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STEP BY STEP EXAMINATION OF TAIL MOVEMENT SEQUENCES REVEALS FUNCTIONAL DIFFERENTIATION IN SIGNALS OF SPOTTED TOAD-HEADED AGAMAS *Phrynocephalus guttatus* (GMELIN, 1789) (REPTILIA: AGAMIDAE)

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Phrynocephalus lizards are well-known for their remarkable tail movements. Possible function of such displays still remains unclear. We present a new approach for studying displays of *Phrynocephalus*, analyzing them as a sequence of movements. Here, we describe four tail movements of *Phrynocephalus guttatus* on the basis of observations on the population from the surroundings of Astrakhan, Russia. We found that movement sequences are structured and two main stereotyped patterns for movement sequences are suggested to distinguish depending on function they perform — aggressive or submissive. We also explain differences in preference and structure of movement sequences for lizards of different sex and age groups from the point of their social status.

Keywords: display; agonistic behavior; social behavior; visual signaling; lizard.

INTRODUCTION

Among other vertebrates, lizards preferably use visual signaling for social interactions and establishing spatial structure in populations (Ord et al., 2002). A complex behavior that consists of various body movements, such as raising and lowering of head and dewlap in the green anole *Anolis carolinensis* (Carpenter, 1967; Jensen and Rothblum, 1977), is called display. Different studies suggest that individuals exhibiting different social statuses are expected to develop differences in their display behaviors (Lopez et al., 2004; McElroy et al., 2007). Still, while various push-ups and dewlap demonstrations are described and revised thoroughly for many reptile taxa, other forms of signaling behavior remain studied poorly.

Toad-headed agamas (*Phrynocephalus* Kaup, 1825) are believed to have variety of movements for communication performing the function of maintaining the spatial structure of the population (Ross, 1989; Dunayev, 1996; Qi et al., 2011). Researchers have noticed relatively

simple repertoire of expressive postures and movements, that can easily be observed and recorded due to facts that these diurnal lizards have comparatively small individual home range, live in open space with preference of elevations and have simple spatial organization (Wang et al., 2004; Qi et al., 2012). The most evident behavioral element of toad-headed agamas is different tail curlings. Some authors suppose polyfunctionality of those tail movements pointing out the role in deterrence, aggression, submission (Ross, 1995; Qi et al., 2011; Peters et al., 2016) or on their spontaneous expression, with no apparent external stimulation. However some researchers (Panov et al., 2004) suggest that displays of toad-headed agamas may decrease nervous tension level. They regard these displays as a counteraction to nervous system overload. From their point of view displays are supposed to be stimulated endogenously. Nonetheless, signal function of these movements is not rejected, although it is supposed to play secondary role. Thereby, the issue of display's possible function remains unclear. In this paper, we describe the repertoire of *Phrynocephalus guttatus*'s tail movements and use a new approach for analyzing displays, considering them as movement sequences, that allows us to clarify features of their composition. Further, we investigate whether statistically significant differences in movement sequences exist between sex and age

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groups with special attention to possible function of different movements.

MATERIAL AND METHODS

Observations were made in July and August 2015 in a desert near the village of Dosang, Astrakhan region, Russia (46°54'41.22" N 47°55'36.81" E). In total, 35 mature individuals (15 males, 20 females) and 20 juveniles, of *P. guttatus* have been caught, measured and marked with individual number. We identified sexes by gently pressing the cloaca exposing males' hemipenis. Observations took place from 10:00 till 14:00 and from 15:00 till 18:00 every day in accordance with the conception of agamas' daily activity peaks (Adolph and Porter, 1993). Lizards' displays were recorded with a video camera from a distance of 3 – 5 m. We recorded 231 movement sequences: 143 were performed by males (9 individuals), 32 — by females (5 individuals) and 56 — by juvenile lizards (10 individuals) (Table 1).

We used Markov Chain Analysis in Past 3.14 (Hammer et al., 2001) to build transition matrixes of different tail movements (Table 2). Further analyses were performed using Statistica 8.0. Displays of at least five individuals were used to compose datasets. To avoid biased sampling, we analyzed five longest movement sequences from each individual for every dataset. To compare observations from different age and sex groups' samples we carried out χ^2 test, which performs pairwise comparison of transitions between different movements. To analyze role of different movements we examined context in which they were performed (Table 2). We distinguish four different situations taking place after lizard's display: 1 — fight (lizard rushing towards opponent), 2 — retreat of recipient (lizard flees after or during display), 3 — retreat of initiator (lizard flees after display), 4 — absence of reaction (absence of any external responses to signal). We used criterion of difference between two proportions to determine whether interaction context depends on display's structure.

