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Ecological Significance of Geographic Differences in Growth Rate of The Sand Lizard, *Acanthodactylus boskianus*

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Abstract: In the present study a combination of laboratory and field enclosure experiments were carried out to investigate the sources of variation in growth rates among two elevationally distinct populations of the sand lizards, *Acanthodactylus boskianus*. Two experiments were conducted to identify the factors that explain the pattern of geographic variation of growth rates in this species. The hatchlings from the two elevation sites reared under identical laboratory conditioned grew at the same rate irrespective of their origin. This finding suggests that the observed differences in growth rate between these two populations were driven by environmental factors. On the other hand, the effect of site where hatchlings were reared was investigated by raising the hatchlings from high elevation site in outdoor enclosures located at low and high elevation sites. Lizards located in the high elevation site grew faster than lizard located at low one. This finding is consistent with the observed differences in growth between the natural populations inhabiting the two localities and emphasize that environmental factors may play a major role in explaining geographic variation in growth as an important parameter in life history traits.

Key words: Lizard ecology-elevational gradient- growth rate- *Acanthodactylus boskianus*

Introduction

Field studies of lizard growth have made a significant contribution to knowledge of life history evolution (Andrews, 1982; James, 1991; Shine and Charnov, 1992). Growth rates may reflect environmental conditions such as food availability and thermal environment (Stamps, 1977; Jenssen and Andrews, 1984; Smith and Ballinger, 1994). Consistent relationships between growth and other life history parameters, such as age at maturity and adult survival, have also been established in several reptile taxa (James, 1991; Shine and Charnov, 1992; El-Mouden *et al.*, 1997).

Geographic variation is an expression of among-population variability in organismal traits for a given species. Species with broad ranges often display a large amount of geographic variation in life-history traits. Geographic variation in life-history traits has received both theoretical and empirical attention, with the aim of testing hypotheses of life-history evolution, and investigating possible sources of variation which include environmental and genetic factors, as well as the interaction between them.

A number of environmental factors may affect life-history traits in natural populations. For instance, lizard life-history traits, such as growth rate, age at first reproduction and fecundity, have been shown to depend on temperature, food availability, etc. (Dunham, 1978; Jones *et al.*, 1987; Sinervo, 1990; Sinervo and Adolph, 1994). Recently, Adolph and Porter (1993) developed a model on the proximate effects of temperature on lizard life-history traits. Their model showed that patterns of life-history variation may predicted without invoking any genetic basis for variability in life history traits, underlying the thermal adaptation to the environments.

Juvenile survival and growth rate are probably the most important traits responsible for the shape of trade-offs among life-history traits in lizards. A small variation in juvenile survival induces a high variation in the population growth rate. On the other hand, individual growth rate is a very good predictor of age at first reproduction, which in turn is likely to affect fecundity (Bauwens *et al.*, 1986;

Ferguson and Talent, 1993).

There are few clearer instances of adaptive responses of lizard demographic characters to Egyptian habitat structures and environmental imposed constraints. In this study we used a combination of laboratory and field enclosure experiments to investigate the sources of variation and the factors that explain the pattern of geographic variation of growth rates of two populations of the sand lizard, *A. boskianus* along two different elevation gradients in Burg El-Arab region, part of western Mediterranean desert of Egypt. The results of the present study may explain many of the observed characteristic differences in growth rate in this species of lizards inhabiting the same habitat.

Materials and Methods

Study sites and organism: The study site is Burg El-Arab region, 50 km west of Alexandria on western Mediterranean coastal region of Egypt. This site has been selected for the present study because of its characteristic environmental features and the variety of its habitat topography. The studied regions were Mallahat Mariut depression of the lower elevation (about 5 m below the sea level) and Gabal Mariut region of highest elevation (35 m above the sea level). The two sites differ with respect to climate, vegetation cover, food abundance, etc. (Table 1, Hussein, 1992).

