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SIGNALING, AGONISTIC BEHAVIOR, AND LIFE-HISTORY TRAITS OF STEPPE AGAMA (*Trapelus sanguinolentus*) IN PRAGUE ZOO

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Life history traits are influenced by many factors, such as social structure, social displays and aggressive interactions. We investigated signalling and agonistic behavior in relation to body condition and lifespan in *Trapelus sanguinolentus*, a small, semi-arboreal, oviparous agamid lizard from the Central Asia. We individually examined basic morphological characteristics, number of performed signal displays and relative success in agonistic interactions (via Clutton-Brock index). Life expectancy of males did not differ from life expectancy of females. Overall variability of signals was low and simple push-up display was prevalent signal type for both sexes. Frequency of performed signals differed between sexes with males signalling more. For both sexes number of signals was not associated with life expectancy. Interaction of life expectancy and sex was also not significant. In females — body condition influenced number of performed signals when individuals in better body condition signalled more. Most of agonistic interactions was solved by means of signal displays and did not lead to a direct physical combat. While in males association between CBI and number of signals was not significant, in females higher value of CBI means more performed signals. Conditions of our study (sex ratio 4:1 in favor of females, 20 individuals on 16.5 m² of terrarium) means that agonistic signals have greater importance for females. The agonistic interactions in females led to direct physical combat more frequently could reflect more competitive intra-sexual environment. Females in better body condition probably used higher signalling activity and better performance in direct combat for access to mates and to places for sunbathing and oviposition.

Keywords: lizards; Agamidae; signaling; agonistic behavior; social structures; captive breeding.

INTRODUCTION

Life history is commonly defined as a set of evolved strategies, including behavioral, physiological and anatomical adaptations that more or less directly influence survival and reproductive success (Ricklefs and Wikelski, 2002). Animals face environmental, social and physical perturbations, which can jeopardize not only their immediate survival but also other key life-history factors such as reproduction. Individuals may need to respond to

similar challenges with considerably different strategies dependent on the social and environmental context (Moore and Jessop, 2003). One of important pacemakers of evolutionary change exposing animals to new selection pressures or allowing them to evade such pressures with direct consequences for survival or reproduction is behavior, including social behavior mediated by communication or direct interaction with conspecifics (Kappeler et al., 2013). The social environment is a critical determinant of fitness and, in many taxa, is often shaped by individuals' behavioral discrimination among different social contexts (Oh and Badyaev, 2010).

Reptiles were often wrongly regarded as primary “non-social” animals in contrary to mammals or birds though their social repertoire is much more diverse than it was formerly assumed (Doody et al., 2012). In specific case of squamata reptiles, limited cooperative behavior and parental care offer opportunities to study various levels of social behavior and living in aggregations as a step

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in the evolution of more complex sociality (Gardner et al., 2015). Lizards are good model organisms for various studies as they are relatively easy to observe in the field and (especially smaller species) can be successfully studied in laboratory conditions (Tokarz, 1995). Dominance hierarchies and (or) male territoriality act an important role in social systems of lizards from a diverse array of phylogenetic lineages (Masters and Shine, 2003). Diurnal territorial lizards from agamid lineages often perform stereotyped visual signal displays at high frequencies and usually in response to social stimuli (e.g., Macedonia and Clark, 2001). In most agamid species, males are larger than females (male biased SSD) because it facilitates winning aggressive encounters with other males and as consequence leads to more frequent mating (Znari and El Mouden, 1997). Visual displays and opponent assessment have a prominent role as mediators of social behavior in Agamidae (Ord et al., 2002) and it was observed that more aggressive males signalize more intensively in terms of display frequency (Osborne, 2005).

While studies on *Lophognathus gilberti* recorded no female-female aggression (Thompson and Thompson, 2001), studies on *Rankinia diemensis* suppose direct female – female competition as a tool of resource defense (Stuart-Smith et al., 2007). More recent studies on *Phrynocephalus vlangalii* suggest that female – female aggression is not only restricted to resource defense (such as burrows in burrow-dependent species) but also plays a role in mate defense and probably improves mating success in female-biased systems (Wu et al., 2018).

