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ALLOMETRY, SEXUAL SIZE DIMORPHISM, AND NICHE PARTITIONING IN THE MEDITERRANEAN GECKO (*HEMIDACTYLUS TURCICUS*)

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ABSTRACT—*Hemidactylus turcicus* is a small gekkonid lizard native to the Middle East and Asia that is known to exhibit sexual dimorphism in head size. Several potential explanations exist for the evolution and maintenance of sexual dimorphism in lizards. We tested 2 of these competing hypotheses concerning diet partitioning and differential growth. We found no differences in average meal size (volume) or in any single dimension of prey size for similarly sized males and females. Allometric patterns of increases in head size also were measured in males and females. We found that males exhibited a mixture of isometric and positively allometric patterns of head size increase, whereas females exhibited isometric and negatively allometric patterns. Thus, we concluded that sexual dimorphism in head size is not the result of diet partitioning but instead of differential growth patterns following sexual maturity in males and females.

RESUMEN—*Hemidactylus turcicus* es una pequeña lagartija nativa del Medio Oriente y Asia que exhibe dimorfismo sexual en el tamaño de la cabeza. Varias posibles explicaciones existen para la evolución y el mantenimiento de dimorfismo sexual en lagartijas. Probamos dos de estas hipótesis contrarias referentes a fragmentación de dieta y crecimiento diferenciado. No encontramos ninguna diferencia en el tamaño medio del alimento (volumen) o en ninguna única dimensión del tamaño de la presa para machos y hembras de tamaños semejantes. Patrones alométricos de aumento del tamaño de la cabeza fueron medidos en machos y hembras. Encontramos que los machos exhibieron una mezcla de patrones isométricos y positivamente alométricos de aumento del tamaño de la cabeza, mientras que las hembras exhibieron patrones isométricos y negativamente alométricos. Concluimos que el dimorfismo sexual en el tamaño de la cabeza no es el resultado de la fragmentación de la dieta sino de patrones diferenciales de crecimiento después de la madurez sexual de machos y hembras.

Male biased sexual dimorphism in head size is common among lizards and is thought to evolve through 3, not mutually exclusive, selection pressures (Verwaijen et al., 2002). Male biased sexual dimorphism could arise via differential mating success between large and small individuals. In this classic explanation of sexual dimorphism, large males gain greater access to females by improved success in aggressive contests with smaller males (Trivers, 1976; Anderson and Vitt, 1990). Another hypothesis potentially explaining male biased sexual dimorphism is the dietary divergence hypothesis (Schoener, 1967; Stamps, 1977; Preest, 1994; Verwaijen et al., 2002), in which large males are able to consume larger and harder prey items relative to females, thus reducing intersexual competition. Finally in lizards, it has been proposed that large males, males with larger head size, or large males in both attributes have greater mating success than small males because they have more powerful copulatory biting behaviors and, thus, are better able to ensure fertilization (Herrel et al., 1996).

Alternative models of the evolution of sexual dimorphism suggest that it can arise as a consequence of non-adaptive processes (Anderson and Vitt, 1990; Karubian and Swaddle, 2000; Cox et al., 2003). For example, size dimor-

phism will develop regardless of selection on size if differential growth rates resulting from physiological, behavioral, and ecological differences exist between the sexes (Anderson and Vitt, 1990; Cordes et al., 1995; Sugg et al., 1995; Cox et al., 2003). The concept is that females devote energy toward reproduction immediately upon reaching sexual maturity, whereas males continue to devote energy toward growth.

The Mediterranean gecko (*Hemidactylus turcicus*) was introduced into the United States approximately 90 years ago and is now widespread throughout the Southeast (Stegneger, 1922). Many aspects of the biology of this species have been investigated in the United States (e.g., Rose and Barbour, 1968; Selcer, 1986; Trout and Schwaner, 1994). It is presumed that its biology (e.g., diet, association with rocky and artificial structures) is generally the same as in its native range; however, little ecological data exist on this species in its natural habitat to test this presumption. Regardless, *H. turcicus* exhibits male-biased sexual dimorphism in head size, but not snout-vent length (SVL) (Saenz and Conner, 1996). Saenz (1996) found that female *H. turcicus* consume more ground dwelling prey, while males prey upon a greater proportion of flying prey, suggesting dietary partitioning between the sexes. However, the absolute difference in head size between males and females was small (Saenz and Conner, 1996). Thus, the biological significance of the dimorphism seems questionable. If a biological explanation for the dimorphism is not apparent, then it seems likely that it might have developed as the result of a non-adaptive process, such as differential growth.

