

Sexual dimorphism in *Trapelus ruderatus ruderatus* (Sauria: Agamidae) with notes on the natural history

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Abstract.—We studied sexual dimorphism and some aspects of natural history and behavior of the Persian agama (*Trapelus ruderatus ruderatus*) from a population in Dehloran Township, Ilam Province, southwestern Iran. Findings were obtained by personal observations and using SPSS 13 statistical package. Based on the analyses, some characters show differences between males and females. All findings for *T. ruderatus* in this paper are reported for the first time.

Key words. Agamidae, *Trapelus ruderatus*, statistical analyses, Ilam, Iran, dichromatism, sexual selection, natural selection

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Introduction

The genus *Trapelus* Cuvier, 1816, comprises four species on the Iranian Plateau as follows: *T. agilis* (Olivier 1804), *T. lessonae* (De Filippi 1865), *T. ruderatus* (Blanford 1881) (*sensu* Rastegar-Pouyani 2000) and *T. megalonyx* (Günther 1865). The distribution of *T. ruderatus* in Iran is limited to southern and southwestern regions of the Iranian Plateau (Anderson 1999; Rastegar-Pouyani 2000; Fathinia 2007; Rastegar-Pouyani et al. 2008). Among the Iranian species of the genus *Trapelus* the study of sexual dimorphism has already been carried out in *Trapelus agilis* (Rastegar-Pouyani 2005). In this relation, study of sexual dimorphism, coloration and color pattern, and natural history of the Persian agama (*Trapelus ruderatus*) is of interest and importance.

As genetic correlation between the sexes is very high for most morphological traits, it is often believed that long periods of time are required to overcome genetic constraints and to evolve sexually dimorphic morphological traits (e.g., Lande 1980; Hedrick and Temeles 1989; Kratochvíl et al. 2003). Moreover, the evolution of sexual dimorphism may be limited by physiological and ecological constraints as well (Kratochvíl et al. 2003).

In agamid lizards, both sexual selection and natural selection influence the form of dimorphism in secondary sexual traits (Stuart-Fox and Ord 2004). Sexual dimorphism (SD) in body shape as well as overall body size is a widespread and common trait among animals (Ji et al. 2006; Kaliontzopoulou et al. 2007), most species being dimorphic rather than monomorphic (Schoener 1977; Mouton and van Wyk 1993; Andersson 1994). Different evolutionary mechanisms have been proposed for the de-

velopment of sexual dimorphism in various animal taxa. However, most of these mechanisms can be summarized by three major forces differentially acting on males and females of a population: sexual selection, fecundity, and natural selection (Olsson et al. 2002; Cox et al. 2003). In many taxa, competition between males over resources characteristically produces an asymmetry in body size between the sexes. Thus, the advantages of larger size for males typically results in sexual size dimorphism (SSD) (Terry et al. 2001). Sexual selection acts on competition between males, often resulting in larger body size and in larger sizes of morphological structures related to fight (Darwin 1874; Verrastro 2004). Anderson and Vitt (1990) suggest that the causes of sexual dimorphism in size could be related to several factors: competition between males; differential mortality between sexes due to differences in longevity; larger amount of energy allocated by females for reproduction; males are more active because they need to search for females and thus present a larger predation risk.

In this paper, the patterns of sexual dimorphism in the Persian agama, *T. ruderatus*, in relation to environmental issues are discussed.

Materials and methods

This survey was carried out in Dehloran area at an elevation of 202 m, approximately 5 km around the city of Dehloran, Ilam Province. The coordinates of study site are 33.5°39'N, and 45°18'E. The information was accessed by a GPS model Etrix. The study area has an annual precipitation of 244.2 mm, and an annual average maximum