Central Asian agamids remain, despite their ecological diversity (ranging from specialized to generalist species), abundance in the region, and hence probable ecological importance, relatively poorly studied (Clemann et al., 2008; Melville et al., 2009). One of them is Steppe agama (*Trapelus sanguinolentus*), a species representing an example of broadly distributed, successful and taxonomically debatable species (Wagner et al., 2011). Ethological studies on this species were previously conducted by Russian research teams (e.g., Bogdanov, 1960; Panov and Zykova, 1985, 1986, 2016; Zykova and Panov, 1986).

As studied species has developed signalling behavior, we aimed to describe and analyse signal displays and agonistic behavior of the Steppe agama. We analysed aforementioned behavioral patterns considering social structure and hierarchy of studied group with control for morphological characteristics, sex and lifespan in conditions of breeding facilities of in Prague Zoological Garden. Observed variability of signal displays was low and thus we focused mainly on quantitative analysis of simple push-up display as a prevalent signal type for both sexes.

METHODS

Studied species and environment

Steppe Agama (*Trapelus sanguinolentus*) is a small-sized, diurnal, semi-arboreal, oviparous agamid. This species exhibits a male-biased SSD with body length in males not exceeding 118 mm and maximal weight about 45 g (Bannikov, 1977). Male individuals from genus *Trapelus* in comparison with females of the same genus tend to have longer and wider heads with possibly better bite performance (e.g., Rastegar-Pouyani et al., 2013; Eskandarzadeh et al., 2015). In natural conditions, *T. sanguinolentus* males are territorial and their territories usually do not overlap, while female territories overlap widely (Zykova and Panov, 1986).

It inhabits great area of Central Asia from Russian Dagestan across Kazakhstan, Uzbekistan, Turkmenistan, Tajikistan, and Kyrgyzstan up to northern Iran and Afghanistan southward and up to north-western China (Xinjiang) eastward (Ananjeva et al., 2011). It is a generalistic species present in various habitats, mainly in arid and semi-arid areas up to 1200 m a.s.l. (Bannikov, 1977) with a preference for places with natural shelters like shrubs or rodent burrows (Clemann et al., 2008). Coloration is variable and can change quickly (Sigmund et al., 1994). It also changes during ontogenesis and exhibits male-specific blue coloration of ventral body parts (Bannikov, 1977). *T. sanguinolentus* exhibits a seasonal periodicity of activity, being active during spring/summer/autumn months and hibernating from late October to late February/early April (Szczerbak, 2003). Sexual maturity is reached in the second year of life, and in each season, two or three clutches of 4 – 18 eggs are laid (Bannikov, 1977).

We realized our study in the terrarium named “The Reptiles From The Central Asian Deserts,” situated in Prague Zoo (Czech Republic), which is designed as a small arid biotope covering a surface of 16.5 m² (Fig. 1). It has mixed sandy and rocky surface with basking places and artificial heating stones. General (ambient) illumination is provided by 5 high-pressure vacuum lamps (2 × 400 W, 3 × 150 W) and 2 LED panels (100 W each). These lamps are located 2.5 m above the surface. Local lighting and heating are provided by two Osram Ultra Vitalux 30 W lamps, suspended 40 cm above the surface, which are also a source of UVB radiation. In the exhibit there are 5 thermal spots, consisting of thermal cables 200 and 100 W, cast in artificial rocks. Ambient temperature in the terrarium varies between 30 – 37°C in summer, reaching 55 – 59°C in heated spots. The bottom is molded into an artificial dune by a set of upward tanks filled with 40 cm of fine sand. The sand is regularly



Fig. 1. Exposition “Reptiles of the Central Asian Deserts” terrarium from a frontal view.

sprinkled to keep the sand wet under the surface so that lizards can dig up burrows.