Allometry is the change of shape of a morphological structure (or structures) with size (Emerson and Bramble, 1993). Because the head is a 3 dimensional, complex structure, changes in its shape during growth might have important ecological and functional implications for the organism. Determining allometric trajectories, or scaling relationships, for head size in *H. turcicus* will establish how head size dimorphism comes about during growth. As an example, males might exhibit isometric scaling, a 1:1 relationship (slope = 1.0) between head size and body size during growth, and females might show negative allometry, a slope of less than 1. Such a pattern would suggest that female heads get proportionately smaller for their size as they grow and not that males are under positive selection for greater head size.

The objectives of the current study were the following: first, we examined the relationship between prey size and sex to test the hypothesis that sexual dimorphism is correlated with differences in prey size (i.e., the dietary divergence hypothesis); second, allometric trajectories in head dimensions (length, width, depth) were estimated to quantify how patterns of growth were responsible for the male-biased sexual dimorphism in head size (i.e., differential growth hypothesis). Examination of these hypotheses is not only important for our understanding of the causal mechanisms behind the generation and maintenance of the sexual dimorphism, but also for future comparative morphological and ecological work on this species in its native habitat.

METHODS—Adult *H. turcicus* were collected on the campus of Stephen F. Austin State University, Nacogdoches, Texas (94°38′50W, 31°37′10N) between 19 April and 15 October 1990. Adults of this species are defined as those individuals greater than 44 mm SVL (Selcer, 1986). Individuals that had not yet reached sexual maturity (i.e., those <44 mm SVL) were not included in the sample because we were unable to reliably determine sex after preservation. Thus, the hypotheses tested concerned post-maturational responses in diet and growth. All 90 adults were fixed in 10% formalin and stored in 70% ethanol. Snout-vent length, head length (premaxillary to the quadrate; HL), maximum head width (HW), and maximum head depth (HD) were measured to the nearest 0.1 mm for 90 individuals (45 male, 45 female). Stomachs were removed from preserved individuals, and all prey items were individually measured (length, width, and depth). For these same individuals, the average volume of all prey items in the stomach (i.e., meal size; mm³) was computed. This average served as a general estimate of prey size. However, it is possible that a particular component of prey size (length, width, or depth) is limiting rather than prey volume. Thus, a separate analysis was performed to test if the sexes differed in any maximal dimension (prey length, width, depth) of the largest prey item in the stomach.

To address the dietary divergence hypothesis, we examined the relationship between meal size and prey size between males and females. Despite having shorter SVLs, male lizards have larger heads (Saenz and Conner, 1996). Thus, a multiple analysis of covariance (MANCOVA) was performed on meal size

TABLE 1—Mean ($\pm SD$) of morphometric data and the results of RMA regressions for *Hemidactylus turcicus* from Nacogdoches, Texas. Snout-vent length was the independent variable, and HL, HW, and HD were dependent variables. The null hypothesis of isometry was rejected if the confidence intervals did not encompass 1.0.

Parameter	Mean $\pm$ SD	Slope	CI	R^2	Allometry
Head depth (HD)					
Males	6.30 $\pm$ 0.93	1.465	1.194–1.735	0.429	Positive
Females	5.80 $\pm$ 1.12	1.085	0.926–1.245	0.689	Isometric
Head length (HL)					
Males	12.25 $\pm$ 1.23	0.9432	0.773–1.113	0.455	Isometric
Females	11.52 $\pm$ 1.72	0.8489	0.738–0.960	0.754	Negative
Head width (HW)					
Males	9.91 $\pm$ 1.02	0.9929	0.825–1.161	0.520	Isometric
Females	9.17 $\pm$ 1.38	0.8420	0.749–0.935	0.824	Negative

by using head length, width, and depth as covariates. These same analyses were repeated using the maximal dimension of the largest prey item in the stomach as the dependent variable rather than meal size.

To characterize differential growth patterns (allometry), data on lizard head size were logarithmic transformed and subjected to a reduced major axis (RMA) regression (Sokal and Rohlf, 1995; Fairbairn, 1997; RMA software, Bohonak, 2002). Snout-vent length was entered as the independent variable and HL, HW, and HD as the dependent variables. The null hypothesis of isometry is a slope of 1.0; thus, if the confidence intervals for the slope of a given independent variable overlap 1.0, the null hypothesis of isometry is accepted. If the null hypothesis of isometry is rejected, the slope is inspected to determine positive and negative allometry (slope > 1.0 = positive allometry, slope < 1.0 = negative allometry). All data were normally distributed following a logarithmic transformation. Statistical tests were performed using JMP software (version 5.1, SAS Institute, Inc., Cary, North Carolina).

