

Motor Coordinations in the Behavior of the Toad-Headed Agama, *Phrynocephalus mystaceus* (Reptilia, Agamidae): Signal Functions and Endogenous Rhythms

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Abstract—Long-term observations and videotape recording of the behavior of territorial animals were used to study its temporal organization in male toad-headed agamas. The total recording time was 10.5 h, including nine continuous recordings of six mature males totaling more than 6 h. An analysis was made of the temporal pattern of complex tail movements, which proved to be a standard component of male behavior even outside of a social context. The basic element of this behavior is a set of stereotyped tail movements (a cycle) performed in a rhythmic sequence, designated a series. One cycle is approximately 7 s long, and the number of cycles per series varies in a broad range (1–20). The intensity of tail movements comprising the cycle gradually decreases within each series and in consecutive series; the series themselves gradually become shorter, whereas intervals between them increase. The cyclicity of series performance under stationary conditions indicates that this behavior is probably under constant endogenous control, which casts doubt on the concept that the stereotyped tail movements in male toad-headed agamas have primarily a communicative function.

One of the basic concepts of the ethological theory of instinct concerns so-called fixed action patterns, or inborn motor coordinations. By definition, a motor coordination is a manifestation of the genetic program that determines the concordant and consecutive action of functional elements in the muscular ensemble. In addition to distinct species specificity and a stereotyped pattern, these behavioral acts are characterized by spontaneity (automatism); i.e., they are often performed without any apparent reason but simply because the internal clock incites the individual to make such a “display.” This activity appears to be aimless and, hence, irrational.

These views, quintessential in the early variant of the classical ethological concept, were empirically confirmed in a number of studies and were eventually reconsidered from a more recent standpoint (Hinde, 1963). In recent decades, the idea of spontaneity in the performance of stereotyped behavioral acts has attracted the attention of many researchers dealing with the problem of the temporal organization of behavior (for review, see Kortmulder and Feuth-de-Bruijn, 1993; Nepomnyashchikh *et al.*, 1995).

This problem is of special significance for studies on the mechanisms of animal communication. Some specialists disagree with the traditional dialogue scheme of communication, “concrete message—adequate response” (within the framework of the stimulus—response concept), and offer an alternative interpreta-

tion: the behavior of each communicant is largely determined by its own previous actions rather than by signals received from the partner. In other words, the lines of behavior of the two communicants are interpreted as parallel temporal sequences of events organized as so-called Markov chains (for details, see Panov, 1978).

A feasible way to verify (or disprove) the ideas concerning the spontaneity of communicative behavior is to analyze the temporal distribution of some behavioral acts that are *a priori* considered to perform a signal function. A convenient empirical model for such studies can be found among species in which direct interactions of individuals are relatively rare, whereas the frequency of the aforementioned behavioral acts is fairly high (vocal signals in songbirds are an illustrative example).

It should be emphasized that a striking difference between the frequencies of the two classes of events is a warning that communication is not necessarily the main function of the observed stereotyped acts. It may well be that their basic purpose is to maintain an individual at a certain emotional level; in different terms, they allow an individual to expend “excess” energy and, thus, provide for self-regulation of its energy budget (Dol’nik, 1986). In this case, the signal function is no more than a by-product of the homeostatic function.

Taking this into account, we deliberately avoid the term “display” (which is a synonym of “communicative

signal”) in describing the behavioral stereotypes of the model species chosen for this study, i.e., the well-differentiated and extravagant tail movements in male toad-headed agamas, *Phrynocephalus mystaceus* Pall., 1776. Instead, the functionally neutral terms “stereotype” and “motor coordination” are used below.

The toad-headed agama satisfies a number of requirements for a model species used in such a study. The behavioral repertoire of these lizards is very limited, and the aforementioned tail movements are virtually the only behavioral component observed with a high frequency. The spatial structure of their population is specific: individuals and, therefore, the centers of their activity are spatially separated, and the possibility of long-distance visual contact is minimal due to the specific topographical features of the study area. Environmental disturbances were rare during the observation period, and conditions in the foci of activity of individual animals remained constant from the observer’s standpoint. This provided a basis for the assumption that, in this situation, the series of tail movements regularly alternating with periods of inactivity were spontaneous; i.e., they were determined by endogenous processes rather than stimulated by some external factor.

The same tail movements are observed during agonistic contacts between individuals of the same sex and during male–female interactions, which is evidence for their signal (communicative) function.

The first part of this study is devoted to the detailed description and structural analysis of stereotyped tail movements. The hypothesis that this behavior is governed by some endogenous rhythms is discussed in the second part.