The daylight in terrarium is controlled during season from 9 up to 15 h per day. During two winter months (December, January) there is reduced lighting and heating regime adjusted to simulate conditions of winter hibernation. Besides *T. sanguinolentus* it is inhabited by two turtle species (*Agrionemys horsfieldii*, *Geochelone elegans*), two Gekko species (*Cyrtopodion fedtschenkoi*, *Teratoscincus scincus*), two lacertids (*Eremias arguta*, *E. grammica*), and three agamids (*Saara loricata*, *Paralaudakia lehmanni*, *Phrynocephalus mystaecus*).

All *T. sanguinolentus* individuals breed in Prague Zoo are descendants of 20 individuals sampled in the wild (exclusively by second author) in April 2012 on two localities in southern Uzbekistan: on steppe locality of Uban-Tau Hills north-west of Muzrabot (37°32'55.22" N 66°43'10.04" E), Surxondaryo Region and on a sandy desert locality of Kattakum (37°21'34.26" N 67°16'14.09" E), Surxondaryo Region, northward from the city of Termiz.

Data collection

Data collection started on 10th of February 2016 with releasing total number of 20 *Trapelus sanguinolentus* individuals (4 males and 16 females) of different age into exposition.

Prior to releasing of animals into terrarium, each individual was measured (SVL, to nearest 1 mm), weighted (to nearest 1 g), and marked in such way that every individual was recognizable to observer outside of exposition. Ethanol markers of three colors (red, green, blue) which did not influence health and physical condition of studied animals (see Bennett, 1999) were used for marking. We defined a simple code for each individual, according to number, color and body position of the marks.

As social-functioning patterns involved in visual signaling are placed on ventral body side, we placed color marks on dorsal body parts (shoulder blade, dorsal area near pelvis, hind limbs — thighs). As color marks on lizard's body parts became less visible after skin-shedding, we needed to renew them. Renewing of marks was repeated on 28th May 2016. Life expectancy (number of

days between hatching and death) was also recorded for each individual (even after experiment). In case of 1 male and 3 female individuals we could not assess life expectancy because of unknown date of hatching. We based our data collection on ad libitum observation (conducted by first author) (Altmann, 1974), recording all types of observed behavior. Nevertheless, in quantitative analysis presented in this study we focused exclusively on signalling and agonistic behavior of each individual. Lizards signalled mostly in a form of “push-up” displays. This signal occurred in both sexes. It occurred more frequently than any other display type and was always present in social situations connected with threat, aggression and possibly also with precopulatory (receptivity) signalling.

Thus, this signal type was fundamental for our quantitative analysis. Regarding agonistic interactions we analysed: i) interactions without direct physical combat (where individuals approached to each other and subsequently, one of the participating individuals repelled its rival by threat-displays) and ii) interactions where direct physical combat involving biting appeared (and in some cases led to bleeding injuries).

Given our time possibilities, we always realized one observational session per day. We conducted observational sessions according to Zoo opening hours from 9 am to 16 pm, with each session lasting 60 min. Observation was realized altogether in 59 days. No new individuals were added to the terrarium during the observational period.

Statistical analysis

We used a Clutton-Brock index (CBI) (Clutton-Brock et al., 1979). It is an index of dominance that consider for each individual both: (1) direct and (2) indirect wins and losses against other individuals (Bang et al., 2010). It is therefore used to assess relative success of each individual in agonistic encounters within studied group. With an exception of CBI index, that we calculated manually, all other data were analysed using R software version 2.15.1 (R Development Team, 2012).