RESULTS

Toad-headed agamas were performing displays in any position — lying or standing — so description of movements was made exclusively on the basis of tail movements. As a result, we distinguish four different tail movements in *P. guttatus* (Fig. 1).

1) Movement A — curled tail is slowly uncurled upwards. This movement was always single.

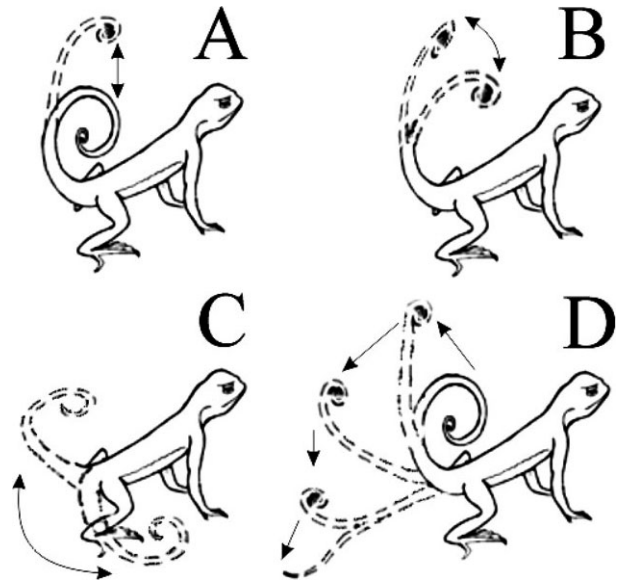


Fig. 1. Repertoire of tail movements by *Phrynocephalus guttatus* (modified from Dunayev, 1996).

2) Movement B — curled tail is slightly waved from side to side.

3) Movement C — tail lashing with effort from side to side. Movement C is often accompanied with digging-like movements of fore and hind limbs.

4) Movement D — tail is curled and uncurled upwards multiple times lowering gradually to the ground.

Contrary to the movement A, other three movements were observed to be repetitive (up to 14 times). To explore this complex behavior, we consider display of *P. guttatus* as a sequence of different tail movements (Table 1).

For a first look we analyzed sequences performed by males ($n = 13$) (transition frequencies differ significantly from expected frequencies, $P < 0.001$). As a result, we present a general scheme of transitions and describe a composition of different sequences (Fig. 2): sequence usually begins with movement A, it is followed by movement B, then movement B can be followed by any other movement almost equiprobably; first option is movement A occurs again, forming a cycle of A – B, that can be repeated multiple times; other options are movements C and D; in case of both movements C and D the next most frequent transitions are either movement A, thereby forming a longer cycle (A – B – C or A – B – D), that can also be repeated multiple times, or the ending of sequence.

The A – B transition is very stereotyped, these movements were rarely observed separately. At the same time movements C and D seem to be mutually exclusive, as

TABLE 1. Sequences of Tail Movements

Initiator	Recipient	Time, sec	Sequence	Comments
♀	♀	8.7	CABABC	Fight
♀	♀	6.9	ABABD	
♀	♀	6.5	ABD	retreat of initiator
♀	♀	12.7	ABABD	
♀	♀	11.2	ABABD	
♀	♀	5.7	ABD	
♀	♀	4	ABC	Digging-like movements with C
♀	♀	5.9	ABABD	
♀	♀	2.4	ABC	Digging-like movements with C
♀	♀	8.6	ABDABD	
♀	♂	3.7	ABC	
♀	♂	4	C	Fight, digging-like movements with C
♀	♂	4.7	ABCAB	Interrupted because of feeding behavior
♀	♂	7	ABABD	
♀	♂	9.1	ABABABD	
♀	♂	3	D	
♀	♂	5.7	ABD	
♀	♂	1.9	ABC	Retreat of recipient
♀	juv	10.6	ABD0	
♀	juv	7.1	ABABD	
♀	juv	6.1	ABD	
♀	juv	6.5	ABC	Retreat of recipient
♀	juv	10.9	CABCABC	Digging-like movements with C
♀	juv	3.7	ABC	Fight
♀	juv	7.8	ABABD	
♀	juv	1.1	B	
♀	juv	3.3	C	Fight
♀	juv	6.2	ABABC	Retreat of recipient
♀	juv	7.1	ABD	
♀	juv	4.7	D	Retreat of recipient
♀	juv	8.4	D	Retreat of recipient
♀	juv	1.8	C	
♂	♀	12.2	ABACD	Digging-like movements with C, retreat of recipient
♂	♀	30.4	ABCABCABCABCD	Fight, digging-like movements with C
♂	♀	8	ACABC	Fight, digging-like movements with C
♂	♀	7.2	ABCAC	Fight, digging-like movements with C
♂	♀	15.9	ABABCACAC	Fight
♂	♀	11.9	ABD	
♂	♀	12.4	ABABAC	Fight, digging-like movements with C
♂	♀	19.5	ABABDBABABD	
♂	♀	37.8	CABDBABDC	
♂	♀	12.1	CABABD	Retreat of recipient
♂	♀	19	CABABD	
♂	♀	6	CABC	Fight
♂	♀	20.7	ABCABDABD	
♂	♀	12.9	ABABDCAC	Fight
♂	♀	14.4	ABABABD	
♂	♀	17.6	ABABD	
♂	♀	13.2	ABD	