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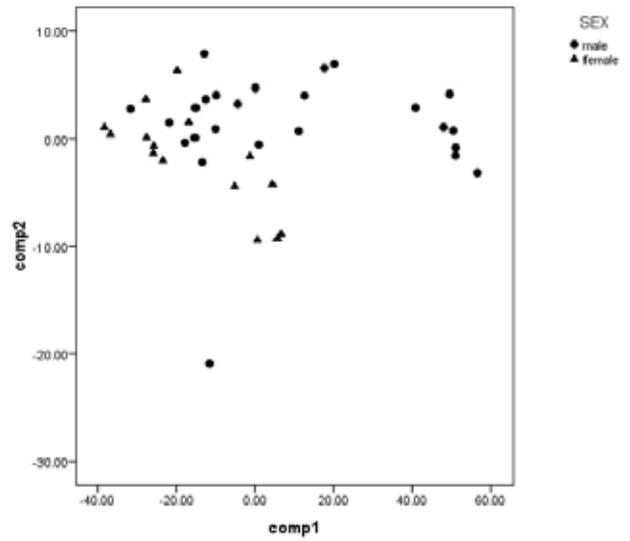


Figure 1 (left). Dorsal view of a male (right) and a female (left) of *Trapelus r. ruderatus*.

Figure 2 (above). Ordination of the individual males and females of *Trapelus r. ruderatus* on the first two principle components. Note the relative degree of isolation of males and females.



Figure 3. The color pattern of an adult male *T. ruderatus* during the hottest hours of the day.

Sexual dimorphism in *Trapelus ruderatus ruderatus*



Figure 4. An adult male *T. r. ruderatus* capturing a spider while foraging.



Figure 5. The occurrence of *T. r. ruderatus* with *Uromastyx loricatus* in the same hole.

Table 1. The comparison of 16 characters in males and females of *Trapelus r. ruderatus*. SEM: standard error of mean; D. of d.: Direction of difference; M. of d.: Mean of differences. All measurements in millimeters (mm).

SEX	IL	IN	NP	SDL	SVL	TL	HL	RP	SL	SBEH	LFL	LHL	LFH	VL	HW	CT
♂	Mean	16.84	5.76	8.48	21.48	127.25	21.66	1.16	18.08	15.48	31.68	44.91	42.64	8.75	19.10	15.92
	N	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25
	SEM	0.27	0.24	0.78	0.36	2.75	0.66	0.11	0.24	0.48	1.35	1.19	1.8	0.37	0.61	0.282
♀	Mean	16.06	5.73	2.86	21.33	106.8	19.53	0.40	16.40	15.20	27.32	39.59	37.57	6.54	17.54	13.86
	N	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15
	SEM	0.37	0.36	0.76	0.42	2.82	0.66	0.1393	0.45	0.35	0.87	0.97	1.72	0.3	0.6	0.29
M. of d.	0.78	0.03	5.62	0.15	9.9	18.85	2.13	0.76	1.68	0.28	4.36	5.32	5.07	2.21	1.56	2.06
D. of d.	M>F	M>F	M>F	M>F	M>F	M>F	M>F	M>F	M>F	M>F	M>F	M>F	M>F	M>F	M>F	M>F

and minimum temperature of 31.6°C and 17.8°C, respectively (Abdali 2009). The study area classified as open habitat based on Stuart-Fox and Ord (2004) which is a semi-desert, alluvial fan area. A total of 40 adult specimens of *T. r. ruderatus* (25 males, 15 females) were examined in this survey. Of these, three were borrowed from RUZM (Razi University Zoological Museum, Kermanshah) while the 37 remaining specimens were collected during September 2008 to September 2009 in the study area. Many of the specimens (12 males and 8 females) were dissected to determine sex and then preserved for further studies. The largest male and female were 111.76 mm and 92.72 mm SVL, respectively. The 17 remaining specimens were caught, measured, and released in the study area. Measurements included 16 metric and meristic characters, based on Rastegar-Pouyani (1999, 2005) and Torki (2007). The metric characters included: SVL: snout-vent length, from end of mental to cloaca; TL: tail length, from cloaca to tip of tail; HL, head length, from end of rostral to anterior border of ear opening; HW: maximum head width; LFL: length of fore limb; LHL: length of hind limb; LFH: length between fore limb and hind limb, from axil to groin; VL: vent length.