First we compared by *t*-tests (with normal distribution of errors) if sexes differs in snout-vent length and weight. Than we compared sexes by generalized variation of this test also for life expectancy and number of performed signals that are integers (therefore, we used Poisson distribution of errors). Because sexes differs in number of performed signals we then run separate generalized mixed models with Poisson error distribution for males and females to determine if the number of performed signals (independent variable) is affected by body condition or life expectancy. Due to low number of indi-

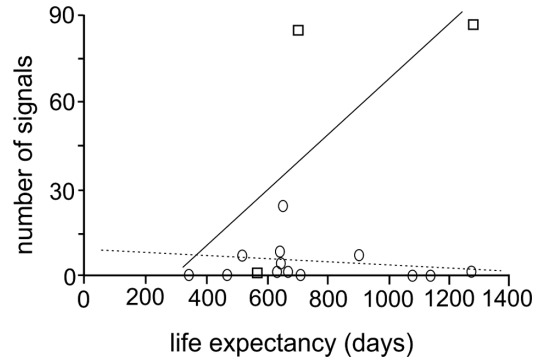


Fig. 2. Relationship between life expectancy and number of signals performed by males and females of *Trapelus sanguinolentus* during a year’s observation at Prague Zoo.

viduals, we compensate for overdispersion (present in all cases) by refitting the models using quasi-Poisson distribution. We used a level of significance with $\alpha = 0.05$

RESULTS

In our statistical analysis, we included a total of 20 individuals (4 males and 16 females). Males did not differ in studied group from females in respect to snout-vent length (*t*-test: $t = 1.17, P = 0.26$), when males measured 100 mm in average (SD = 10.30, SE = 5.15) and females 96 mm (SD = 4.89, SE = 1.22). Similarly weight was not significantly different between the sexes (*t*-test: $t = -0.06, P = 0.95$), when males weights 32.2 g (SD = 5.34, SE = 2.67) and females 32.4 g (SD = 6.69, SE = 1.67).

Life expectancy of males (mean = 866 days, SD = 383.54, SE = 221.35, $n = 3$) did not differ from life expectancy of females (mean = 749, SD = 272.86, SE = 75.47, $n = 13$) (GLM: *t*-value = 0.63, $P = 0.54$). However, number of performed signals differed between sexes with males signalling more (mean = 50.50, SD = 42.58, SE = 21.31) than females (mean = 5.44, SD = 7.81, SE = 1.95) (GLM: *t*-value = 4.44, $P < 0.001$). Number of performed signals was not associated with life expectancy in both sexes (GLM: males: *z*-value = -0.50, $P = 0.63$; females: *z*-value = 0.71, $P = 0.61$) while trend between sexes here was the opposite (Fig. 2). Interaction of life expectancy on factor sex was also not significant (GLM: *z*-value = 0.95, $P = 0.36$). Number of performed signals was significantly and positively associated with individual body condition in females (GLM: *z*-value = 3.42, $P < 0.01$) (Fig. 3), while in males the relationship was not significant (GLM: *z*-value = -0.32, $P = 0.78$) and had opposite trend, nevertheless interaction between

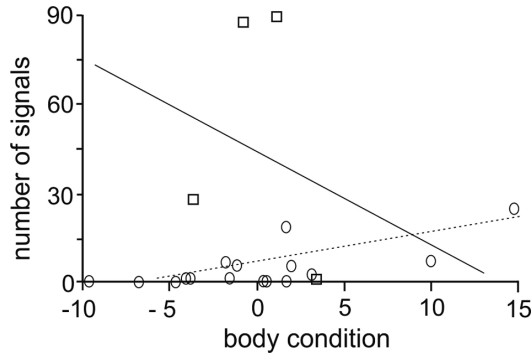


Fig. 3. Relationship between body condition and number of signals performed by males and females of *Trapelus sanguinolentus* during a year's observation at Prague Zoo.

body condition and sex was not significant (GLM: z -value = -1.60 , $P = 0.13$).

Most of observed agonistic interactions did not led to a direct physical combat (93% of total number of interactions for males, 86% for females). CBI values ranged 0.86 – 1.33 for males and 0.52 – 2.4 for females. In males, the association between CBI and frequency of performed signals was not significant (GLM: t -value = 1.33 , $P = 0.32$), whereas in female, higher value of CBI means more performed signals (GLM: t -value = 2.09 , $P < 0.05$).

