 3·6	Bn,Zn	2·1 ± 1	32·5(Bn,Zn)	Bn,Zn	1·087
Qushan	67	37·2 ± 2·4	Bn,**Zc**	2·1 ± 0·9	31·3(**Ba**,Zn)	Bn,**Zc**	33	39·1 ± 4	Bn,Zn	2·1 ± 1	27·3(Bn,Zn)	Bn,Zn	1·052
Taohua	52	35·8 ± 2·5	Bn,Zn	2·1 ± 0·9	34·6(**Bb**,Zn)	**Ba**,Zn	47	39·7 ± 4	Bn,Zn	2·2 ± 1	34(Bn,Zn)	Bn,Zn	1·108
Dachangtu	69	37·2 ± 2·7	Bn,**Zc**	1·9 ± 0·9	24·6(Bn,Zn)	Bn,**Zc**	31	39·2 ± 3·1	Bn,Zn	2·3 ± 1	41·9(Bn,Zn)	Bn,Zn	1·054
Daxie	66	37·9 ± 3	**Bb,Zc**	2·1 ± 0·9	28·8(Bn,Zn)	**Bb,Zc**	28	39·6 ± 2·7	Bn,Zn	2·2 ± 1	39·3(Bn,Zn)	Bn,Zn	1·045
Xiushan	43	36·5 ± 2·8	Bn,**Za**	2·1 ± 0·9	32·6(**Bb**,Zn)	Bn,**Za**	57	39·9 ± 2·8	Bn,**Za**	2·1 ± 0·9	28·1(Bn,Zn)	**Ba,Za**	1·093
Sijiao	64	39·8 ± 2·9	**Bc,Zc**	2·2 ± 0·9	37·5(**Bc**,Zn)	**Bc,Zc**	31	40·5 ± 3·4	**Ba,Zb**	2·4 ± 1	41·9(Bn,Zn)	**Ba,Za**	1·017
Meishan	65	35·5 ± 2·4	**Bb**,Zn	2·2 ± 0·9	36·9(**Bc**,Zn)	**Bb**,Zn	34	39·5 ± 2·1	Bn,Zn	2·2 ± 1	32·4(Bn,Zn)	Bn,Zn	1·114
Xiashi	78	36·4 ± 3·9	Bn,Zn	2·1 ± 1	39·7(**Bc**,Zn)	Bn,Zn	22	40 ± 3·3	Bn,**Za**	2·4 ± 1	45·5(**Ba,Za**)	Bn,Zn	1·104
Cezi	52	38·1 ± 2·6	**Bb,Zc**	2 ± 0·9	23·1(Bn,Zn)	**Bb,Zc**	44	41·2 ± 5·6	**Bb,Zc**	2·4 ± 1·1	45·5(**Ba,Za**)	**Bb,Zb**	1·083
Dengbu	64	38·8 ± 2·9	**Bc,Zc**	2·1 ± 0·9	32·8(**Bb**,Zn)	**Bc,Zc**	30	40·3 ± 2·7	**Ba,Za**	2·3 ± 1·1	40(Bn,Zn)	**Ba,Za**	1·04
Xiaochangtu	73	41·4 ± 3·3	**Bc,Zc**	2·3 ± 0·9	39·7(**Bc**,Zn)	**Bc,Zc**	27	42·8 ± 2·4	**Bc,Zc**	2·4 ± 1	44·4(Bn,**Za**)	**Bc,Zc**	1·033
Changbai	66	39·3 ± 3·1	**Bc,Zc**	2·2 ± 1	36·4(**Bc**,Zn)	**Bc,Zc**	28	40·9 ± 2·6	**Bc,Zb**	2·3 ± 1·1	46·4(**Ba,Za**)	**Bb,Zb**	1·042
Fodu	68	39 ± 2·2	**Bc,Zc**	2·2 ± 1	39·7(**Bc**,Zn)	**Bc,Zc**	31	43·9 ± 4·1	**Bc,Zc**	2·3 ± 1·1	41·9(Bn,Zn)	**Bc,Zc**	1·125
Dayushan	69	40·4 ± 3·1	**Bc,Zc**	2·3 ± 1	39·1(**Bc**,Zn)	**Bc,Zc**	27	43·3 ± 2·9	**Bc,Zc**	2·2 ± 1·1	37(Bn,Zn)	**Bc,Zc**	1·071
Damao	83	39·9 ± 2·3	**Bc,Zc**	2·2 ± 1	37·3(**Bc**,Zn)	**Bc,Zc**	23	43·4 ± 4·6	**Bc,Zc**	2·4 ± 1·1	43·5(Bn,**Za**)	**Bc,Zc**	1·088
Huni	64	40·6 ± 3	**Bc,Zc**	2·4 ± 1·1	45·3(**Bc,Za**)	**Bc,Zc**	29	43·5 ± 3·6	**Bc,Zc**	2·3 ± 1	44·8(Bn,**Za**)	**Bc,Zc**	1·072