The peculiar tail movements of toad-headed agamas were first described by Polynova (1982). Unfortunately, she arbitrarily divided this integrated behavioral pattern into a series of fragments and subsequently considered each fragment separately; as a result, this pattern was markedly distorted in her description. However, in defense of this author, mere visual observations, without videotape recording and image processing, are insufficient for adequate analysis of such a complex stereotype.

MATERIALS AND METHODS

Studies were performed in Dagestan between July 7 and 13, 2002. In the vicinity of Makhachkala, a dense isolated population of toad-headed agamas inhabits the so-called Kumtorkala sand hill (approximately 2 km² in area). The hill is 60 m high, and its central (top) part is bare, whereas the depressions dividing the lower parts of its slopes are covered with sparse vegetation in which giant ryegrass and wormwood prevail.

Toad-headed agamas occur mainly in these vegetation-covered depressions and also in adjoining bare areas but avoid the middle and upper parts of the hill slopes. The field of view in such habitats is limited, so that visual contact between individuals occurs sporadically. Thus, the microrelief and vegetation in the preferable habitats of toad-headed agamas of the Kumtorkala population sharply differ from those of habitats typical of the species as a whole.

In females, an individual zone of activity is more or less circular, approximately 20 m in diameter, with the burrow in the center. As the sandy ground easily caves in, the female has to dig a new burrow every two to three days, at a distance of up to 6 m from the old burrow. Thus, the activity zone is displaced, remaining within an area ca. 30 m in diameter. This area is the home range of a given female. Individual zones of activity virtually never overlap, whereas the home ranges may overlap to some extent. The activity zone has a size allowing the female to keep it under visual control. No agonistic interactions of females were observed, although the owners of neighboring home ranges often approached each other to within a distance of less than 2 m.

In juvenile males, the spatial pattern and size of home ranges are the same, and they are distributed independently of female home ranges. Young males generally avoid contact with one another, although an occasional fight may occur. Attempts to come in contact with a female were rare.

The zones of activity of mature males were more than 100 m in diameter and markedly overlapped. Each zone covered several home ranges of females and juvenile males. Mature males did not make burrows but simply buried themselves in the sand during the hot time of day and for the night, without preference for any definite place. Their movements over the home range resembled patrol work: the animal periodically moved for 10–100 m, remaining in each new place for several minutes to one hour, and this continued throughout the daily activity period. Neither permanent centers of activity nor preferable patrol routes were revealed.

Mature males could not see each other most of the time. Their visual contact was rare (only a few instances over the activity period) and was virtually always accompanied by mutual aggression. Responses of mature males to the presence of juvenile males had no definite pattern, and we failed to reveal the factors provoking their aggressive behavior. Coming in contact with females, mature males often behaved indifferently. In some cases, a male remained in the center of the female’s activity zone or made an attempt at mating.

Our observations concentrated on mature males. Their tail movements have a more differentiated pattern

and are repeated with a much higher frequency than in animals of other sex and age groups. Due to well-manifested territoriality, mature males are spatially segregated from one another, and the possibility of long-distance visual contact between them (and with juveniles and females) was largely limited by physical barriers (rough terrain, shrubs, and grass stand). Hence, the situation during observations and video recording of their behavior remained generally unchanged.

To accomplish the purpose of this study, it was necessary to continuously record the behavior of a male on videotape over periods of time that markedly exceeded the typical duration of intervals between two consecutive series of tail movements. Recording was suspended upon any change in animal behavior (and, apparently, state of mind) that was caused by some external factor, e.g., when the male took a run to catch an insect, attacked a conspecific male entering its home range, or visited a center of a female's activity.

We used a Sony CCD TR570E video camera with a 12× zoom lens and a 48× digital zoom. Animal behavior was recorded throughout the activity period, in the morning and the earlier part of the day (the onset and cessation of activity on each particular day depended on air temperature and wind velocity). The total recording time was 10.5 h, including nine continuous recordings of six mature males that varied in length from 6 to 85 min (in the aggregate, more than 6 h). Observations made between the breaks caused by the aforementioned external factors were used to analyze the putative endogenous rhythms. To this end, we studied 17 recordings that varied from 8 to 33 min (a total of more than 5 h) and included 130 episodes of tail movements (together with 23 additional episodes recorded in the period of animal exposure to external stimuli).

To analyze tail movements in the course of social interactions, we videotaped three episodes of agonistic contact between males and four interactions of three different males with females (a total of 75 min). In addition, the behavior of three solitary juveniles was recorded for a total of 129 min. One episode of contact between a mature male and one of these juveniles could be normal or homosexual mating.

Video recordings were processed using the Pinnacle Studio computer program at the Laboratory of Comparative Ethology and Biocommunication, Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences.

