INTER-POPULATION VARIATION IN LIFE-HISTORY TRAITS OF A CHINESE LIZARD (*TAKYDROMUS SEPTENTRIONALIS*, LACERTIDAE)

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Detecting inter-population differences in life-history traits is the first step in exploring the proximate and ultimate causes of such variation. We measured maternal body size and reproductive output of the lacertid lizard *Takydromus septentrionalis* from two island populations in eastern China to quantify inter-population variation. We captured female *T. septentrionalis* from the field and conducted a "common garden" experiment in the laboratory to measure their reproductive output. The study revealed major divergences in female body sizes, clutch mass and egg mass, but no significant difference in these traits was found between the first clutch and the later clutches. This suggests that the inter-population divergences persisted when the same groups of females were maintained in identical conditions in captivity. In contrast, there were no inter-population differences in size-adjusted fecundities, clutch size and relative clutch masses. Therefore, maternal body size plays an important role in determining female reproductive output in this species, but it does not account for all variation in reproductive traits. The egg size is less variable than the clutch size in each population, which gives support to the optimal egg size theory.

Key words: body size, fecundity, inter-population variation, offspring size, reproductive output

INTRODUCTION

Life-history traits are directly related to organismal fitness and hence are major targets of natural selection. Species differ substantially in life-history traits, reflecting both genetic and environmental effects. Even geographically separate populations of a single species can evolve different life histories depending on local ecological conditions (Roff, 2002). As ectotherms, squamates are highly dependent upon climatic conditions and have thus attracted considerable research on the contribution of the environment to life-history variation (Dunham *et al.*, 1988; Adolph & Porter, 1993; Niewiarowski, 1994; Angilletta *et al.*, 2004). Whereas earlier studies on this topic focused on interspecific variation in life histories (e.g. Tinkle *et al.*, 1970; Dunham *et al.*, 1988), inter-population variation in life histories has been emphasized more recently (e.g. Forsman & Shine, 1995; Niewiarowski *et al.*, 2004). The inter-population comparison may lend considerable insight toward our understanding of genetic and environmental causes of life-history variation and the evolution of life histories (Niewiarowski, 1994; Angilletta *et al.*, 2004; Niewiarowski *et al.*, 2004). To achieve this end, we need a broad collection of data sets describing inter-population variation in life histories of squamates. However, such studies mainly focus on North American and European species (e.g. Dunham *et al.*, 1988; Castilla & Bauwens, 1989; Niewiarowski, 1994), whereas the information on Asian taxa is quite limited (but see Hasegawa,

1994). Therefore, life-history data on Asian species, even descriptive data, should be very useful in completely understanding life-history evolution in squamates.

For inter-population studies of life histories, while the geographic pattern of life-history variation such as latitudinal and altitudinal variations has attracted a great number of studies (Ballinger, 1983; Dunham *et al.*, 1988; James & Shine, 1988; Grant & Dunham, 1990), islands have been of special interest to ecologists because of the rapid adaptive shifts possible in island taxa with small and discrete populations, living under different conditions and selective pressures (Case, 1982). Compared with parallel studies on geographically separated populations in the continent – for example, elevational comparisons (e.g. Ballinger, 1977; Grant & Dunham, 1990) – inter-island comparisons can reveal microgeographic variation in life histories for populations with relatively low gene flow or migration among them. Several authors have quantified inter-island variation in morphology and some ecological traits of snakes and lizards (e.g. Shine, 1987; Case & Schwaner, 1993; Hasegawa, 1994; King, 1997; Thorpe & Malhotra, 1998); these studies suggested that the inter-island variation might stem from both genetic and environmental factors.

The northern grass lizard *Takydromus septentrionalis* is a small (up to 80 mm snout–vent length [SVL]) slender-bodied, long-tailed (up to 270 mm) lacertid. Among the 16 or 17 species of grass lizards from the genus *Takydromus* in the oriental and palearctic regions (Arnold, 1997), *T. septentrionalis* is a later evolved species (Lin *et al.*, 2002), and is mainly distributed over a large area of eastern and northern

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TABLE 1. Inter-population variation in seasonal reproductive output of the northern grass lizard, *Takydromus septentrionalis*. One-way ANOVA as well as ANCOVA with maternal SVL as a covariate were used to detect between-island differences in reproductive traits. Symbols immediately after *F* values represent significant level: NS=non-significant, ** = *P*<0.01.