RESULTS—The average meal size (± 1 SE) for females was 1.239 $\pm$ 0.103 mm³; for males, it was 0.847 $\pm$ 0.0785 mm³. The MANCOVA model was significant (Wilk's *lambda* = 0.77, $F_{4,186} = 6.4$, $P < 0.0001$), and the model effect of sex also was significant ($F_{2,93} = 0.24$, $P < 0.0001$), indicating that head shape (L $\times$ W $\times$ D) was different between males and females. However, the covariate term of average meal size was not significant ($F_{2,93} = 0.01$, $P = 0.7783$), indicating that the significance of the whole model was the result of the model effect of sex alone, not differences in meal size. The MANCOVA on maximum prey length, width,

and depth was not significant (Wilk's *lambda* = 0.97, $F_{4,172} = 0.51$, $P < 0.725$). Thus, male and female lizards of a given size did not eat prey that was significantly different in maximal length, width, or depth.

A mixture of positive, negative, and isometric growth trajectories were observed in the specimens studied (Table 1). Head depth in males showed positive allometry, whereas female HD scaled isometricly. In males, HL and HW scaled isometricly, but in females, both parameters showed negative allometry.

DISCUSSION—The hypothesis that sexual dimorphism in head size in *H. turcicus* has evolved due to selection on males to consume larger prey (dietary divergence) could not be supported given that the covariate term in the multivariate model (average meal size) was not significant. Thus, no relationship existed between meal size and sex or head size. Furthermore, there was no difference among any single dimension of prey size between the males and females. Thus, males and females did not eat significantly larger or smaller meals than the opposite sex nor did they eat prey that differed in any particular maximal dimension of length, width, or depth. Instead, the minor dietary differences between males and females were likely due to habitat segregation, with males foraging in slightly different microhabitats (higher perches) than females (lower perches) (Saenz, 1996).

The allometric analysis suggested that sexual dimorphism in HL and HW in *H. turcicus* was

the result of differential growth. The isometric scaling patterns observed in males demonstrated that, following sexual maturity, HL and HW increased at the same rate as overall body size. In contrast, females showed negative allometry for both HL and HW, indicating that growth slowed in these dimensions following sexual maturity. Thus, the differential growth hypothesis for head size dimorphism was supported by the fact that female growth in head size slows but is unchanged in males. These growth patterns could be purely the result of physiological differences between males and females, or they could be due to selection on other characters (e.g., energy devoted to reproduction rather than growth in females). The data collected here cannot support or reject either possibility.

The positive allometry in HD demonstrated that head size increased faster than body size in males, whereas in females, it increased at the same rate (isometry). The benefit to males in having proportionately deeper (or taller) heads could be related to biting performance and, thus, might be under some selective pressure. A taller head could increase gape, which in turn, might facilitate a better ability for males to grasp females during copulatory bites (Herrel et al., 1996). Although not directly tested, ritualistic copulatory bites might play a central role in male mating success, because they are often of long duration and are powerful enough to leave wounds or scars on females (L. D. McBrayer, pers. observ.). A second consequence of an increase in gape is that maximal prey size could be increased. However, because diets seemed to be quite similar in terms of both meal size and prey size, bite performance during copulation might be more likely related to the positive allometry of HD in males.

Aside from gape, a taller head also could allow for increased bite force. A taller head would allow additional space for the jaw adducting musculature and for pinnate muscles. In turn, these modifications would yield greater bite force through an increase in the physiological cross section of the muscle (Herrel et al., 2001). Performance studies, such as bite force (see Arnold, 1983; Wainwright and Reilly, 1994), are needed to understand the functional (causal) relationship of head size, particularly HD, to mating success. Bite force and

morphology have been shown to be related to sexual dimorphism in 3 species of lacertid lizards (Herrel et al., 1996; Verwaijen et al., 2002), and recent studies suggest that bite force is related to both fighting capacity (Lailvaux et al., 2004) and fitness (Lappin and Husak, 2005) in some lizard species.

Finally, we cannot rule out that the male biased sexual dimorphism in *H. turcicus* was due to sexual selection (e.g., female choice) on body size or HD. While males are significantly different in body mass from females (Saenz and Conner, 1996), no behavioral data exist to suggest that females preferentially mate with large, or large headed, males. Female preference for large males has been shown for many species of lizards (Anderson and Vitt, 1990; Vitt and Cooper, 1985), and we suggest that future studies test this hypothesis directly in *H. turcicus*. In addition, we cannot rule out that patterns of sexual dimorphism, diet, or habitat segregation observed in this population in North America exist throughout the native range of *H. turcicus*. Regardless, future studies should integrate allometry with performance (e.g., bite force or winners of agnostic encounter between males) and individual fitness to better understand how phenotypic variation, such as sexual dimorphism, is maintained in lizard populations.

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