The motor coordination under study is a complex pattern of movements (referred to as a series) based on rhythmic repetition of their stereotyped sequences (cycles) (see below). In the course of data processing, we analyzed correlations between (1) the intensity of tail movements (wagging) in a given cycle and its ordinal number in the series, (2) the number of cycles in a series

Table 1. Numbers of cycles in series observed in different situations

Situation	Number of cycles in series	
	≤5	>5
Male patrolling its home range	26	0
Agonistic male–male interactions	9	0
Male–female interactions	16	0
Male remaining in the same place*	44	35

* The frequency of series consisting of more than five cycles was significantly higher than those recorded in all other situations ($p < 0.01$).

and the ordinal number of this series in the record, (3) the length of a series and its ordinal number in the record, and (4) the duration of an interval between series and its ordinal number in the record. We considered only continuous series and records, i.e., those not interrupted by any extraneous activity (e.g., hunting). The series consisting of less than eight cycles and the records including less than eight series were excluded from the analysis. As the intensity of tail wagging was graded visually, the distribution of this and several other parameters differed from the normal distribution. Hence, the nonparametric Spearman rank correlation coefficient (R) was used for statistical analysis.

The parameters listed above varied markedly even in the same animal: the number of series per record varied from 4 to 12; the number of cycles per series, from 2 to 20; and the length of a series, from 9 to 194 s. Hence, correlations were calculated for each record and series separately, without pooling the data on different animals.

For one lizard (male no. 1), a fairly long record was obtained, which covered the period from 11:12:00 to 11:34:24 (July 7, 2002). This allowed us to perform two-way ANOVA for the dependence of the intensity of cycles on their ordinal number in the series (factor 1) and the ordinal number of the series in the record (factor 2). Series 1–4 were used, and only the first six cycles in each series were analyzed.

To compare the distributions of the number and intensity of cycles in the series recorded in different situations, Fisher's exact test was used. All statistical comparisons were made using the Statistica 6.0 program package (StatSoft Inc.).

RESULTS

Stereotyped Tail Movements: Temporal Pattern

This element of behavior in toad-headed agamas is based on a set of stereotyped tail movements (a cycle) performed in a rhythmic sequence (a series). One cycle

Table 2. Attenuation of tail movements recorded in male toad-headed agamas in the absence of external stimulation

Time of the beginning and end of series and the total record	Statistical assessment of dependence in pairs of parameters		
	parameter	spearman coefficient, <i>R</i>	probability of error, <i>p</i>
Series	1. Intensity of wagging in the cycle		
11.13.47–11.16.32	2. Ordinal number of the cycle	–0.96	<0.001
11.48.54–11.49.53		–0.96	<0.001
11.52.31–11.54.04		–0.73	0.007
11.58.16–11.59.23		–0.97	0.007
12.21.24–12.22.50		–0.83	0.002
Record	1. Number of cycles in the series	–0.66	0.070
11.12.00–11.34.24	2. Ordinal number of series in the record		
	1. Duration of the series	–0.71	0.047
	2. Ordinal number of series in the record		
	1. Duration of intervals between series	+0.86	0.014
	2. Ordinal number of the interval in the record		

is approximately 7 s long, and the number of cycles per series varies in a broad range. In an extreme case, a series consists of only one cycle, which may be as if incomplete. During social interactions, series usually include no more than five cycles. Long series (more than 5 and up to 20 cycles) are observed only in mature males in situations where they remain for a long time in the same place under apparently unchanging conditions (Table 1). In the longest series, the cycles are often separated by short periods of locomotor activity (the animal turns around, walks forward, or makes a short run).

In mature males, one cycle can be reduced to tail coiling and uncoiling repeated three times. As a rule, tail movements are more differentiated in the first cycle of a series (Fig. 1). In the first movement, the animal coils the tail very rapidly and slightly wags its distal (tightly coiled) part from side to side. After uncoiling the tail, the animal extends it at an angle of about 45° to the substrate, remaining in this posture for some time. In the second movement, the tail is coiled in two stages (coiled, slightly loosened, and tightly coiled again); upon uncoiling, it is directed almost vertically. After the third coiling, when the distal part of the tail is directed forward, the animal begins to wag it. These rapid lateral movements are repeated as the tail is extended posteriorly, so that it eventually moves parallel to the substrate. The picture is most impressive at the middle stage of wagging, when the animal extends the tail almost vertically and moves it with an amplitude of up to 180° (Fig. 2).

The amplitude and intensity of tail movements gradually decrease in the following cycles of a series. The second cycle is often reduced to three instances of “simple” coiling, with wagging observed only after the last one. The number and especially the amplitude of

these lateral tail movements further decrease in the subsequent cycles. The same applies to tail coiling: in the last cycles, the animal merely raises the tail three times virtually without coiling it. This attenuation of movements is especially conspicuous when the male remains for a long time in the same place and is inactive except for the above tail movements.