	Beiji island (*n*=40)		Dongtou island (*n*=27)		ANOVA $F_{1,74}$	ANCOVA $F_{1,73}$
	Mean ± SE	Adjusted mean±SE	Mean±SE	Adjusted mean±SE		
Number of clutches	2.0±0.2	1.9±0.2	1.9±0.2	1.9±0.2	0.46[NS]	0.004[NS]
Seasonal fecundity	5.2±0.4	4.9±0.4	4.7±0.5	5.1±0.5	0.71[NS]	0.05[NS]
Seasonal total egg mass (g)	1.60±0.11	1.49±0.11	1.14±0.13	1.24±0.13	6.42**	0.19[NS]

China (Zhao & Adler, 1993). These insectivorous lizards are primarily diurnal and terrestrial; females produce clutches of 1–5 elongate eggs from April to July (Ji *et al.*, 1998; Du, 2003). *T. septentrionalis* has relatively small energy reserves and therefore the energy to produce a clutch of eggs mainly come from the current food intake (Du et al., 2003). The lizards are locally abundant on two offshore islands, Dongtou and Beiji, 13 km apart off the eastern coast of China. These two islands have similar annual average air temperature and annual total precipitation (Zhejiang Bureau of Meteorology). Microhabitats for lizards are grassy areas. However, the grassy habitat is partly covered by pine trees (*Pinus massoniana*) on Dongtou island, but is quite open on Beiji island. Therefore, this system provides us with an excellent model to explore life-history variation in lizards between islands with similar climate conditions but different microhabitat features. Here we investigate life-history characteristics of adult northern grass lizards from the two islands. To determine whether or not local populations diverged from each other in these life-history traits, we recorded body size of the lizards and conducted a "common-garden" experiment to detect their reproductive traits.

MATERIALS AND METHODS

On 10 April 1999, we collected 117 adult *Takydromus septentrionalis* (76 females and 41 males) from two offshore islands, Beiji island (27°35' N, 120°10' E) and Dongtou island (27°50' N, 121°28' E), in Zhejiang province, eastern China. All animals were caught by hand or noose and transported to Hangzhou Normal College. Immediately after arrival, the animals were weighed (±0.001g), measured SVL (±0.01mm) and individually marked (toe-clipped). The lizards were randomly allocated to terraria (60×40×30cm, each containing 9-10 females plus 5-6 males) with sand and grass to mimic natural habitats where these lizards are found. A 60W light bulb suspended 15 cm above the floor provided opportunities for behavioural thermoregulation from 0700 h to 1700 h. Food (larvae of *Tenebrio molitor*) and water (containing mixed vitamins and minerals) were provided ad libitum. We palpated the abdomens of each female every five days, and any animal with oviductal eggs was transferred to a small glass terrarium (20×15×20 cm) filled with 2 cm-deep moist sand. Each small terrarium was checked at least three times a day for freshly laid eggs. All eggs were weighed (± 0.001g) promptly so as to minimize potential changes in mass due to water exchange. Postpartum females were returned to their original terraria. The experiment was carried out between 10 April and 10 July.

We calculated relative clutch mass (RCM) as the ratio of clutch mass to maternal postoviposition mass (Shine, 1980). The difference in RCM between populations was tested using an analysis of covariance with clutch mass as the variable and body mass as the covariate. Linear regression was used to detect the relationship between maternal body size and reproductive traits. To detect divergence between populations and among clutches, we conducted analyses of variance (ANOVA) for reproductive traits that were independent of maternal SVL and analysis of covariance (ANCOVA) for variables correlated with maternal SVL.

RESULTS

TIMING OF OVIPOSITION AND TOTAL SEASONAL FECUNDITY

Females from the Beiji population laid their eggs after being captured for 27.2±1.4 days (*n*=49), which was earlier than for Dongtou females (38.0±2.5, *n*=27; $F_{1,74}$=16.04, *P*<0.001). Total seasonal reproductive output of Beiji females was higher than that of Dongtou females in terms of total egg mass, but no differences in number of clutches or seasonal fecundity were found between the two populations (Table 1). Because larger females produced more eggs, and a greater total egg mass (SVL vs total seasonal fecundity, r^2=0.084, $F_{1,74}$=6.82, *P*<0.01; vs total seasonal clutch mass, r^2=0.135, $F_{1,74}$=11.59, *P*<0.01), we then reanalysed inter-population variation in fecundity after including maternal SVL as a covariate. This analysis indicated that total clutch size and total seasonal clutch mass at the mean SVL of 66.68 mm did not differ significantly between the two island populations (Table 1).