SSD, sexual size dimorphism; SVL, snout-vent length.

Frogs' ages ranged from 8 months or 1–4 years for males and 1–4 years for females on each island and the mainland. There were no differences in the average age of both sexes among the two sites on the mainland and the islands (Kruskal–Wallis test, $\chi^2 = 26{\cdot}998$, d.f. = 21, $P = 0{\cdot}152$ for males; $\chi^2 = 16{\cdot}847$, $P = 0{\cdot}72$ for females) (Table 1).

The proportion of old-aged frogs (ages 3 and 4) ranged from 22·5–45·3% for males and 15·4–46·4% for females on the islands and at two sites on the mainland (Table 1). The proportion of old-aged frogs for both sexes did not differ between Guoju and Sanhecun on the mainland. The proportion of old-aged frogs for males on 13 islands, and for females on Cezi, Xiashi and Changbai, was higher, but, on Zhoushan, it was lower than it was in the Guoju region. The proportion of old-aged frogs for both sexes on Huni and for females on Xiashi, Cezi, Xiaochangtu, Changbai and Damao, was higher, but, on Zhoushan, it was lower than it was in the Sanhecun region.

An ANCOVA showed that, after age was controlled for, significant differences still emerged in the corrected body size for males and females among the islands and the two sites on the mainland ($F = 25{\cdot}318$, d.f. = 21, $P < 0{\cdot}001$ for males; $F = 8{\cdot}534$, $P < 0{\cdot}001$ for females). Trends in the differences in the body sizes between most islands and the two mainland sites were similar before and after the variable of age was controlled for (Table 1).

The Beilun region in the mainland had 44 predator species of rice frogs, whereas the Zhenhai region had 38 species, which was a much higher number than (seven to 23 predator species) on any island (Table 2, Appendix S1, Supporting Information).

Rice frog density, prey availability and prey size for the frogs differed among two sites on the mainland and the islands (one-way ANOVA, $F = 6{\cdot}114$, d.f. = 21, $P < 0{\cdot}001$ for the density; $F = 3{\cdot}112$, $P < 0{\cdot}001$ for prey availability; $F = 8{\cdot}044$, $P < 0{\cdot}001$ for prey size). There were no differences in the rice frog density, prey availability and prey size between the two sites of the mainland (Table 2). However, the rice frog density, prey availability and prey size for the frogs on most islands were higher than those on the two sites of the mainland.

EFFECTS OF FOUR PRIMARY FACTORS ON BODY SIZE, SSD AND OTHER FEATURES OF RICE FROGS ON THE ISLANDS

The body size and other features (e.g. average age, proportion of old-aged frogs, and density) of rice frogs on the

Table 2. Island area, distance to the mainland (DTM), predator species richness, rice frog density, prey availability and prey size (sample size) for rice frogs on 20 islands of the Zhoushan Archipelago and in two regions of nearby mainland China. The least significance test was used for comparisons of rice frog density, prey availability and prey size between an island and a region of the mainland (see text). Bn (or Zn) = no significance between an island (or a region) and Beilun (or Zhenghai); Ba, Bb and Bc (or Za, Zb and Zc) = significant at 0·05, 0·01 and 0·001 (in bold type)