The meristic characters included: CT: crossbars on dorsal side of tail; IL: number of infralabial scales; SL: number of supralabial scales; SBEH: scales between eyes across head; SDL: subdigital lamellae under the fourth toe; IN: number of internasals; NP: number of preanal callose scales; RP: rows of callose preanal scales. The metric and meristic characters were measured in mm to the nearest 0.01 mm using digital caliper model Shoka Gulf and/or stereomicroscope. To test the significance of sexual dimorphism, the ANOVA test as well as the Principle Component Analysis (PCA: correlation matrix) were employed. The SPSS software version 13 was used for carrying out the statistical analyses. In addition to the study of sexual dimorphism, some aspects of the ecology of the species including color pattern and color changes of concealed and exposed body regions, behavior, and habitat type and vegetation were considered carefully. According to Stuart-Fox and Ord (2004) the lateral regions of the head, the throat, chest and ventral regions were regarded as “concealed,” whereas the remaining body regions were considered as “exposed.” Plant species were determined based on “Flora of Ilam” (Mozaffarian 2008).

Results

Statistical analysis

A summary of the 16 measured characters is shown in Table 1. There are obvious differences between males and females for 10 characters NP, SVL, TL, HL, RP, SL, LFL, LHL, VL, and CT. For all the significant characters the males have greater values than females. Based on this

Table 2. Extraction of principle components 1-4 using the component matrix.

Characters	PC1	PC 2	PC 3	PC 4
IL	0.239	0.575	-0.355	0.239
IN	-0.402	0.450	0.586	0.032
NP	0.715	0.370	-0.175	-0.322
SDL	-0.086	0.410	0.180	0.666
SVL	0.960	-0.206	0.096	-0.022
TL	0.955	-0.062	0.015	-0.043
HL	0.910	-0.204	0.264	-0.056
RP	0.542	0.648	-0.028	-0.205
SL	0.356	0.747	0.100	0.303
SBEH	-0.221	0.256	0.781	-0.372
LFL	0.601	-0.274	0.186	0.241
LHL	0.967	-0.070	0.006	0.110
LFH	0.937	-0.233	0.015	0.032
VL	0.877	0.201	0.088	0.075
HW	0.925	-0.255	0.156	0.054
CT	0.320	0.646	-0.269	-0.377

study, in most cases the color pattern in females is paler than in males (Fig. 1).

The results of a PCA performed on *T. r. ruderatus* are summarized in Table 2. With 16 variables there are 16 principle components. Details of the first four principle components are given in Table 3. As is shown, the first four principle components (PC1-PC4) account for 48.57%, 16.41%, 8.57%, and 6.94% of the total information, respectively. Jointly they explain 80.45% of the total information.

In the PC1 which contains 48.57% of the total information, the characters NP, SVL, TL, HL, LHL, LFL, VL, and HW having greater values, hence having more contribution and importance in sexual dimorphism. The PC1 highlights a size (metric) difference. The scores of the males along this axis (Fig. 2) show an overlap with those for females, indicating that although sexual dimorphism occurs between males and females, the two sexes are not completely separated from each other in these characters.

The second axis (PC2) contains 16.41% of the total variation and is a meristic axis that records individuals at one end with relatively large IL, NP, RP, SL, and CT and small SVL, HL, LFL, LFH, and HW, compared with individual with relatively small IL, NP, RP, SL, and CT and large SVL, HL, LFL, LFH, and HW.

The third axis (PC3) contains 8.57% of the total variation, and is a meristic axis that records individuals at one end with relatively large IN and SBEH and small

IL and CT, compared with individuals at the other end with relatively small IN and SBEH and high values for IL and CT.

The fourth axis (PC4) contains only 6.94% of the total difference, highlighting a meristic axis showing individuals at one end with relatively large SDL and small CT, SBEH, and NP, compared with individuals at the other end with small SDL and large CT, SBEH, and NP.

Color changes

The Persian agamid, *T. r. ruderatus*, changes its color and adjusts itself based on environmental requirements. During hot hours of the day, the dorsal color of *T. ruderatus* turns to paler in comparison to the cooler hours. During the hot hours, the vertebral stripe becomes lighter, dorsal regions of the body and tail and temporal regions turn to brick, color of flanks becomes vinous and ventral surfaces of body and head turn to whitish (Fig. 3).

The brick color of the dorsal region of tail is more conspicuous than the rest of the body. Color changes look more prominent when a lizard is alarmed. When frightened, the lizard stands on forelimbs, protrudes gular fold and gets ready to bite. The case is true for both males and females. During this defensive posture, the dorsal region of the tail turns brick red while flanks, gular fold, lower surfaces of the eyes, and upper surfaces of limbs (especially the forelimbs) turn to dark blue (Fig. 4). The specimens that collected during September were lighter in color than those collected in April. It seems that so far color changing during reproductive season have not yet been documented for *T. r. ruderatus*, hence this case needs further investigation.