FEMALE BODY SIZE AND RELATIVE CLUTCH MASS

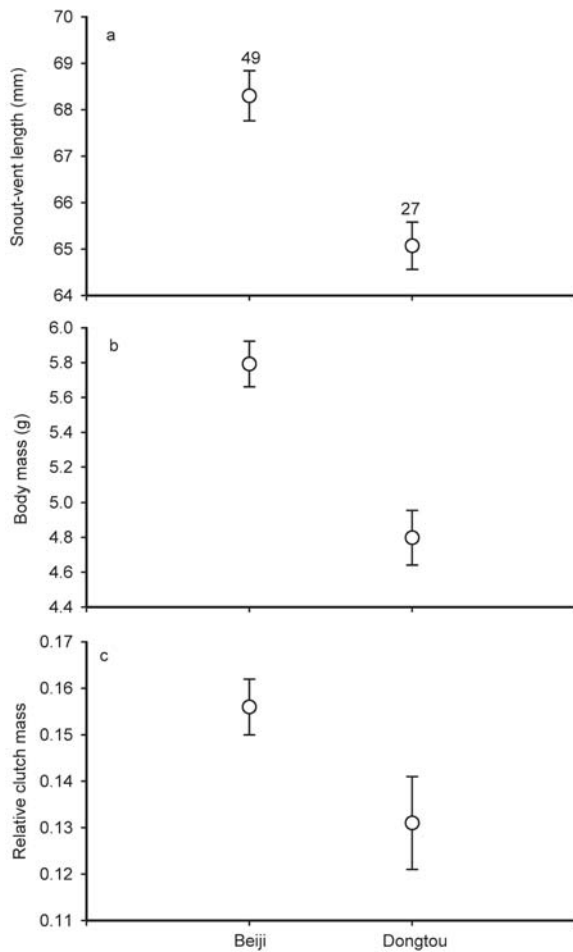Female body size at maturity differed significantly between the two populations. The SVLs of minimal re-

FIG. 1. Variation in maternal body size (A), mass (B) and relative clutch mass (C) in the northern grass lizard *Takydromus septentrionalis* between Beiji and Dongtou island populations. Graphs show mean values and associated standard errors. Numbers above the error bars in the upper graph are sample sizes, and apply to all graphs within this figure.
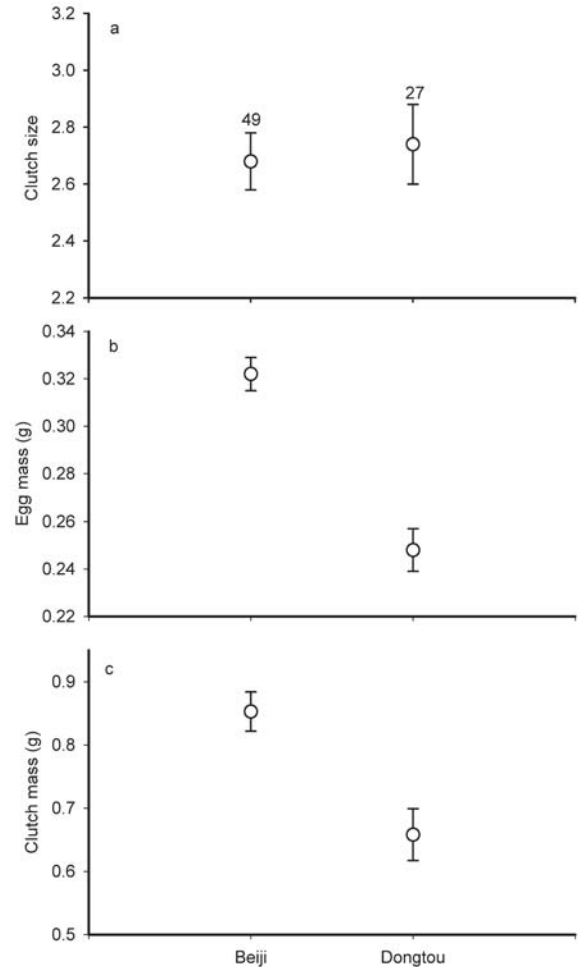

FIG. 2. Variation in clutch size (A), egg mass (B) and clutch mass (C) of the northern grass lizard *Takydromus septentrionalis* between Beiji and Dongtou island populations. Analyses of covariance were performed to detect the inter-population variation. Maternal snout–vent length was used as the covariate, which was set at 66.68 mm. Graphs show adjusted mean values and associated standard errors. Numbers above the error bars in the upper graph are sample sizes, and apply to all graphs within this Figure.

productive females on Beiji and Dongtou islands were 57.5 mm and 54.5 mm, respectively. Sexually mature females from the Beiji population were larger than those of the Dongtou population both for mean SVLs ($F_{1,74}$=15.38, P<0.001; Fig. 1A) and body masses ($F_{1,74}$=22.15, P<0.001; Fig. 1B). Relative clutch mass (RCM) also varied between populations, with the RCM of Beiji females being higher than that of Dongtou females ($F_{1,73}$=10.74, P<0.01; Fig. 1C).