				Rice frog density							
Location	Area (km^2)	DTM (km)	Predator species richness	No. transect	Frogs per m per transect	*P*	Prey availability (mm^3 per 100 sweeps)	*P*	Prey size (mm^3 per prey)	*P*
Beilun mainland			44	10	0·12 ± 0·05		37·8 ± 28·3		10·8 ± 6·6(33)	
Zhenhai mainland			38	5	0·1 ± 0·02	Bn,	28·7 ± 36·8	Bn	12·8 ± 17·2(10)	Bn
Zhoushan	468·7	9	23	6	0·12 ± 0·03	Bn,Zn	59·5 ± 39·1	Bn,Zn	17 ± 10·8(21)	**Ba**,Zn
Daishan	100	37	20	5	0·16 ± 0·05	Bn,Zn	61·5 ± 37·1	Bn,Zn	25·6 ± 18·8(12)	**Bc,Zb**
Liuheng	92·75	7	16	5	0·17 ± 0·02	Bn,Zn	59·3 ± 69·2	Bn,Zn	14·3 ± 10·4(20)	Bn,Zn
Jintang	76·4	3·6	18	5	0·16 ± 0·04	Bn,Zn	74·5 ± 77·9	Bn,Zn	23·3 ± 10·6(16)	**Bb,Zb**
Qushan	59·9	58·5	11	5	0·2 ± 0·04	**Ba, Za**	160·8 ± 163·6	Bn,Zn	38·3 ± 25·8(21)	**Bc,Zc**
Taohua	41	8·8	11	5	0·19 ± 0·05	Bn, **Za**	255·7 ± 180·3	**Bb,Zb**	32·8 ± 23·1(39)	**Bc,Zc**
Dachangtu	33·3	37·6	13	5	0·2 ± 0·05	**Ba,Za**	235·1 ± 120·9	**Bb,Zb**	33·6 ± 17·5(35)	**Bc,Zc**
Daxie	28·2	0·4	15	4	0·18 ± 0·02	Bn,Zn	300·8 ± 234·8	**Bb,Zb**	40·1 ± 35·3(30)	**Bc,Zc**
Xiushan	23	54·5	11	5	0·23 ± 0·13	**Bb,Zb**	217·5 ± 167	**Bb,Zb**	30·2 ± 19(36)	**Bc,Zc**
Sijiao	22·3	26·8	8	3	0·25 ± 0·07	**Bb,Zb**	242·3 ± 113·5	**Ba,Zb**	33 ± 14·7(22)	**Bc,Zc**
Meishan	21·86	0·5	11	4	0·25 ± 0·1	**Bb,Zb**	244·4 ± 180·2	**Bb,Zb**	63·9 ± 113·8(14)	**Bc,Zc**
Xiashi	16·7	13·2	8	4	0·25 ± 0·05	**Bb,Zb**	201·1 ± 66·7	**Bb,Zb**	30·9 ± 13·7(26)	**Bc,Zc**
Cezi	14·9	16·5	12	4	0·26 ± 0·12	**Bb,Zb**	143·2 ± 26·7	**Ba,Zb**	16·5 ± 7·9(34)	**Ba,Za**
Dengbu	13·31	14·1	10	4	0·27 ± 0·07	**Bc,Zb**	164·8 ± 79·7	**Ba,Zb**	27·5 ± 20·9(24)	**Bb,Zb**
Xiaochangtu	10·8	31·1	12	4	0·3 ± 0·09	**Bc,Zc**	143·8 ± 64·8	**Ba,Zb**	16·9 ± 10·6(34)	**Ba,**Zn
Changbai	10·24	37·6	12	3	0·3 ± 0·06	**Bc,Zc**	262·3 ± 166	**Bb,Zb**	41·4 ± 32·7(19)	**Bc,Zc**
Fodu	7	7	9	5	0·32 ± 0·05	**Bc,Zc**	210·2 ± 116·9	**Bb,Zb**	45·1 ± 36·4(23)	**Bc,Zc**
Dayushan	6·2	42·8	7	4	0·36 ± 0·15	**Bc,Zc**	265·8 ± 188·3	**Bb,Zb**	34·3 ± 35·2(31)	**Bc,Zb**
Damao	5·7	8·8	8	4	0·34 ± 0·12	**Bc,Zc**	382·8 ± 266·4	**Bb,Zc**	36·5 ± 35·7(42)	**Bc,Zc**
Huni	1·37	10·88	8	4	0·37 ± 0·09	**Bc,Zc**	225·3 ± 164·4	**Ba,Zb**	20 ± 30·9(43)	Bn,Zn