The lizard, *Acanthodactylus boskianus* (Reptilia, lacertidae) was chosen as the study organism because it is abundant and easily captured. This lizard is common in most parts of Egypt, especially in semi-deserts, living among stones and loose soil. This lizard is diurnal and rarely seen in winter. Adult snout-vent length (SVL) ranges from 64 to 86 mm and body mass ranges from 21.2 to 38.1 g. Mating takes place in the first days of June, gravid females were seen one month later and hatching takes place after two weeks. The growth rates in the field were estimated in two distinct populations of *A. boskianus* in low elevation site (Mallahat Mariut) and high elevation site (Gabal Mariut). At mid-July 1999, 60 hatchlings were captured. SVL to the nearest

Table 1: Differences in site characteristics and resource abundance of the study populations (from Hussein, 1992)

Differences	Gabal Mariut Region	Mallahat Mariut region
Elevation (m)	35m above the sea level	5m below the sea level
Annual rainfall (cm)	172.00	100.90
Vegetation cover (%)	14.90	08.70
Food abundance (item per trap h ⁻¹)	3.14	0.66

ANOVA for comparing the resource levels by sites

	F _{2,122}	P
Annual rainfall	3.546	0.033**
Vegetation cover	4.809	0.008**
Food abundance	2.932	0.047*

*P<0.05, **P<0.01

0.1mm and body mass to the nearest 0.1 g were recorded for all the collected individuals, then they were released to the field after being marked by toe-clipping. The growth rate data were obtained from individuals that were recaptured each two weeks (i.e. at 1, 15 August and 1, 15 September). Each captured lizard was measured, weighed and returned to the field.

To investigate the sources of variation in growth rate among the two elevationally distinct populations of the sand lizard *A. boskianus* and to identify the factors that explain the pattern of geographic variation in growth among this species, two experiments were conducted.

First experiment: In this experiment, the hatchlings of the gravid females collected from the two elevationally distinct populations (low and high) were reared under identical laboratory conditions. At the beginning of July 1999, twelve gravid females were collected from the population of each site. These females were transferred to a field laboratory in the Faculty of Science research station located in Burg El-Arab region near the field of work. The gravid females were measured (SVL) and weighed. They were housed in plastic terraria (90X45X45 high) with damp soil, some strong paper for shelter, water and small beetles as food *ad libitum*. They were exposed to a natural photoperiod (12 hours daily) and to incandescent lamps for heat for six hours/ day. Terraria were checked twice daily for hatchlings. Hatchlings were measured (SVL), weighed, marked by toe-clipping, and randomly assigned to a terrarium with damp soil and a shelter, within one day of hatching. Each terrarium contained five unrelated hatchlings. They had water and were fed *ad libitum* with small insects caught in the field. Hatchlings were also exposed to the same above cited conditions of photoperiod and heat. On 1 and 15 August and 1, 15 September, all hatchlings were measured and weighed which allowed us to estimate growth rates during the first two months of life. Statistical analysis of growth rates among lizards coming from the two elevationally distinct populations and univariate tests were carried out (MANCOVA, Bailey, 1981) to find the site effect and the interaction between the site and initial SVL for populations throughout the four growth periods.

Second experiment: In this experiment, the hatchlings of the gravid females from the high elevation population were reared in outdoor enclosures located at low and high elevation sites. At the beginning of July 1999, twenty

gravid females were captured in only one population located at Gabal Mariut (high elevation site). Gravid females and their offspring followed the same treatment as in the first experiment. After two weeks, all gravid females laid their eggs. Each hatchling was randomly assigned to one of four enclosures (5X3X0.75m high) either in low or high elevation site. The hatchlings released in the enclosures in the subsequent day of hatching. The enclosures were located near the natural population and contained the common vegetation types represented in the natural site (e.g. *Ammophila arenaria* and *Euphorbia paralias*). At 15 August and 15 September, i.e., after the first and second months of life respectively, the lizards were captured. Each lizard was measured, weighed and returned to the enclosure. The results obtained were analyzed statistically according to Bailey (1981). Main effects of site on growth rate were analyzed by ANOVA test. Statistical significance was inferred at P < 0.01.

Results

Field studies of both populations showed that all the gravid females laid their eggs in mid-July. Females lay an average of five (range: 2 to 12) unshelled eggs under vegetation and common shrubs in the environment that hatch immediately after being laid. Gravid females from Gabal Mariut were slightly larger than females from Mallahat Mariut (P < 0.01, Table 2). Numbers of eggs, hatchling SVL and mass did not differ significantly between sites, although number of eggs from Gabal Mariut tended to increase (P > 0.05, Table 2).