DISCUSSION

In case of our study, we did not find significant association between frequency of signalling and life expectancy nor CBI nor individual body condition in males. However, our graphic results show higher value of CBI that is positively associated with higher rate of signalling, better physical condition that is negatively associated with higher rate of signalling and longer lifespan that is positively associated with higher rate of signalling. The first trend is corresponding while the second and third trends are opposite in comparison with trends found out for females. These results are probably influenced by low number of male individuals in the studied group. Therefore, further investigation is needed.

For females, better physical condition occurred in individuals that signalled more actively. Moreover, high rate of signalling was significantly positively associated with high value of CBI. We can hypothesize that females in better physical condition used their relatively high signalling activity and — as we observed in certain situations — better performance in direct combat to attain a “socially despotic” status and to achieve and defend their access to mates (see Wu et al., 2018).

Simultaneously, males, as an object of female – female competition, seemed to be stimulated in their mating effort by the same signal displays of “dominant” females that in this intersexual context could serve as receptiveness-related. This probably support findings of Panov and Zykova (2016) that consider push-up displays in *Trapelus sanguinolentus* as polyfunctional signals varying its meaning according to context of situation.

It is important to notice that condition is an index of body weight and body length and thus, a presence of egg clutches in abdominal cavities of these females can be an important factor here. We did not monitor number of eggs laid by particular females, therefore one of the possibilities of more signals and higher CBI in case in some females is their readiness to lay eggs and hence need for egg fertilization.

It seems probably that our initial precondition of male territoriality and polygynous reproduction that we applied in our experiment via highly female-biased sex ratio (4:1) of observed group strongly influenced intrasexual competition in both sexes. In our specific conditions females signal displays seem to be of a greater importance in comparison with males. Males probably faced less problematic conditions for establishing stable social relationships of “dominance” and “subordination” due to their low numbers. Hierarchical structure among males was established quickly after entry into the terrarium. On the other hand, females probably faced more competitive intra-sexual environment. This difference could arise from intersexually different numbers of individuals in terrarium.

Most agonistic interactions (for both males and females) in our study did not lead to direct physical combat. Nevertheless, the fact that agonistic interactions in females led to direct physical combat more frequently than in males (though this proportional difference was not particularly high) could reflect more competitive intrasexual environment in case of females. In this perspective, it is evident that resource-defence and/or mate-defence directed female – female aggression known for an Asian agamid *Phrynocephalus vlangalii* (Wu et al., 2018) can exist in *Trapelus sanguinolentus* in context of our study as well. Nevertheless, we have to be cautious with generalization of this statement as we studied a *T. sanguinolentus* group in altered conditions of terrarium. According to Zykova and Panov (1986), female *T. sanguinolentus* usually feed during the day-time in a zone of 1 to 14 m² and also irregularly use adjacent zones beyond this area. A total surface of terrarium chosen for our study is 16.5 m². In southern Uzbekistan, where ancestors (founder-individuals) of current breeding group in Prague Zoo were collected, *T. sanguinolentus* was never observed in large aggregations in one small area

(Velenský, personal advice). Thus, a society of 20 or more individuals in one terrarium with abovementioned surface could stimulate agamas to enhanced competition over reproductive opportunities that this species probably do not experience in nature.

Future studies on captive *T. sanguinolentus* could focus on seasonal periodicity of female signalling and agonistic behavior to test a precondition of reproductive cycle-influenced signalling activity and female – female aggression (see, e.g., Wu et al., 2019). Details on possible intersexual differences in signalling can be important as well (see, e.g., Patankar et al., 2013). The fact that simple push-ups were a strongly prevalent signal display in conditions of our study should be confronted with finding of Panov and Zykova (2016) that push-up displays are not a stable component of the agonistic or precopulatory behavior in *T. sanguinolentus* and various entirely different forms of signal behavior are included in behavioral repertoire of this species. Last but not least, detailed observation of egg laying and determining breeding females could provide interesting insight into motivation and following intensity of signalling behavior of *T. sanguinolentus*.