islands were positively correlated with one another (body size and average age: *r* = 0·663, *P* < 0·001 for males; *r* = 0·718, *P* < 0·001 for females; body size and the proportion of old-aged frogs: *r* = 0·512, *P* = 0·021 for males; *r* = 0·692, *P* = 0·001 for females; body size and rice frog density: *r* = 0·731, *P* < 0·001 for males; *r* = 0·948, *P* < 0·001 for females; average age and proportion of old-aged frogs: *r* = 0·908, *P* < 0·001 for males; *r* = 0·929, *P* < 0·001 for females; average age and rice frog density: *r* = 0·818, *P* < 0·001 for males; *r* = 0·706, *P* = 0·001 for females; the proportion of old-aged frogs and density: *r* = 0·777, *P* < 0·001 for males; *r* = 678, *P* = 0·001 for females). By contrast, SSD was not associated with any other features (*r* = 0·182, *P* = 0·443 for males' average age; *r* = 0·199, *P* = 0·401 for females' average age; *r* = 0·312, *P* = 0·181 for the proportion of old ages for males; *r* = 0·211, *P* = 0·371 for the proportion of old ages for females; *r* = 0·342, *P* = 0·14 for rice frog density).

For environmental variables, the island area ranged from 1·37 km^2 for Huni to 468·7 km^2 for Zhoushan (Table 2), and the distance to the mainland ranged from 0·4 km for Daxie to 58·5 km for Qushan. Large islands usually had more predator species and higher prey availability than small ones did. There was a positive correlation between predator species richness, prey availability and island area (Fig. 2a,b), between predator species richness and prey availability (Fig. 2c) and between prey availability and prey size (Fig. 2d). However, the distance to the mainland was not related to any of the other variables (*r* = −0·073, *P* = 0·761 for island area; *r* = −0·191, *P* = 0·42 for predator species richness; *r* = −0·074, *P* = 0·756 for prey availability; *r* = −0·113, *P* = 0·653 for prey size). Both island area and predator species richness were not related to the prey size (*r* = 0·052, *P* = 0·827 for island area; *r* = −0·221, *P* = 0·349 for predator species richness).

The body size and other features (e.g. average age, proportion of old-aged frogs, and density) of the rice frogs on the islands were negatively associated with the island area and the predator species richness (Table 3). Moreover, the female body size and other features were positively related to prey availability. SSD was not correlated with the island's area, predator species richness, prey availability or prey size (Table 3).

Table 4 shows the results of the multi-model inference based on the information-theoretic approach (also see Appendix S2, Supporting Information). For body size and other features, the relative importance values of prey species richness ranged from 0·5938 to 0·99811; prey availability ranged from 0·01961 to 0·34272; the prey size varied from 0·01941 to 0·38756 and the distance to the mainland varied from 0·00705 to 0·12817. For SSD, all four primary factors had small relative importance values between 0·09699 and