Variation in the Stereotyped Pattern of Tail Movements

When the entire sequence of movements is reproduced (which is often observed only in the first cycle of a series), no apparent differences in their performance by different males can be distinguished. In other words, the motor coordination at the peak of its manifestation is species-specific. On the other hand, the rate of tail coiling and wagging gradually decrease in most series, with rare exceptions (see above). We estimated the intensity of tail wagging on a five-grade scale: grade 0 corresponded to the absence of wagging, and grade 4 showed that up to six lateral tail movements with an amplitude of about 180° were recorded. Using this approach, we studied the attenuation of tail wagging in four randomly chosen consecutive series performed by the same male on July 7. Our record looked as follows:

Onset of activity 11:56; seven cycles (total duration 50 s): 4, 3, 3, 3, 4, 3, 0; inactivity period 74 s.

Onset of activity 11:58; nine cycles (67 s): 4, 3, 3, 3, 2, 2, 1, 1, 0; inactivity period 9 s.

Onset of activity 11:59; three cycles (23 s): 1, 1, 0; inactivity period 27 s.

Onset of activity 12:00; three cycles (22 s): 1, 1, 0; inactivity period 80 s, then male runs away.

Data on the temporal pattern of this male's behavior were processed statistically, and the results are shown

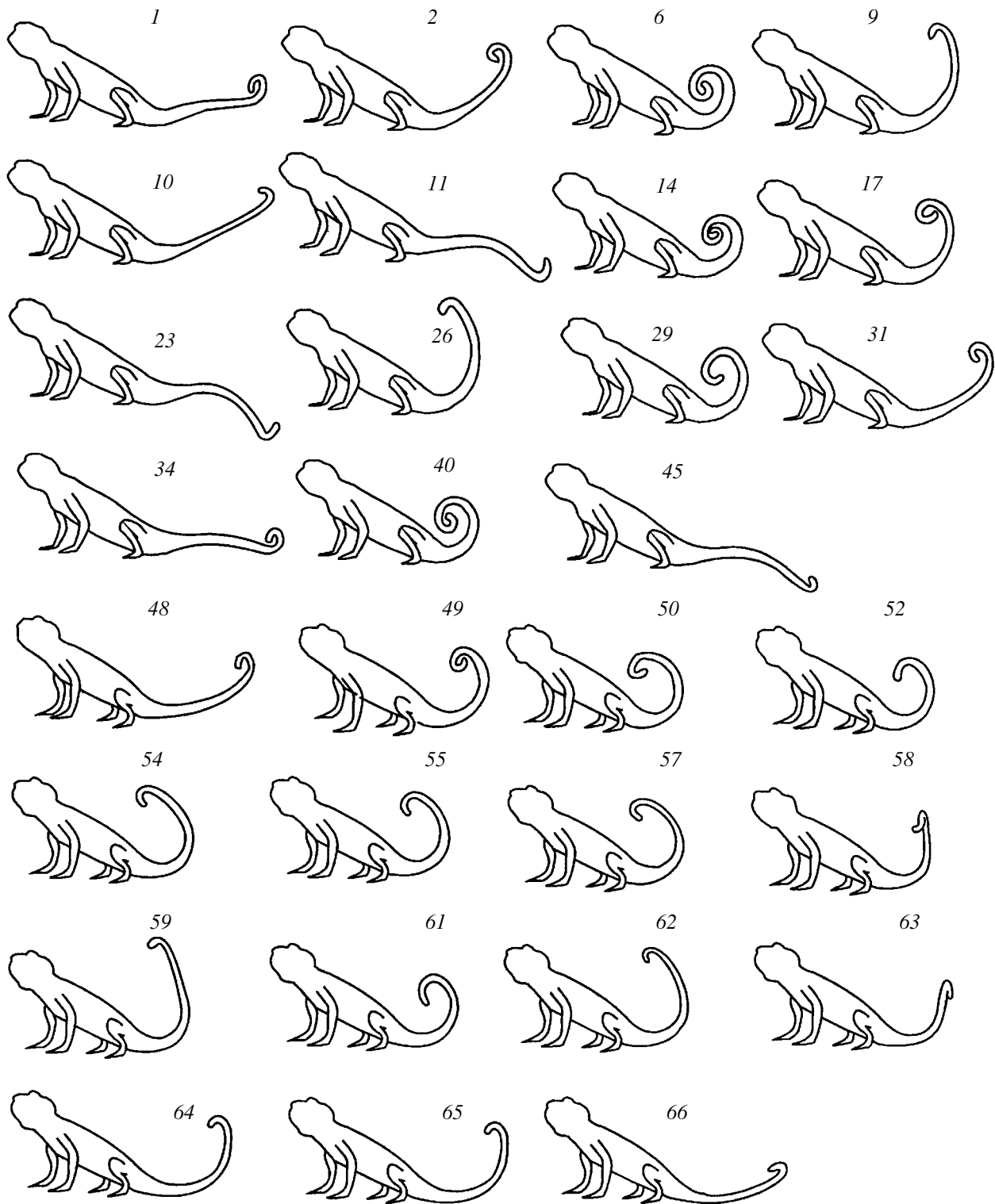


Fig. 1. Cycle of tail movements in a male toad-headed agama (without final intensive wagging). Figures show the ordinal numbers of frames in a continuous recording made at 25 frames per second. The male coils its tail (1-6) and then extends it at a certain angle to the substrate (10). Tail coiling is repeated four more times, twice completely (11-17 and 31-40) and twice incompletely (26-28 and 49, 50), and the cycle is finished with lateral tail movements (56-65). In deleted frames (e.g., 7-9), the tail is in the same (or almost the same) position as in the previous frame (e.g., 6).

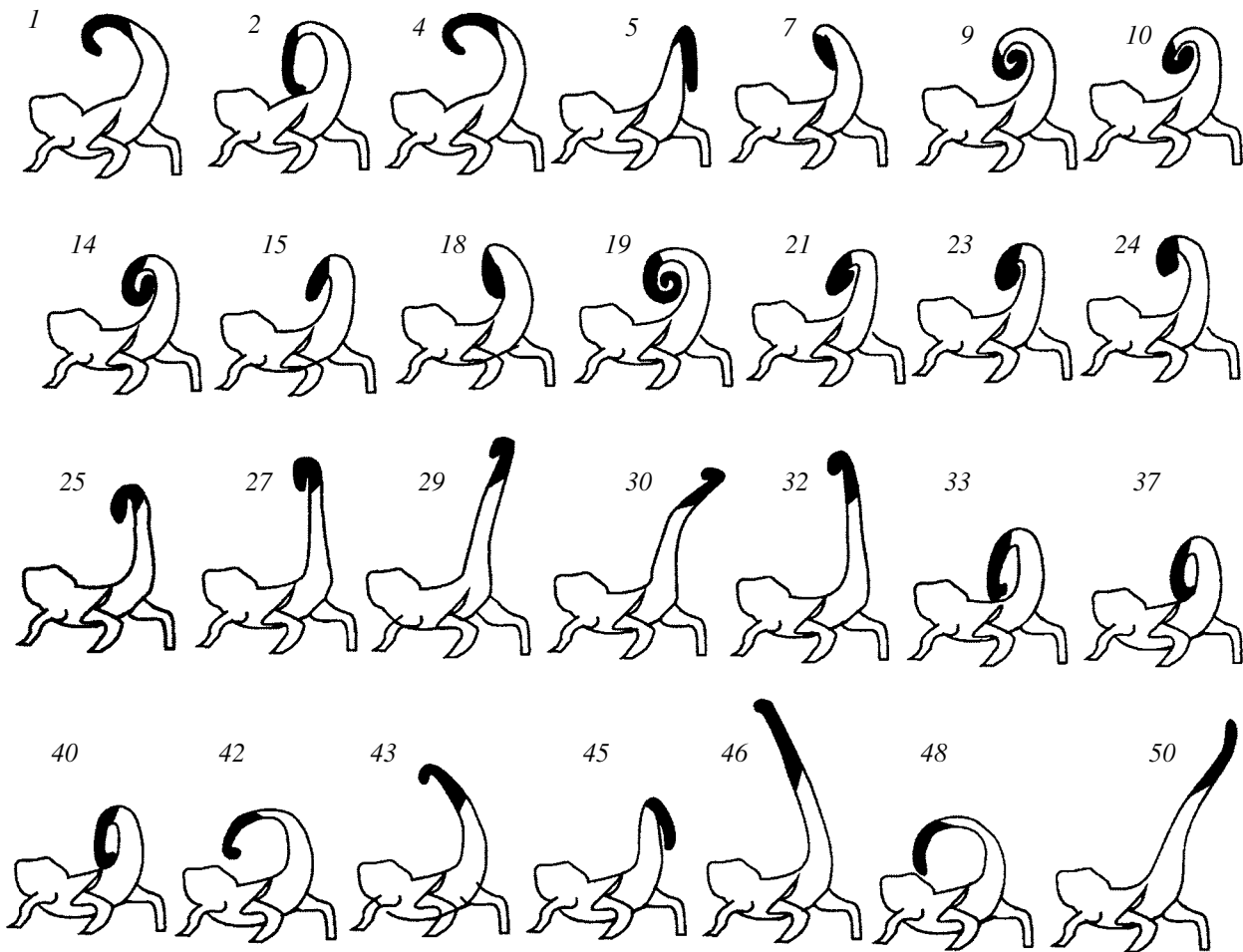


Fig. 2. Visual effect produced by movements of the tail with a contrasting color pattern (white on the ventral side and coal black at the tip). The cycle consists of incomplete tail curling (1–4), complete curling (7–24) with the tail then raised high above the substrate (27–32), and a second complete curling (33–37) followed by intensive wagging (43–50). Lateral movements of the coiled distal part of the tail are readily seen (7–10, 15–18, and 21).