In the field, hatchlings of the lizard *A. boskianus* among the two elevationally distinct populations showed an ascending slope pattern of growth in SVL and body mass with evidence of rapid growth during the first month after hatching, after which rates were slightly decreased (Fig. 1). The hatchlings of both elevations grow at similar relative rates but reach different values. Lizards located in high elevation site grow faster than lizards located in the low elevation site.

Growth rates did not differ between lizards coming from the two populations and reared in the same environmental conditions (First experiment, Fig. 2). The results of MANCOVA test showed that neither the site effect nor the interaction between the site and the initial SVL were significant (Table 3). Univariate tests also showed that the growth rates did not differ between populations of any of the four periods (Table 3). Therefore, hatchlings from low and high elevation sites grew at the same rate when reared in the same environmental conditions.

The results of the second experiment in which the hatchlings from the high elevation population were reared in outdoor enclosures located at low and high elevation sites showed that the site where hatchlings were reared had a large impact on growth. Lizards located in the high elevation site grew faster than lizards located in the low elevation site (Fig. 3). These findings are consistent with the field observed differences in growth rates between the natural populations inhabiting the two localities.

Discussion

This study demonstrate that growth rate is flexible traits of the sand lizard *A. boskianus*. This flexibility can explain the geographic variation between a low and high elevation population of this lizard. It is clear from the results that

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Table 2: Comparisons of population characteristics of the study sites

Characteristics	Gabal Mariut		Mallahat Mariut		P
	$\bar{x} \pm S.D$	Range	$\bar{x} \pm S.D$	Range	
Graavid female SVL (mm)	77.2 ± 0.98	65.5-86.2	73.2 ± 0.88	64.5-81.4	<0.01
Graavid female mass (g)	34.4 ± 1.22	29.8-38.1	26.8 ± 0.63	21.2-31.6	<0.01
Number of eggs	5.9 ± 0.58	2.0-12.0	5.6 ± 0.21	2.0-11.0	>0.05
Hatchling SVL	22.3 ± 1.44	19.0-23.0	22.2 ± 1.09	19.0-23.0	>0.05
Hatchling mass (g)	1.9 ± 1.59	1.6-3.4	1.9 ± 0.84	1.6-2.2	>0.05

P > 0.05: Insignificant difference, P < 0.01: Significant difference

Table 3: MANCOVA data on four growth periods. Site is the population of origin, initial SVL is snout-vent length at hatching

Growth rate	Period	Sources of Variation	F	P
1	15 Jul. - 1 Aug.	Site	0.69	0.233
		Initial SVL	21.88	0.001
2	1 Aug. - 15 Aug.	Site X Initial SVL	1.22	0.245
		Site	0.77	0.427
3	15 Aug. - 1 Sep.	Initial SVL	26.12	0.001
		Site X Initial SVL	0.61	0.466
4	1 Sep. - 15 Sep.	Site	0.88	0.370
		Initial SVL	24.30	0.001
		Site X Initial SVL	0.92	0.321
		Site	0.97	0.246
		Initial SVL	28.22	0.001
		Site X Initial SVL	0.99	0.253