Natural history

The specimens were observed and collected in different habitats, including sandy areas, alluvial fans, and gravel areas in alluviums. *Trapelus ruderatus* occupies territories with special plants and bushes including *Alhagi camelorum*, *Malva parviflora*, *Ziziphus numularia*, *Capparis spinosa*, *Chrozophora tinctoria*, and hand-planted trees such as *Prosopis juliflora*. Most specimens were collected during the hot hours of midday under *C. tinctoria*. *Trapelus ruderatus* is sympatric with *T. lessonae* in

Table 3. Total variance for the first four principle components. Extraction method: Principle Component Analysis.

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
PC1	7.772	48.575	48.575	7.772	48.575	48.575
PC2	2.626	16.411	64.986	2.626	16.411	64.986
PC3	1.371	8.570	73.555	1.371	8.570	73.555
PC4	1.105	6.904	80.459	1.105	6.904	80.459

the Dehloran region. Some individuals make holes under aforementioned plants and others use deserted holes of other reptiles or rodents. *Trapelus ruderatus* sometimes lives with *Uromastyx loricatus* in the same hole (Fig. 5). Moreover certain species of reptiles, some arthropods such as members of the family Gnaphosidae (ground spiders) were observed during excavation of a hole of *T. ruderatus*. It seems that *T. ruderatus* depends strongly on the aforementioned vegetation, as they: A) provide shelter against predators, B) provide shadow during hot summer mid days, C) attract specific types of arthropods and D) serve as ambush for prey. In one case, the senior author found an adult *T. ruderatus* on *C. spinosa* a distance from its burrow of more than 20 meters. This may be indicative of the importance of vegetation in the life history of this lizard. *Trapelus ruderatus* is usually territorial but in one case two adult male specimens were observed under the same *Z. numularia*; both were collected while the tail of the smaller specimen was bitten by the larger one.

Discussion

Sexual size dimorphism is the evolutionary result of selection operating differently on the body size and other characters of males and females (Andersson 1994, Torki 2007). Sexual and/or natural selection can act on both sexes, resulting in the morphological patterns. Genetic correlations between the sexes, as well as phylogenetic inertia, could be factors affecting the observed morphologies (Kaliontzopoulou et al. 2007). Although direct sexual selection can have a major role in the evolution of neomorphic structures, sexual differences are often related to allometric patterns and heterochronic processes (Bruner et al. 2005). Sexual dimorphism is widespread in lizards, with the most consistently dimorphic traits being head size (males have larger heads) and trunk length (Torki 2007). The case is true for *T. r. ruderatus*. Since head dimensions are directly related to bite force, it seems likely that bite force, through its effect on dominance, is a performance trait under sexual, and also, natural selection. Bite force is decisive in species that engage in physical combat (Huyghe et al. 2005). Theoretically, fecundity selection favors large females and sexual selection favors larger males. The two selective pressures could cancel each other out and, consequently, result in a lack of SSD between males and females. For example, selection via male contest competition is the ultimate factor resulting in increased male size in *Eumeces chinensis* and *E. elegans*, whereas selection acting on fecundity or litter mass is the main cause for increased female size in *Phrynocephalus vlangualii* (Ji et al. 2006). So the male contest may be the main pressure resulting in larger SVL in the males of *T. r. ruderatus*. Both sexes have evolved different body or head sizes to use different niche dimensions, such as habitat type, perch height, or diet (“intraspecific