in Table 2. As follows from this table, a statistically significant inverse correlation between the intensity of movements in a cycle and its ordinal number is observed in the series consisting of more than seven cycles. In other words, the intensity of tail wagging decreases as the cycles follow one another in a series. Likewise, both the number of cycles in a series and the duration of a series correlate inversely with its ordinal number in the record (i.e., the series gradually become shorter in the course of their performance). On the other hand, the intervals between series increase, as follows from a direct correlation between the duration of an interval and its ordinal number. According to the results of ANOVA, tail wagging is attenuated both in consecutive cycles of a series and in consecutive series:

Ordinal number of a cycle in a series: $df = 3$, $F = 7.35$, $F_{crit} = 2.90$; $p = 0.006$.

Ordinal number of a series in the record: $df = 5$, $F = 5.12$, $F_{crit} = 3.27$; $p = 0.003$.

These descriptions concern only the stereotyped tail movements of mature males. Mature females simply raise the tail and slightly coil it at the tip, without wagging. The same applies to juvenile males, in which, however, slight wagging (grade 2) can be detected in rare cases. This fact indicates that the motor coordination of interest may be under hormonal control.

Stereotyped Tail Movements As Related to Other Components of Behavior

The above sequences of tail movements are independent of the animal's posture at the moment of their performance. The animal may be standing (with all legs straightened), sitting like a dog, or lying flat. Tail movements may be observed even when a male buries itself

in the sand so that only the head and the distal part of the tail remain above the surface.

During aggressive encounters between males, an animal often moves the tail while digging the substrate with its legs: both the fore and the hind legs of the same side of the body abruptly move to the rear (usually twice), throwing out jets of sand, and then the legs of the other side do the same. In another form of agonistic behavior, a male raises and lowers the anterior part of the body by straightening and bending the forelegs, with the lower jaw touching the substrate when the body is down. These movements are analogous to the push-ups recorded in rock agamas (Panov and Zykova, 1999). A mature male makes them immediately before dashing toward an adversary and attacking it. Thus, the digging movements and push-ups are definitely related to aggression, whereas the stereotyped tail movements are invariant in the cases of aggressive, sexual, and neutral behavior. In other words, the system of motivation underlying this stereotype is different.

This stereotype is most closely related to the overall locomotor activity. In many cases, a short walk or crawling, often with a turn around the vertical, precedes a series of tail movements. The same acts or longer runs for a distance of up to 10 m may take place between two cycles in a series of tail movements. Such cases were regarded as so-called compound series. For example, the following sequence of events was recorded on July 14, 2002: 4, 3 – a walk forward – 4 – a run – 3, 2, 2 – a run – 3, 3, 3, 2 – a walk forward and a 90° turn – 2, 1, 1. Making the most intensive tail movements, the male often treads on the substrate with all four feet, remaining in the same place.

The above relationship is distinctly manifested when the male patrols its home range (see below): after each run to a new place, the male stops for 1–3 s and performs a short series of tail movements.

Very intensive tail movements, with wagging assessed at a high grade, are always observed when the animal catches and consumes prey.

Specific Features of Tail Movements in Different Situations

The pattern of stereotyped tail movements in a mature male engaged in conflict with another male or interacting with a female is virtually the same, contrary to the opinion expressed by Polynova (1982). However, when a male prepares for an attack on an adversary, the series of tail movements usually begins not with coiling but with intensive wagging (grade 4) involving the posterior part of the body, with the animal pressing its chest against the substrate and throwing sand with its hind legs (see above). In the next cycle, which is often the last in the series, tail coiling is often interrupted and is not followed by wagging. Thus, such a short (“defi-

Table 3. Relative intensity (%) of tail wagging in the first cycles of series observed in different situations

Situation	Intensity of wagging (grade)		
	4 or 3	<3	number of series, <i>n</i>
Male patrolling the home range	51.4	48.6	37
Agonistic male–male interactions*	87.2	11.8	13
Male–female interactions	46.1	53.9	26
Male remaining in the same place*	60.6	39.4	71

* The intensity of wagging in the first cycles of the series was significantly higher than in all other situations ($p < 0.02$).

cient”) series consists of two incomplete cycles, the first without coiling and the second without wagging. A similar series is sometimes performed by a male dealing with a female, although the intensity of wagging is usually lower (grade 3) than in the former case.