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REFERENCES

- Altmann J. (1974), “Observational study of behaviour: sampling methods,” *Behaviour*, **49**(3), 227 – 267.
- Ananjeva N. B., Guo X., and Wang Y. (2011), “Taxonomic diversity of agamid lizards (Reptilia, Sauria, Acrodonta, Agamidae) from China: A comparative analysis,” *Asian Herpetol. Res.*, **2**(3), 117 – 128.
- Bang A., Deshpande S., Sumana A., and Gadagkar R. (2010), “Choosing an appropriate index to construct dominance hierarchies in animal societies: a comparison of three indices,” *Animal Behav.*, **79**(3), 631 – 636.
- Bannikov A. G. E., Darevsky I. S., Ischenko V. G., Rustamov A. K., and Szczerbak N. N. (1977), *Key to Amphibian and Reptile Fauna of the USSR*, Prosveshchenie, Moscow [in Russian].
- Bennett D. (1999), *Expedition Field Techniques: Reptiles and Amphibians, Geography Outdoors*, Royal Geographical Society with IBG, London.
- Bogdanov O. P. (1960), *Fauna of the Uzbek SSR. Vol. 1. Amphibians and Reptiles*, Izd. AN UzSSR, Tashkent [in Russian].
- Clemann N., Melville J., Ananjeva N. B., Scroggie M. P., Milto K., and Kreuzberg E. (2008), “Microhabitat occupation and functional morphology of four species of sympatric agamid lizards in the Kyzylkum Desert, central Uzbekistan,” *Animal Biodiv. Conserv.*, **31**(2), 51 – 62.
- Clutton-Brock T. H., Albon S. D., Gibson R. M., and Guinness F. E. (1979), “The logical stag: adaptive aspects of fighting in reed deer (*Cervus elaphus* L.),” *Animal Behav.*, **27**(1), 211 – 225.
- Doody S. J., Burghardt G. M., and Dinets V. (2012), “Breaking the social – non-social dichotomy: A role of reptiles in vertebrate social behavior research,” *Ethology*, **119**, 1 – 9.
- Eskandarzadeh N., Rastegar-Pouyani N., Rastegar-Pouyani E., and Zinati L. (2015), “Sexual dimorphism in *Trapezus agilis agilis* (Olivier, 1807) (Sauria: Agamidae) from Tabas Region, Northeastern Iran,” *Russ. J. Herpetol.*, **22**(2), 123 – 127.
- Gardner M. G., Pearson S. K., Johnston G. R., and Schwarz M. P. (2015), “Group living in squamate reptiles: a review of evidence for stable aggregations,” *Biol. Rev.*, **91**(4), 1 – 12.
- Kappeler P. M., Barrett L., Blumstein D. T., and Clutton-Brock T. H. (2013), “Constraints and flexibility in mammalian social behaviour: introduction and synthesis,” *Philosoph. Trans. Roy. Soc. B*, **368**(1618), 1 – 10.
- Macedonia J. M. and Clark D. L. (2001), “Headbob display analysis of the Grand Cayman anole, *Anolis conspersus*,” *J. Herpetol.*, **35**(2), 300 – 310.
- Masters C. and Shine R. (2003), “Sociality in lizards: family structure in free-living King’s Skinks *Egernia kingii* from southwestern Australia,” *Zoologist*, **32**(3), 377 – 381.
- Melville J., Hale J., Mantziou G., Ananjeva N. B., Milto K., and Clemann N. (2009), “Historical biogeography, phylogenetic relationships and intraspecific diversity of agamid lizards in the Central Asian deserts of Kazakhstan and Uzbekistan,” *Mol. Phylogen. Evol.*, **53**(1), 99 – 112.
- Moore I. T. and Jessop T. S. (2003), “Stress, reproduction and adrenocortical modulation in amphibians and reptiles,” *Hormones Behav.*, **43**(1), 39 – 47.
- Oh K. P. and Badayev A. V. (2010), “Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies,” *Am. Naturalist*, **176**(3), 80 – 89.
- Ord T. J., Blumstein, D. T., and Evans C. S. (2002), “Ecology and signal evolution in lizards,” *Biol. J. Linn. Soc.*, **77**(1), 127 – 148.
- Osborne L. (2005), “Information content of male agonistic displays in the territorial tawny dragon (*Ctenophorus decre sii*),” *J. Ethol.*, **23**, 189 – 197.
- Panov E. N. and Zykova, L. Yu. (1985), “Comparative biology of Steppe and Caucasian Agamas (*Agama sanguinolenta*, *A. caucasica*) in Sumbar River basin,” in: *Flora and Fauna of the Western Kopet Dagh*, Ashkhabad: Ilym, pp. 185 – 204 [in Russian].
- Panov E. N. and Zykova L. Yu. (1986), “Notes on the *Agama sanguinolenta* behavior, 2. Everyday and communicative behavior,” *Zool. Zh.*, **65**(2), 235 – 246 [in Russian].
- Panov E. N. and Zykova L. Yu. (2016), *Rock Agamas of Eurasia*, KMK Scientific Press, Moscow.