TABLE 1 (continued)

Initiator	Recipient	Time, sec	Sequence	Comments
♂	♀	5.3	ABD	
♂	♀	13.5	CABCABD	Retreat of recipient
♂	♀	4.2	BABA	Interrupted because of feeding behavior
♂	♀	24.3	ABDABDABD	
♂	♀	6	ABD	
♂	♀	23.4	ABDABABD	
♂	♀	11.2	ABABD	
♂	♀	6.6	ABD	
♂	♀	15.2	CABCABC	Fight
♂	♀	8.8	ABABD	Retreat of recipient
♂	♀	6.8	ABABA	Interrupted because of feeding behavior
♂	♀	29.1	ABABABCABABCABABC	Digging-like movements with C, fight
♂	♀	13.8	ABCABCABC	Digging-like movements with C, fight
♂	♀	2.5	ABC	Fight
♂	♀	8.7	ABABD	
♂	♀	6.4	ABABD	
♂	♀	7.7	ABD	
♂	♀	9.2	ABCABC	Digging-like movements with C, retreat of recipient
♂	♀	21.8	ABCABCABABABABC	Fight
♂	♀	4.1	ABC	Retreat of recipient
♂	♀	4.9	ABC	Retreat of recipient
♂	♀	12.3	ABD	
♂	♀	3.7	BABC	Retreat of recipient
♂	♀	8.2	ABD	
♂	♀	11.4	ACABD	Fight
♂	♀	4.8	ABCAB	
♂	♀	5.9	CBABA	Interrupted because of feeding behavior
♂	♀	12.8	DABD	
♂	♀	17.1	ABDABD	
♂	♀	7.6	ABD	
♂	♀	14.7	CABCABD	Retreat of recipient
♂	♀	8.6	ABD	Retreat of recipient
♂	♀	12	ABD	
♂	♀	16.1	ABACD	Retreat of recipient
♂	♂	18.9	ABABABD	
♂	♂	11.2	ABABD	
♂	♂	11.4	ABABABC	
♂	♂	12.4	ACABD	
♂	♂	26.4	CACABCABD	Digging-like movements with C
♂	♂	13.3	CABD	Digging-like movements with C
♂	♂	16	CABABD	Digging-like movements with C
♂	♂	16	ACABCAB	Digging-like movements with C, retreat of recipient
♂	♂	18.5	ACABD	Digging-like movements with C
♂	♂	25.3	ABACABAC	
♂	♂	6.2	ABD	
♂	♂	4.9	ABCABCABC	Fight
♂	♂	17.5	ABABDAB	
♂	♂	7.1	ABD	
♂	♂	28.4	ABCACAC	Digging-like movements with C, fight

TABLE 1 (continued)