When a male periodically moves its tail while remaining in the same place in the absence of apparent external stimuli, the pattern of these stereotyped movements does not differ from that accompanying both types of social interactions. The difference concerns the intensity of tail wagging, which is usually lower even in the first cycle of a series (Table 3). Moreover, the series proper may be very long (which is never observed during social interactions), with the intensity of all tail movements decreasing to the absolute minimum.

These data show that such an important parameter as the number of cycles per series largely depends on the situation in which the corresponding behavior is observed. As follows from Table 1, short series of one to three cycles obviously prevail in both variants of direct social interactions (male–male and male–female). The same applies to the behavior during out-breaks of locomotor activity, when the male systematically moves over its home range. These movements resemble patrolling, although they are not aimed at protecting the boundaries of the home range, as is the case with some other agamid species (Zykova and Panov, 1986).

In the above situations, the animal appears to reduce the number of cycles in a series to save time for purposeful forms of behavior, such as chasing and attacking an adversary or establishing contact with a female. Conversely, when the male remains in the same place and is not exposed to external stimulation, a series may consist of 12, 14, and even 20 cycles. Thus, series are generally longer when tail movements appear to be spontaneous and shorter when these movements per-

form a communicative function (male–male and male–female contacts) or a putative social function (patrolling). As follows from Table 1, this difference is statistically significant.

Repetition of the series of tail movements under stationary conditions (the animal remains in the same place in an unchanging environment) indicates that this behavior may be determined primarily by endogenous rhythms (see Rogovin, 1989).

DISCUSSION

The data confirm the validity of classical ethological concepts concerning a class of behavioral stereotypes that are generally considered to perform only a signal function (or such a function as the main one). In agreement with this viewpoint, the stereotypes of interest are social adaptations (beneficial to an individual as a member of a population). In classical ethology, they have been considered primarily in the context of discussion regarding the structure of individual behavior and have been assigned a homeostatic, “antistress” function providing for regular relief of tension in the nervous system. According to this concept, these stereotypes reflect cyclic processes in the nervous system; hence, it is normal that they are performed in the absence of external stimulation, as spontaneous acts.

The above views are based on the energy model of motivation (Hinde, 1963). Its main postulates are as follows: (1) readiness to perform an act increases proportionally to the time elapsed after the previous performance of this act, and (2) the intensity of performance decreases in a series of repeated acts, probably due to relief of nervous tension in this course.

This fully applies to the temporal pattern of stereotyped tail movements in male toad-headed agamas. The intensity of tail wagging gradually decreases within each series and in consecutive series; the series proper gradually become shorter, whereas the intervals between them increase (Table 2). These facts suggest that the motivation underlying this behavioral act is attenuated in the course of its repeated performance. Furthermore, periodic tail movements occur in the absence of apparent external stimulation, with the number of cycles per series being greater than in the situations where they may be regarded as a component of purposeful communicative behavior (Table 1). It is noteworthy that the animals are ready to perform these movements in response to unspecific stimuli (e.g., while catching and consuming prey) and that they are an indispensable component of locomotor activity. On this basis, it can be assumed that stereotyped tail movements are a manifestation of general arousal (Panov, 1978; Rogovin, 1989) and are governed by endogenous rhythms.

In view of these data, it is logical to question the validity of the concept that the stereotyped tail movements in male toad-headed agamas perform primarily a signal function, although at first glance this is self-evident and any doubt appears groundless. The intricate pattern of these movements and the visual effect they produce contradict the idea that they merely reflect the dynamics of nervous processes and have no definite address.

However, there is ample evidence that the signal function is absolutely subordinate in this case (see Rogovin, 1989). Only a few out of many dozens of series of tail movements are associated with real social interactions, and these interactions are successfully accomplished without preliminary “tail signaling.” In toad-headed agamas, the male forces the female to mate, and success depends only on its ability to run fast and hold the female tight. However, the series of intensive tail movements are observed immediately after mating, when they appear to be purposeless.

The same applies to the aggressive behavior of males. The aggressor moves its tail while several meters (in some cases, several tens of meters) away from its adversary. These movements *per se* do not make the other male flee, and this allows the aggressor to run it down in the next moment. Tail movements do not precede the attack proper but are performed while the male bites its fallen adversary and immediately after that, when the latter runs away. In both these situations, tail signaling appears purposeless: the fallen lizard simply cannot see these movements, and signaling in the second case is obviously behind time. Thus, stereotyped tail movements during agonistic and sexual interactions reflect increasing general arousal during immediate contact with another individual rather than inform the latter about the intentions of the active partner.