- R Development Core Team** (2012), *R: a Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Vienna.
- Rastegar-Pouyani N.** (1999), “Analysis of geographic variation in the *Trapelus agilis* complex (Sauria: Agamidae),” *Zool. Middle East*, **19**(1), 75 – 99.
- Ricklefs R. E. and Wikelski M.** (2002), “The physiology/life-history nexus,” *Trends Ecol. Evol.*, **17**(10), 462 – 468.
- Sigmund L., Hanák V., and Pravda O.** (1994), *Zoologie strunatců*, Karolinum, Prague.
- Stuart-Smith J., Swain R., and Wapstra E.** (2007), “The role of body size in competition and mate choice in an agamid with female-biased size dimorphism,” *Behaviour*, **144**(9), 1087 – 1102.
- Szczerbak N. N.** (2003), *Guide to the Reptiles of the Eastern Palearctic*, Krieger Publishing Company, Malabar, Florida.
- Thompson G. G. and Thompson S. A.** (2001), “Behaviour and spatial ecology of Gilbert’s dragon *Lophognathus gilberti* (Agamidae: Reptilia),” *J. Roy. Soc. W. Austral.*, **84**(4), 153 – 158.
- Tokarz R. R.** (1985), “Body size as a factor determining dominance in stage agonistic encounters between male brown anoles (*Anolis sagrei*),” *Animal Behav.*, **33**(3), 746 – 753.
- Wagner P., Melville J., Wilms T. M., and Schmitz A.** (2011), “Opening a box of cryptic taxa — the first review of the North African desert lizards in the *Trapelus mutabilis* Merrem 1820, complex (Squamata: Agamidae) with descriptions of new taxa,” *Zool. J. Linn. Soc.*, **163**(3), 884 – 912.
- Wu Y., Ramos J. A., Qiu X., Peters R. A., and Qi Y.** (2018), “Female – female aggression functions in mate defence in an Asian agamid lizard,” *Animal Behav.*, **135**, 215 – 222.
- Wu Y., Whiting M. J., Fu J., and Qi Y.** (2019), “The driving forces behind female – female aggression and its fitness consequences in an Asian agamid lizard,” *Behav. Ecol. Sociobiol.*, **73**(73), 1 – 11.
- Znari M. and El Mouden E.** (1997), “Sexual dimorphism, reproductive and fat body cycles in Bibron’s agama (*Agama impalearis*, Boettger, 1874) (Sauria: Agamidae),” *Herpetologica*, **53**(4), 411 – 422.
- Zykova L. Yu. and Panov E. N.** (1986), “Notes on behavior of Steppe Agama. General pattern of biology, using of space and social behavior,” *Zool. Zh.*, **65**(1), 99 – 109 [in Russian].