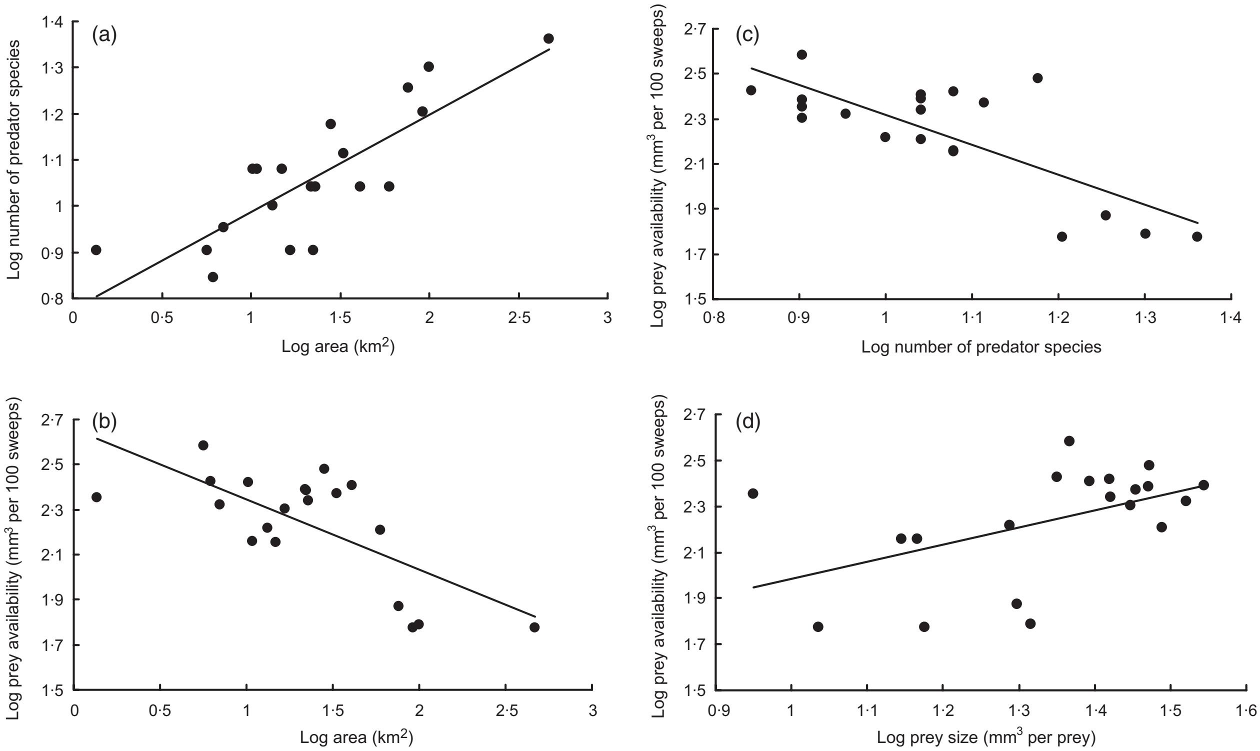

Fig. 2. The relationships among island characteristics on 20 islands of the Zhoushan Archipelago. (a) Predator species richness and area (r = 0·82, P < 0·001). (b) Prey availability and area (r = −0·705, P = 0·001). (c) Predator species richness and prey availability (r = −0·767, P < 0·001). (d) Prey availability and prey size (r = 0·502, P = 0·024).

Table 3. Coefficients and probabilities (in parentheses) of the Pearson correlation among the features of rice frogs and island characteristics on 20 islands of the Zhoushan Archipelago in China

Features of rice frogs	Island area	Predator species richness	Prey availability	Prey size	Distance to mainland
Male body size (log SVL, mm)	−0·649 (0·002)	−0·481 (0·032)	0·316 (0·175)	−0·341 (0·141)	0·294 (0·208)
Female body size (log SVL, mm)	−0·930 (< 0·001)	−0·776 (< 0·001)	0·620 (0·004)	−0·039 (0·870)	0·132 (0·578)
SSD (female body size per male body size)	−0·416 (0·068)	−0·429 (0·059)	0·427 (0·061)	0·389 (0·09)	−0·219 (0·353)
Average age for males (year)	−0·769 (< 0·001)	−0·722 (< 0·001)	0·494 (0·027)	−0·096 (0·688)	0·075 (0·753)
Average age for females (year)	−0·736 (< 0·001)	−0·658 (0·002)	0·551 (0·012)	−0·039 (0·872)	0·073 (0·761)
Proportion of old-aged males (%)	−0·737 (< 0·001)	−0·766 (< 0·001)	0·553 (0·011)	0·044 (0·853)	0·040 (0·869)
Proportion of old-aged females (%)	−0·759 (< 0·001)	−0·570 (0·009)	0·509 (0·022)	−0·041 (0·863)	0·057 (0·811)
Density (log frogs per m per transect)	−0·952 (< 0·001)	−0·838 (< 0·001)	0·651 (0·002)	−0·035 (0·884)	0·181 (0·445)

SVL, snout-vent length; SSD, sexual size dimorphism.