Initiator	Recipient	Time, sec	Sequence	Comments
♂	♂	1.8	C	Digging-like movements with C
♂	♂	18.6	ABC	Digging-like movements with C, fight
♂	♂	16.3	ABABDABD	
♂	♂	4.8	ABA	
♂	♂	11.9	ABCABD	
♂	♂	20.1	CABCABACABAB	Retreat of recipient
♂	♂	3.3	BDBDB	Retreat of initiator
♂	♂	4.9	ABD	
♂	♂	13.3	ABACABD	Retreat of recipient
♂	♂	9	ABABD	
♂	♂	7.8	BCAD	Retreat of recipient
♂	♂	9.5	CABCABC	Fight
♂	♂	3.6	BDB	Fight
♂	♂	8.8	ACABC	Fight
♂	♂	13.3	ABABABD	
♂	♂	9	ABABAC	Fight
♂	♂	10.1	BABD	
♂	♂	4.8	ABAD	
♂	♂	5.9	BABD	
♂	♂	6.4	ABD	
♂	♂	16.1	ABABABCACAC	Digging-like movements with C, fight
♂	♂	4	ABC	Fight
♂	♂	6.8	ABABAC	Fight
♂	♂	15.7	ABABD	Retreat of recipient
♂	♂	19.9	ACABABACAC	Digging-like movements with C, fight
♂	♂	3.4	ABC	Fight
♂	♂	8.2	ABCAC	Fight
♂	♂	14.9	ABDABD	
♂	♂	11.6	ABD	
♂	♂	5.7	ABD	
♂	♂	19.7	ABABABACABCAC	Retreat of recipient
♂	♂	6.2	ABD	Retreat of recipient
♂	♂	25	ABABABABDABAC	Fight
♂	♂	3.2	AC	Fight
♂	♂	6.1	ABD	
♂	♂	5.1	ABD	
♂	♂	7.4	ABD	
♂	♂	7.8	ABD	
♂	♂	12.4	ABCABCABC	Digging-like movements with C, fight
♂	♂	9.3	ABCD	Retreat of recipient
♂	♂	12.5	ABD	
♂	♂	28.6	BABCABCABABDABABC	Fight
♂	♂	21.9	CABCABCABDABABC	Digging-like movements with C
♂	♂	15.3	ABABCABD	Retreat of recipient
♂	♂	14.7	ABDABD	
♂	♂	11.8	ACABAC	Fight
♂	♂	11.9	ABCABAC	Fight
♂	♂	15.7	ABABDABD	
♂	juv	2.6	C	Digging-like movements with C, fight

TABLE 1 (continued)

Initiator	Recipient	Time, sec	Sequence	Comments
♂	juv	22.1	ABACABCABD	Retreat of recipient
♂	juv	17.1	CABCABCAC	Digging-like movements with C, fight
♂	juv	29.5	ABABDABCABCABC	Digging-like movements with C, fight
♂	juv	10	ABABD	
♂	juv	14.1	ABDABD	
♂	juv	5.4	DAB	Interrupted because of feeding behavior
♂	juv	8.8	ABD	
♂	juv	14.2	ABDABD	
♂	juv	7.5	CABC	Digging-like movements with C, fight
♂	juv	8.2	ABD	
♂	juv	10.4	ABABD	
♂	juv	11.5	ABD	
♂	juv	11.6	ABD	
♂	juv	9.3	ABABD	
♂	juv	6.4	ABD	
♂	juv	6.5	ABD	
♂	juv	19.3	ABCABABCABCABC	Digging-like movements with C, fight
♂	juv	4.9	ABABC	Fight
♂	juv	13.8	ABD	
♂	juv	29.2	ABCABCABACABCABAC	Fight
♂	juv	14.7	ABD	
♂	juv	12.1	ABCABD	
♂	juv	4.4	ABD	
♂	juv	3.1	CABC	Digging-like movements with C, fight
♂	juv	9.1	ABABD	
♂	juv	7.3	ABD	
♂	juv	4.2	ABC	Fight
♂	juv	33	CABDABACABDCABABCD	Retreat of recipient
juv	♀	17.2	ABCABC	
juv	♀	17.3	ACABCABD	Digging-like movements with C
juv	♀	26.2	ABCABCACABCABD	
juv	♀	8.2	ACAD	
juv	♀	9.1	CABD	
juv	♀	5.3	ABAB	Retreat of initiator
juv	♂	2.5	DC	Retreat of initiator
juv	♂	18.8	BABABABABD	
juv	♂	7.3	ABD	
juv	♂	6	ABABAC	
juv	♂	14.1	ABD	
juv	♂	17.9	ABABDABD	
juv	♂	8.8	ABD	Retreat of initiator
juv	♂	6.3	D	
juv	♂	30.4	ACABDABABD	Digging-like movements with C
juv	♂	5.9	BABC	Fight
juv	♂	6.4	ACABD	Digging-like movements with C, fight
juv	♂	9.6	CABCAC	Fight
juv	♂	21	ABDBABABD	
juv	♂	4.9	C	Digging-like movements with C, retreat of initiator
juv	♂	17.1	ABABD	