Periodic tail movements of a solitary male may be regarded as a kind of beacon informing potential intruders that the home range is occupied. In this respect, as well as in the temporal pattern, these movements appear to be largely similar to bird songs. However, it should be noted that the population studied inhabits sandy areas with a well-developed plant cover and males usually perform the series of tail movements while sitting at the base of a shrub or amid tall grass, where they are poorly visible. Under such conditions, active protection of home ranges (see above) is apparently the main factor maintaining reliable segregation of territorial males. In any case, visual signals are a much less effective means of distant communication than acoustic signals (bird songs).

A strong argument in favor of the idea that signaling is the main function of stereotyped tail movements is circumstantial and, hence, cannot be fully corroborated. It issues from the concept of ritualization,

according to which excessive forms of behavior evolve on the basis of relatively simple structures and eventually become components of species-specific communicative systems. In the case of toad-headed agamas, as in many other cases, an idea suggests itself that their tail coloration (a contrasting black-and-white pattern, which is conspicuous against the background of pale desert colors) and tail movements accentuating this species-specific identification mark are a result of coupled evolution.

The validity of this reasoning is confirmed by the fact that sharp lateral tail movements (with the tail being straightened) are observed in rock agamas of the genus *Laudakia*, which are closely related to toad-headed agamas (*Phrynocephalus*). These poorly differentiated movements (wagging) are performed in the state of general arousal and can be regarded as an accessory element of the behavioral repertoire, similar to the aforementioned push-ups in toad-headed agamas. It appears that the evolution of communicative signals in these two groups followed different pathways: in toad-headed agamas, it provided for the development of complicated tail movements (Rogovin, 1989; Semenov, 1997); in rock agamas, it favored differentiation of push-ups and related morphological structures, such as the gular sac with its conspicuous and species-specific coloration (Panov and Zykova, 1997, 1999). From the evolutionist standpoint, this scenario is conventional and, hence, looks plausible. Unfortunately, the concrete mechanisms of corresponding evolutionary transformations appear to be inexplicable today (provided we give up the notorious theory of sexual selection, which we consider to be largely imaginary).

Thus, we may conclude that the evolution of agamid lizards involved the divergence of behavior as an immanent process whose primary and basic function is to counteract an excessive load on the nervous system. In outward appearance, the resulting forms of behavior have all the attributes of communicative signals (conspicuousness, hierarchical organization of movements, etc.). However, they are poor candidates for this role: the corresponding acts are mainly performed in the absence of a necessary communication scheme, which implies the presence of not only a sender but also a receiver of a signal, as well as the congruence of their actions. In our case, the last two conditions are not satisfied.

However, we do not assert that these acts basically have no signal effect. Stereotyped tail movements observed by conspecific individuals located nearby may influence their behavior in some cases. The character of this influence, however, is unclear because tail movements as a signal provide information only about the sex of the sender and not about its intentions. Remember that the pattern of stereotyped tail move-

ments in the repertoires of both aggressive and sexual behavior is virtually the same.

In any case, the temporal pattern of the series of tail movements in the toad-headed agama conforms to the general principles of organization of so-called serial behavior (exemplified by bird singing). A similar phenomenon has been described in some other lizards. In the steppe agama *Trapelus sanguinolentus*, males periodically perform series of push-ups in the absence of social stimulation (Panov and Zykova, 1986). The same concerns the rock agama *Laudakia caucasica*, in which the complete set of species-specific stereotyped push-ups is usually observed when a male remains alone in its preferable basking site. The pattern of these movements during social interactions appears to be reduced as the male gives priority to relevant purposeful forms of behavior rather than to "signals informing of its intentions" (Panov and Zykova, 1999). This phenomenon is analogous to the reduction of the series of tail movements during social interactions in the toad-headed agama.

A remarkable feature of the motor coordination considered in this study is the definite correspondence between the level of unspecific arousal and the intensity of tail movements. In fact, we are dealing with a perfect continuum: from a sluggish movement limited to raising the distal part of the tail and keeping it above the substrate, through one-time tail coiling (as an element of static posture), to the most intricate motor coordination terminating in the most intensive tail wagging (grade 4). As noted above, this continuum or, more frequently, fragments of it can be observed even within one series of tail movements, when their intensity gradually decreases to a minimum. In our opinion, this phenomenon is a perfect example confirming the validity of the energy model of motivation. Moreover, it deserves special consideration within the framework of the important problem of the degree of stereotypy in inborn motor coordinations and the factors of their variation (Schleidt, 1974).

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