0·36569. Among the four primary factors, predator species richness had the highest relative importance value for each of the features of the rice frogs. Prey availability had higher relative importance value for SSD, average age and the proportion of old-aged female frogs than did the prey size, whereas prey size had a higher relative importance value for male body size than prey availability did. For any of the features of rice frogs, the distance to the mainland had the lowest relative importance value. For all of the features of the frogs, the parameter estimate from model averaging was positive for prey availability and negative for predator species richness. The parameter for prey size was negative for all of the features but the SSD. The parameter of the distance to the mainland was positive on male body size and the proportion of old-aged female frogs, and negative on female body size, SSD, the average age of males and females, and the proportion of old-aged male frogs.

Discussion

Several of the findings in this study confirmed our expectations of the life-history hypothesis related to predation pressures. The body size of rice frogs on about half of the islands was larger before and after the variable of age was controlled

Table 4. Summary of parameter estimates, their variance, and relative importance (in parentheses) of predator species richness, prey availability, prey size and distance to the mainland on the body size, SSD and other features of rice frogs on 20 islands of the Zhoushan Archipelago in China. The parameters were estimated based on model averaging over all 15 models. The relative importance of a predictor variable was calculated by summing the Akaike weights across all of the models for the variable

Features of rice frogs	Predator species richness	Prey availability	Prey size	Distance to the mainland
Male body size (log SVL, mm)	−0·0424 ± 0·00148 (0·5938)	0·09798 ± 0·00015 (0·243)	−0·02403 ± 0·00072 (0·38756)	0·00118 ± 0·00000 (0·12817)
Female body size(log SVL, mm)	−0·11549 ± 0·00099 (0·98469)	0·00113 ± 0·00000 (0·03295)	−0·00161 ± 0·00001 (0·0489)	−0·00001 ± 0·00008 (0·01465)
SSD (female body size per male body size)	−0·03893 ± 0·002 (0·36569)	0·0208 ± 0·00006 (0·34272)	0·02043 ± 0·00005 (0·24961)	−0·00133 ± 0·00000 (0·09699)
Average age for males (year)	−0·65452 ± 0·04279 (0·93989)	0·0216 ± 0·00087 (0·07573)	−0·02345 ± 0·00112 (0·0697)	−0·00013 ± 0·0000 (0·00705)
Average age for females (year)	−0·51429 ± 0·04879 (0·87632)	0·03586 ± 0·00207 (0·13154)	−0·0072 ± 0·00075 (0·03605)	−0·00005 ± 0·00000 (0·01739)
Proportion of old-aged males (%)	−0·33161 ± 0·00672 (0·99406)	0·00051 ± 0·00000 (0·01961)	−0·00098 ± 0·00000 (0·01941)	−0·00021 ± 0·00000 (0·01761)
Proportion of old-aged females (%)	−0·21831 ± 0·02145 (0·69276)	0·04785 ± 0·00115 (0·29226)	−0·00508 ± 0·00001 (0·04603)	0·00009 ± 0·00000 (0·02741)
Density (frogs per m per transect)	−0·1441 ± 0·00152 (0·99811)	0·0005 ± 0·00000 (0·02499)	−0·0031 ± 0·00000 (0·08401)	0 ± 0·00000 (0·01592)

SVL, snout-vent length; SSD, sexual size dimorphism.

for, and rice frog density was higher on most of the islands as compared to two sites from the mainland (although the body size of males differed between the two sites of the mainland). The number of predator species on each sampled island was much lower than that in the two mainland sites. Body size, average age, the proportion of old-aged frogs for both sexes and rice frog density on the islands were all negatively correlated with the number of predator species. Finally, the multi-model inference based on AIC$_c$ showed that the relative importance of predator species richness on body size, average age, the proportion of old-aged frogs for both sexes and rice frog density was larger than that of prey availability, prey size and distance to the mainland, and the parameters for predator species richness were all negative. These results strongly suggested that reduced predation pressures were a dominating factor in shaping shifts in the body size of rice frogs on the Zhoushan Archipelago. A reduction in the number of predator species led to an increase in the body size, average age, proportion of old-aged frogs (ages 3 and 4) and the density of rice frogs on the islands. The results did not agree with the alternative hypothesis that there should be a positive relationship between insular body size and predation pressures on the islands (Meiri 2006; Sinclair, Mduma & Brashares 2003).