CLUTCH SIZE, CLUTCH MASS AND EGG MASS

Clutch size, clutch mass and egg mass were positively correlated with female SVL (clutch size, r^2=0.347, $F_{1,74}$=10.13, P<0.01; clutch mass, r^2=0.529, $F_{1,74}$=28.80, P<0.00001; egg mass, r^2=0.114, $F_{1,74}$=9.52, P<0.01). We thus used two-way ANCOVA with SVL as a covariate to detect variations in reproductive traits arising from inter-population and clutch effects. The analysis indicated that there was a significant difference in reproductive traits between the two populations

($F_{3,111}$=18.77, P<0.00001), but not between the clutches ($F_{3,111}$=1.04, P=0.38). To identify the source of inter-population differences in reproductive traits, we further performed individual analyses of covariance on the three traits. Whereas females from the two populations produced clutches with similar numbers of eggs ($F_{1,73}$=0.11, P=0.75; Fig. 2A), females from Beiji island produced larger eggs ($F_{1,73}$=43.01, P<0.00001; Fig. 2B) and thereby heavier clutch mass ($F_{1,73}$=12.92, P<0.001; Fig. 2C) than did those from Dongtou island. Because the effects of maternal body size have been removed using ANCOVA in our analysis, the significant inter-population difference in egg size was not entirely attributable to maternal body-size variation, though egg mass was highly correlated with maternal SVL. The coefficients of variation of egg size for the Beiji and Dongtou populations were 12.5% and 16.0%, respectively, which was less variable than clutch size in both

populations (26.4% for the Beiji population and 26.2% for the Dongtou population).

DISCUSSION

As reported previously for other reptile species (e.g. *Eumeces okadae*, Hasegawa, 1994), the northern grass lizard showed significant inter-island variation in a wide range of life-history traits. These variations were correlated with maternal body size both between and within populations; such correlation is common in lizards (Fitch, 1985; Dunham *et al.*, 1988; James & Shine, 1988). Nonetheless, inter-island variation in reproductive traits per clutch was not entirely attributable to maternal body-size differences: life-history traits varied significantly among islands even after the effect of differing maternal body sizes was removed from the analysis. The current study found significant inter-island differences in life histories, but, as a descriptive study, there were not enough data to elucidate the ultimate and proximate causes of these variations in life histories. To further clarify the causes for the significant inter-island variation in reproductive traits of *T. septentrionalis,* we would need to take account of the between-island differences in both genetic origins and environmental factors such as food availability, predator pressure and population density. Ideally, reciprocal transplant experiments in the field could identify the respective effects of these factors on the reproductive traits of *T. septentrionalis* (Niewiarowski & Roosenburg, 1993).

Given that variation in adult body size accounted for much of the inter-population divergence in life-history traits of *T. septentrionalis*, we need to consider the factors that influence adult body sizes so as to completely understand life-history variation within this species. Both genetic and environmental factors could affect growth rates and ages at sexual maturity (Reznick & Bryga, 1987; Sinervo and Adolph, 1989; Smith *et al.*, 1994), and in turn be responsible for such inter-population variation in body size. For ectotherms, environmental influence plays an important role in determining body size. Such environmental factors include temperature (Ashton and Feldman, 2003; Angilletta *et al.*, 2004), prey availability and size (Case, 1978; McLaughlin & Roughgarden, 1989; Wellborn, 1995), the intensity of predation (Case, 1982) and demography (King, 1989). As predicted by Case (1982), *E. okadae* from the Izu islands attained larger body sizes on islands with low predation pressure than on those with high predation pressure (Hasegawa, 1994). Unfortunately, because of the absence of data on environmental and ecological parameters, we are currently not able to test these ideas in the island populations of *T. septentrionalis*.

The determinants of egg size reflect selective processes such as the trade-off between clutch size and offspring size, as well as proximate constraints including functional and energetic limitation (Fox & Czesak, 2000; Sinervo *et al.*, 2000). Our study indicated that egg size has a relatively low level of variation compared with that of fecundity in both populations. This greater constancy in egg size than in clutch size accords well with optimality models (Smith & Fretwell, 1974). The difference in egg size existed between the two populations after the effects of maternal body size were removed from the analysis, and persisted throughout all clutches after the females had been kept in an identical laboratory environment for a long period. This result suggests either that the difference in egg size is coded genetically or that it is influenced by events (food supply, temperature, etc.) early in a female's life and is thereafter resistant to change.

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