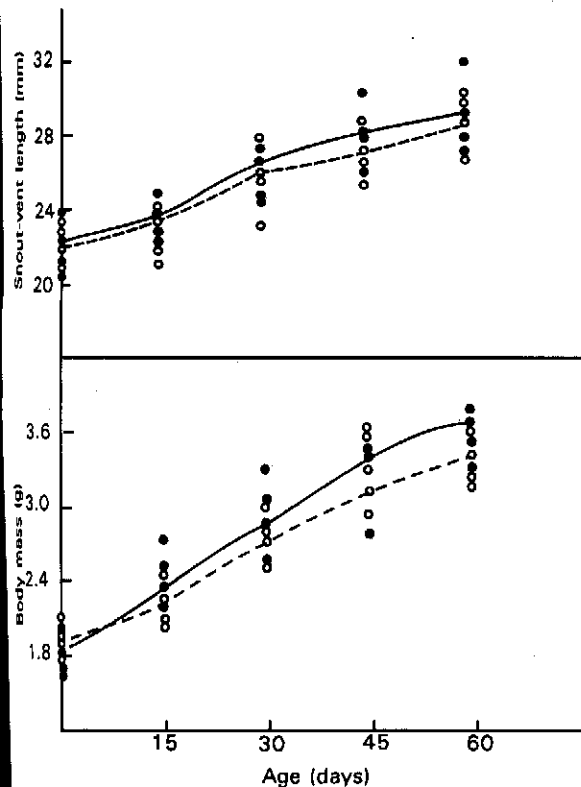


Fig. 1: Snout-vent length and body mass hatchling lizards of Gabal Mariut (closed circles) and Mallahat Mariut (open circles) plotted against age. Continuous and dashed lines represent the mean values

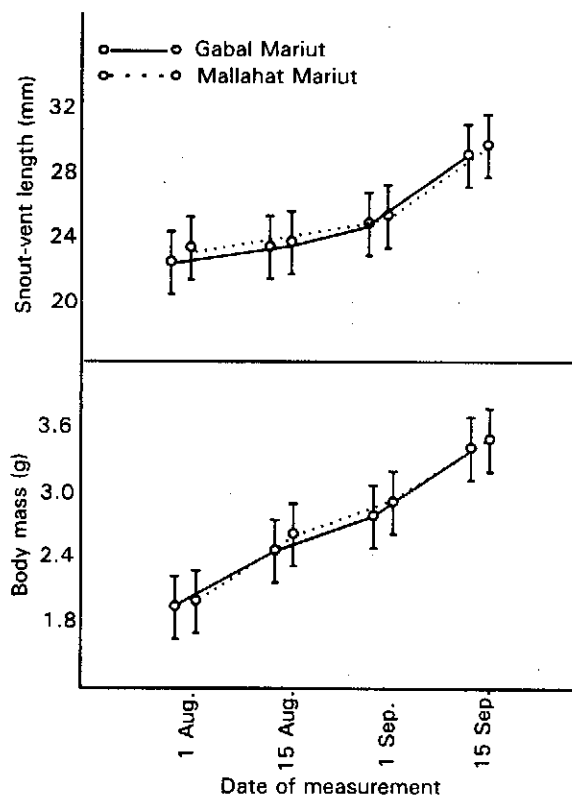


Fig. 2: Growth rate of hatchling lizards collected from different elevation sites and reared under identical laboratory conditions. Points are the mean values and bars represent standard deviations

hatchlings coming from the two populations grew at the same rate when experiencing the same environmental

conditions. On the other hand, the hatchlings from the high elevation population showed significant differences in growth rate when reared at low and high elevations. These

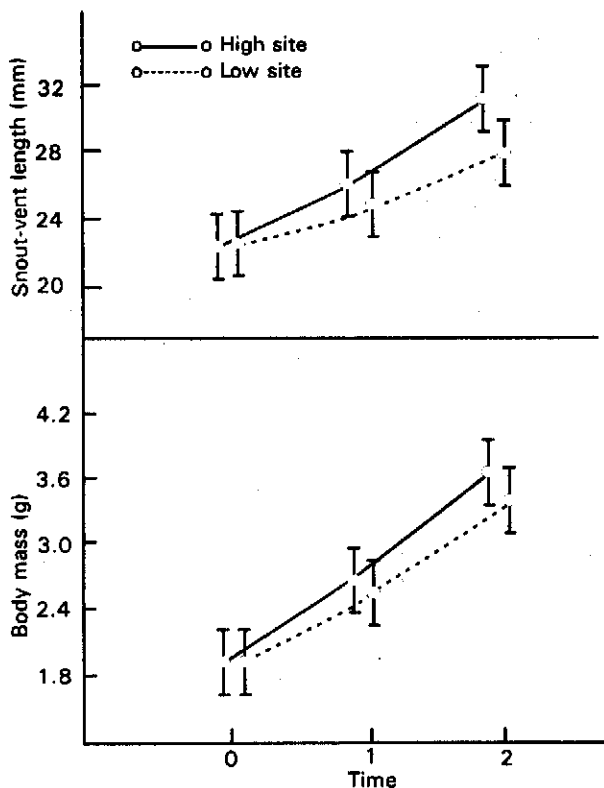


Fig. 3: Snout-vent length and body mass of hatchling lizards from Gabal Mariut population reared in two different environments. The X-axis indicates the three dates of measurements (0: at hatching, 1: after one month, 2: after two months). Bars represent standard deviations