The negative association between insular body size and predation pressures has been documented in the lizard *Eumeces okadae,* found on a host of Japanese islands (Hasegawa 1994); for other insular herbivores, see Meiri (2006). It has been argued that the density of predators rather than the number of predator species is a better indicator of predation pressures affecting the insular body size (Meiri, Simberloff & Dayan 2005). The density of predators might have strong impacts on the shifts in the body size of rice frogs on the Zhoushan Archipelago, which requires further exploration. The negative correlations between average age or the proportion of old-aged frogs for both sexes and the number of predator species indicated that the reduced number of predator species could enable rice frogs to survive longer on the islands. This may be a result of the reduced extrinsic mortality from the reduced predation pressures. Therefore, the predation pressures of rice frogs on the islands were linked to the number of predator species present. Furthermore, the negative relationship between body size and the number of predator species has been reported in insular lizards and rats (Case 1978; Angerbjörn 1986; Smith 1992; Michaux *et al.* 2002). These studies, combined with our findings, demonstrate that the number of predator species can be a good indicator of the predation pressures affecting insular body size.

Reduced predation pressures on the islands could affect the body size of rice frogs in two ways. First, reduced predation pressures could directly increase the foraging rate of rice frogs and therefore result in increasing age and size at maturity (Stearns 1992; Ball & Baker 1996). Such increased body size may be a plastic response of the frogs to the reduced predation pressures over a short-term period. Second, the extrinsic mortality rate from reduced predation pressure could also influence the body size of rice frogs via shifts in the age and size at the maturity reaction norm (Adler & Levins 1994; Palkovacs 2003). Reduced extrinsic mortality would increase individual survival, resulting in increased average age, the proportion of old-aged frogs and the density of rice frog populations. The high population density on the islands would favour a large body size because large individuals have advantages in intra-species competition. This would shift age-size reaction norms. A population with a greater expected future survival rate would increase its fitness by maturing later and at a larger size and therefore have a larger adult body size than the mainland con-specifics (Adler & Levins 1994; Palkovacs 2003). This shift in reaction norms could be an evolutionary (genetic) response over a long-term period.

Recent studies have suggested prey availability as an important factor shaping shifts in insular body size (Wu, Li & Murray 2006; Pafilis *et al.* 2009). Wu, Li & Murray (2006) studied effects of prey availability, prey size and distance to the mainland on the density and body size of rice frogs in seven islands of the Zhoushan Archipelago, and considered that increased prey availability could have contributed to the increased density and body gigantism of insular rice frogs. They did not collect data on predator species richness and the age structure of rice frog populations (e.g. average ages and the proportion of old-aged frogs) in their study. The age structure of insular vertebrate populations has never been studied before. Our study provides weak evidence for the effects of prey availability on the body size of rice frogs on the Zhoushan Archipelago. Resources on islands are usually considered to be limited (Palkovacs 2003; Case 1978; Lomolino 2005). Contrary to this belief, most islands in the Zhoushan Archipelago showed increasing prey availability as compared with two sites on the mainland. Such increasing prey availability in some islands co-occurred with increased body size for males and females (Wu, Li & Murray 2006). However, male body size was not positively related to prey availability on the islands. Furthermore, prey availability had a smaller relative importance (the summing of Akaike weights = 0·243) on changes in the male body size than predator species richness and prey size did. Although there was a positive relationship between female body size or rice frog density and prey availability, the relative importance of prey availability on female body size (the summing of Akaike weights = 0·03295) or the density (0·02499) was very low (Table 4). Prey availability is unlikely to be the main force shaping shifts in body size and the density of rice frogs on the Zhoushan Archipelago.