TABLE 1 (continued)

Initiator	Recipient	Time, sec	Sequence	Comments
juv	♂	7	ABD	
juv	♀	10.4	ABD	
juv	♀	7.1	ABCAC	Digging-like movements with C
juv	♀	6.7	D	
juv	♀	8.2	ABABD	
juv	♀	10	ACABD	
juv	♀	2.2	D	
juv	♀	13.8	CABCABD	Retreat of recipient
juv	♀	5.7	ABD	
juv	♀	5.3	ABD	
juv	♀	1.2	B	
juv	♀	3	BABC	Digging-like movements with C, fight
juv	♀	6.4	ABD	Retreat of initiator
juv	♀	2.2	D	
juv	♀	6.3	ABD	
juv	♀	14.6	ABABABABC	Digging-like movements with C, fight
juv	♀	4.9	ABD	Retreat of initiator
juv	juv	16.7	ACABABACAC	Fight
juv	juv	3.7	ABC	Fight
juv	juv	3.3	ABC	
juv	juv	2.4	D	
juv	juv	3	C	Digging-like movements with C
juv	juv	14.8	ABACD	Retreat of recipient
juv	juv	7.7	ABD	
juv	juv	6.3	ABABC	Digging-like movements with C
juv	juv	9.6	CABCABC	Digging-like movements with C
juv	juv	3.7	C	
juv	juv	9.2	ABABD	
juv	juv	5.7	ABD	
juv	juv	4.3	BABA	
juv	juv	1.5	B	Retreat of initiator
juv	juv	11.3	ABABCABD	
juv	juv	5.4	ABABAB	Retreat of initiator
juv	juv	6.9	ABC	
juv	juv	1.2	C	Digging-like movements with C, fight

there were almost no transitions between them, it is also uncommon to observe both of them in the same sequence. Sequences always ended after movement C or D, with an exception of a few cases, when lizards interrupted their display to catch a prey.

Schemes of transitions derived from observations of movement sequences performed by females ($n = 5$) and juveniles ($n = 8$) have no fundamental differences from the general (male) scheme (transition frequencies also differ significantly from expected frequencies, $P < 0.001$). Comparison of movement sequences by χ^2 test of juveniles vs. females/males does not reveal significant differ-

ences ($\chi^2 = 19.9/23.4$, $df = 19/19$, $p = 0.4/0$, 22 respectively).

Since the A – B transition appears in almost every sequence, we can assume that it is a very stereotypical transition. Therefore, following situation is likely independent to presence of A and B movements in sequence. On the contrary, movements C and D appear separately, so it is reasonable to analyze following situation depending on the presence of movements C and D. Our data shows that sequences containing movement C more often led to an attack on recipient ($P < 0.001$). The most probable result with an involvement of movement D was absence of any reaction ($P < 0.001$).

TABLE 2. Transition Matrixes

Sex	A	B	C	D
Males ♂				
Transition probabilities				
A	0	0.877	0.113	0.009
B	0.329	0	0.311	0.36
C	0.942	0.021	0	0.037
D	0.789	0.083	0.128	0
Transition frequencies				
A	0	271	35	3
B	93	0	88	102
C	129	3	0	5
D	86	9	14	0
Juveniles				
Transition probabilities				
A	0	0.825	0.15	0.025
B	0.371	0	0.143	0.486
C	0.929	0.071	0	0
D	0.722	0.111	0.167	0
Transition frequencies				
A	0	74	8	1
B	31	0	19	29
C	27	1	0	2
D	24	4	4	0
Females ♀				
Transition probabilities				
A	0	1	0	0
B	0.3	0	0.3	0.4
C	1	0	0	0
D	0.933	0.067	0	0
Transition frequencies				
A	0	39	0	0
B	12	0	12	16
C	13	0	0	0
D	14	1	0	0

DISCUSSION

Our lizards reacted to large animals (human, dog, sheep, or bird) by either laying low or fleeing. Few observed sequences were performed with no apparent external stimulation and vast majority of displays took place in the presence of conspecifics, therefore we consider these movements to be signaling behavior. In general, our repertoire description corresponds to previous observations (Dunayev, 1996), thus supporting validity of distinguished movements. We didn't find any evidence if lizard's posture was involved in display performance. That may contribute to the hypothesis, that body position in toad-headed agamas is basically determined by morpho-anatomical features, probably participating in thermoregulation.