differences were consistent with the observed pattern of variation between the natural populations. Several environmental factors can account for flexibility or plasticity of growth rate in reptiles. Thermal environment and food availability are two of the most studied proximal factors likely to affect growth rate (Andrews, 1982; Avery, 1984; Sinervo and Adolph, 1989; Niewiarowski and Roosenburg, 1993; Sinervo and Adolph, 1994). All of these studies showed that individuals living in rich-food environments or environments with higher temperatures had higher growth rates. Therefore, variation in growth rate among lizard populations can largely depend on thermal environments without necessarily invoking genetic adaptation to these thermal environments (Adolph and Porter, 1993).

Our field study shows that the lizards located in high elevation site grow faster than lizards located in low one. There is a close relation, in general, between increasing growth rate and the length of daily activity times. Lizards with longer activity times are likely to spend more time at body temperatures and thus are likely to have high growth rates. Several field and laboratory observations support this prediction (Avery, 1984; Grant and Dunham, 1990; Sinervo and Adolph, 1994). The present results also confirmed and endorsed the finding of Hussein (1992) on the same species and sites who deduced that the activity of lizards at higher elevation site were extended throughout the day but

restricted to mid-day inactivity at the lower site. The differences in daily activity times is a consequence of differences in temperature, habitat and foraging behaviour between populations in both studied regions.

On the other hand, few recent studies have pointed out that phenotypic flexibility or plasticity in growth rates between lizard populations can exist (Stearns, 1986; Gotthard and Nylin, 1995). For instance, *Sceloporus undulatus* lizards transplanted to a new thermally more favorable environment, acquire the same growth rate of individuals belonging to the local populations (Niewiarowski and Roosenburg, 1993). Therefore it is not surprising then to find that hatchlings of the sand lizard, *A. boskianus*, studied here, grew at the same rate when experiencing the same environmental conditions irrespective of their origin, i.e. the environment is the main source of the observed geographic variation.

In fact, correlated variation in life history characters such as growth rate and environmental factors such as resource abundance, has been documented in numerous reptilian systems (Tinkle and Ballinger, 1972; Derickson, 1976; Dunham, 1981; Ballinger and Congdon, 1981; Adolph and Porter, 1993). Patterns of covariation in life-histories and environmental gradients have been referred to as "proximal" in origin or "environmentally induced" (Dunham, 1978; Dallinger, 1983). But this does not necessitate that such variation is entirely non-genetic and thereby irrelevant to selection on life history phenotypes. Environmental genotype interactions exist and can lead to adaptive plasticity in variable and unpredictable environments (Stearns, 1986; Newman, 1988). Although comparative data cannot reveal genetic mechanisms leading to such an interaction, in some cases life history phenotypic response to specific environmental constraints are likely to be adaptive (Tinkle, 1972; Dunham *et al.*, 1989).

The environmental conditions seems to be the main source of variation of growth rate between the two elevationally distinct lizard populations reported here. So, growth rate may still phenotypically variable within population inhabiting different sites. Therefore, the hatchlings from the high elevation population showed significant differences in growth rate when reared in outdoor enclosures located at low and high elevations, i.e. the site where hatchlings were reared had a large impact on growth rate.

Some other recent studies have shown that geographic variation in reptile life-history traits may arise from genetic divergence among populations, and that intrapopulation genetic variation for some of them (e.g. growth rate) exists (Sinervo and Adolph, 1989; Sinervo, 1990; Ferguson and Talent, 1993). Natural selection may operate with different strengths and in different directions in different environments, thus if genetic variation in life-history traits within population exists, they are expected to evolve to different local optima (Sinervo and Adolph, 1994). Natural selection could have favoured different genotypes in different thermal environments resulting in genetic differentiation between populations. This will lead to genetic adaptation to the local environmental conditions which explain the observed differences in growth rate between the natural populations inhabiting different localities. Alternatively, adaptation to local environment may be achieved through optimum levels of phenotypic flexibility. Therefore, the environmental factors may play a major role in shaping patterns of life history association

A. boskianus, and in explaining geographic variation of life histories.

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