Our results did not support the niche expansion hypothesis that competitors may affect rice frog body size on the islands. This hypothesis predicted that insular body size should evolve to be large or small with increased or decreased prey size (Van Valen 1965; Grant 1968; Schoener 1970; Heaney 1978; Dayan & Simberloff 1994; Boback & Guyer 2003). Although prey size for most islands was larger than it was on two sites of the mainland, no positive relationship was detected between body size for both sexes and prey size on the islands. The parameters for prey size on the body size of both sexes were negative, against the prediction of the hypothesis. This result suggested that the reduced competition from other species for prey resources could not have contributed to the changes in the body size of rice frogs on the islands. One explanation for this finding is that rice frogs did not respond to the increased prey size by increasing their body size. An increase in prey size on most islands might be a result of changes in the size of prey left from the extinction of competitors, but such increased prey size did not lead to an increase in the body size of both sexes. Our results contrast with a study that reported that the body sizes of insular carnivores depended on the abundance and size of prey (Meiri 2006).

Insular body size has generally been found to be correlated with the island area and with isolation (Lomolino 2005; Adler & Levins 1994). The effect of the island area on body size is indirect because the area influences the number and distribution of species on the islands (Meiri 2006). The negative correlation between the body size of rice frogs and the island area on the Zhoushan Archipelago may be due to the area of the island affecting the number of predator species: predator species richness was negatively related to the area. The effects of isolation on insular body size often result from the co-linearity between island area and isolation (remoter islands are smaller) or from immigrant selection (Lomolino 2005; White & Searle 2006). Evidence for the immigrant selection idea mainly comes from insular small mammals (Lomolino 2005; White & Searle 2006). The distance to the mainland was not correlated with the island area of the Zhoushan Archipelago. Furthermore, there were no associations between the body size of rice frogs for both sexes and the distance to the mainland. The distance to the mainland had a much lower relative importance on the body size of the frogs than any other factors did. This finding suggested that evidence for the effects of immigrant selection on the body size of rice frogs was weak on the islands, which possibly arose because rice frogs cannot disperse across seas. Salt water is harmful to most amphibian species (Gadow 1901; Yiming, Niemel & Dianmo 1998) and may limit the migration of rice frogs from the mainland to the islands.

Studies have reported no difference in the SSD between the mainland and island populations (Patterson 1983; Meiri, Dayan & Simberloff 2006). Consistent with these studies, no greater or smaller degree of SSD for rice frogs was detected between the islands and two sites on the mainland. The SSD of rice frogs on the islands was not related to the island area, predator species richness, prey availability, prey size or distance to the mainland. All four primary factors had a very low relative importance value on SSD (the summing of Akaike weights from 0·097 to 0·3457). Therefore, there was weak evidence for a difference in the SSD for rice frogs between the Zhoushan Archipelago and the mainland, or there was weak evidence of the effects of predator species richness, prey availability, prey size and distance to the mainland on the SSD on the islands.

In summary, the body size of rice frogs tends towards gigantism on about half of the 20 islands of the Zhoushan

Archipelago. There is strong evidence for the effects of the reduced number of predator species on an increase in body size, average age, the proportion of old-aged frogs and the density of rice frogs on the islands, but weak evidence for the effects of increasing prey availability, increasing prey size and immigrant selection. The SSD of rice frogs did not differ between the islands and the mainland, and evidence for the effects of predator species richness, prey availability, prey size and distance to the mainland on the SSD of rice frogs was weak on the islands.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. The distribution of predator species on rice frogs on 20 islands of the Zhoushan Archipelago and nearby mainland China.

Appendix S2. The multi-model inference of linear regressions on body size, sexual size dimorphism (SSD) and other features of rice frogs on 20 islands of the Zhoushan Archipelago in China. Body size, SSD, average age, the proportion of old-aged frogs (age 3 and age 4 years) and density of rice frogs are response variables, and predator species richness, prey availability, prey size and distance to the mainland are the predictor variables.