So far, peculiar behavior of toad-headed agamas was reviewed in complex, without thorough examination of different movements and the context of their usage (Ross, 1995; Dunayev, 1996; Qi et al., 2011). Only recently Pe-

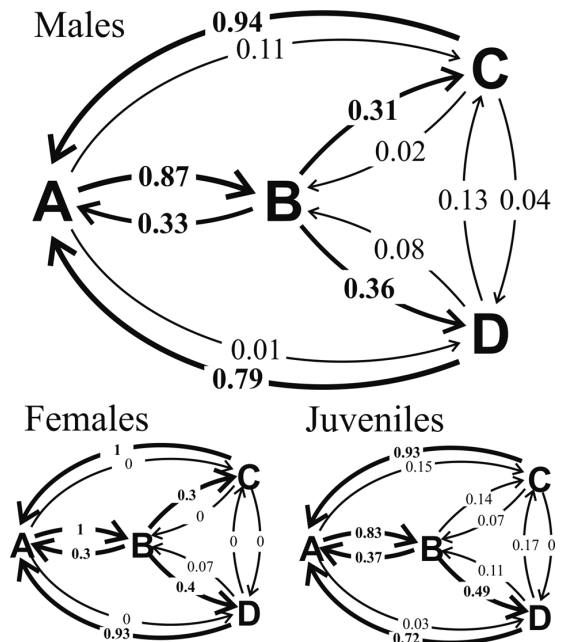


Fig. 2. Scheme of transitions between tail movements performed by males, females and juveniles. Thicker arrows indicate transitions with higher frequencies.

ters with colleagues (Peters et al., 2016) showed that social context affects tail display by *Phrynocephalus vlangualii* lizards. In this paper each particular movement was considered to be different display, so it is unknown whether lizards were able to perform movements in sequences. They described three different types of tail displays: tail lashing (corresponds to movement C described by us), tail coiling (movements A or B) and tail waving (movement D). They suppose that tail coiling and lashing by *P. vlangualii* are aggressive displays used in burrow defense and anticipate that the structure of these signals would vary between individuals in a manner that might reflect motivation or resource holding potential. Tail waving is suggested as a submissive display for juvenile lizards. In contrast to previous studies of lizards, female *P. vlangualii* were as likely to perform displays as males.

Our data clearly shows that movement sequences are structured. The A – B transition is very conservative independently of a context or lizards' age or sex. We have two possible explanations for this. The first is that A – B may function as an advertisement, indicating presence of the lizard on its territory. The second explanation corresponds to the hypothesis proposed for Australian agamas (Peters and Evans, 2003). The idea is that these movements may have introductive purposes, activating and enhancing recipient's perception for further signals. Noteworthy, such a signal proposed to be simple and to have

low frequency and long duration which is highly concordant to comparative characteristics of movement A.

Actual sequence may be composed of several cycles, still we propose to distinguish two simplified patterns: A – B – C and A – B – D. The A – B – C pattern often lasts longer and is composed of more iterations than A – B – D pattern possibly due to different levels of excitement and motivation, which may be higher in case of A – B – C pattern, resulting in a longer display or even triggering a fight. Thus, we consider A – B – C pattern as an aggressive. Though we observed only few attempts of mating, all of them occurred after performing A – B – C pattern, what is generally concordant with an idea that most of lizards do not have special mating behavior, and the success of force mating depends on physical condition of a male. Still our data is insufficient and further observations are needed to test this hypothesis in *P. guttatus*. We suppose that retreats of recipient may also be correlated with A – B – C, however it is statistically insignificant probably because of lack of data. On the contrary, performing A – B – D pattern more often results in absence of reaction or even retreat of lizard that performs a display so it may indicate low level of excitement. Because of that we consider A – B – D pattern as a submissive.

Despite the fact that we recorded more females than males, while trying to observe lizards evenly, majority of recorded displays were performed by males. So, it can be argued that signaling in *P. guttatus* is a prerogative mostly of males as a dominant group while females and juveniles may have a subdominant status. Thus, they can establish hierarchy during interactions in their groups what has already been proposed for *Anolis* and some other lizards (Mahrt, 1998; Jenssen et al., 2000; Radder et al., 2006). Further studies focusing structure of displays are required to elucidate potential functions and social context of this behavior.

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