niche divergence” hypothesis) (Smith and Nickel 2002). This may explain the larger HL observed for males in *T. r. ruderatus*. Sexual dimorphism can also be observed in forelimbs and hindlimbs. Long limbs increase maximum sprint speed, allowing lizards to catch prey or escape predators more efficiently. However, shorter limbs are favored on narrow perches because they enhance agility relative to longer limbs (Calsbeek and Smith 2003). Females, on the other hand, have to cope with the functional challenges posed by egg bearing (Butler and Losos 2002). Males tend to have larger limbs which can increase sprint for an escape from predators or facilitate chasing females for successful mating (Fathinia 2007). Sexual selection for effective territory defense has favored males that are more likely than females to stand their ground when approached by a predator and that this decreased wariness led to predator-mediated natural selection for longer legs and concomitant greater speed in males (Peterson and Husak 2006). Taken together, the mentioned reasons may explain sexual dimorphism in the limbs of *T. r. ruderatus*. The longer tail was assumed to be the result of morphological constraints imposed by the male copulatory organs on tail autotomy, or it may have evolved as a result of improved escape abilities in the sex more likely subjected to heavier predation pressure (Kratochvíl et al. 2003). Males are territorial and large size enhances male reproductive success (Shine et al. 1998). This may explain the longer tail and trunk in the male Persian agama.

Epidermal glands in the cloacal or femoral regions of many lizards have semiochemical function related to sexual behavior and/or territorial demarcation. Signals are passively deposited in the environment during locomotion of the animals within their territory (Imparato et al. 2007). Most males are aggressive, territorial, and male territories can contain several female home ranges. One advantage of chemical signals is that they can be used to obtain information about an individual even when other sensory cues are absent. Thus, females might choose where to establish their home ranges by relying on information coming from the chemical signals left from territorial males (Martin and Lopez 2000).

Animal color patterns have received significant attention from different fields, including ecology, physiology and systematics. One of the main generalizations reached is that color patterns constitute adaptive evolutionary characters, representing a compromise between two main selective forces, sexual and natural selection. In reptiles, sexual selection through female mate choice and/or male-male competition, usually determines the occurrence of colorful males particularly during the reproductive season; females can choose males based, among others, on visual displays in which color patterns are highly relevant. Natural selection acts through predation and thermoregulation. Thus, diurnal reptiles exposed to visual predators experience an intense selection for substrate matching to diminish their vulnerability to these predators. On the other hand, dark colors, which

absorb more heat, occur with higher frequency in animals from environments with lower temperature (Vidal et al. 2007).

Two primary processes may drive the evolution of color change: (1) natural selection for the ability to camouflage (crypsis) against variety of backgrounds and (2) selection for conspicuous social signals. In many color-changing lineages, color change is known to facilitate both crypsis and social communication (Stuart-Fox and Moussalli 2008). It seems that dichromatism of “exposed” body regions is significantly associated with habitat openness: species occupying open habitats are less sexually dichromatic than species in more closed habitats (Stuart-Fox and Ord 2004). The case is true for *Trapelus ruderatus*. Dichromatism of “exposed” body regions is constrained by natural selection, whereas dichromatism of “concealed” body regions is driven by sexual selection. According to predation hypothesis, species occupying open habitats are more vulnerable to visual predators. In the species which live in open habitats both sexes are cryptic and therefore less dichromatic (Stuart-Fox and Ord 2004). This case is observed in both males and females of *T. ruderatus*. Based on the predation hypothesis the extent of sexual dichromatism is related to habitat openness only for body regions exposed to visual predators. Concealed body regions have important roles in intraspecific communication, for example most agamid species flash dewlaps or perform head bobs in social interactions (Stuart-Fox and Ord 2004). Regarding the fact that the Persian agama is an open habitat dweller, aforementioned strategies (natural selection for crypsis, selection for conspicuous social signals, and the predation hypothesis) may explain the relatively weak dichromatism observed in both males and females of this lizard.

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Appendix

Material examined

Trapelus ruderatus ruderatus (n=3): RUZM-AT.12.1 to RUZM-AT.12.3: Iran, Fars province, Lamerd, 20 km south of Lamerd [27° 20' N, 53° 10' E]. RUZM-AT.12.4 to RUZM-AT.12.23 (n=20): Iran, Ilam province, Dehloran township [33.5°39' N, 45°18' E; 202 m above sea level].

Trapelus ruderatus ruderatus (n=17): Examined and then released in the study area.



Behzad Fathenia earned his B.A. and M.S. from Isfahan and Lorestan universities, respectively. His M.S. research focused on "The Biosystematic Study of Lizards of Ilam Province." For the time being, he is a Ph.D. student at Razi University, Kermanshah, western Iran under supervision of Nasrullah Rastegar-Pouyani, Mozafar Sharifi, and Eskandar Rastegar-Pouyani. His dissertation research

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