Behavior of Varanus griseus during Encounters with Conspecifics

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Abstract. - In 1990-1993 in the western region of the deserts of Kyzylkum (Uzbekistan), constant observations of a group of desert monitors in natural conditions were conducted. Described are manifestations of various emotional states of monitors, and common types of monitor interaction. Given are detailed descriptions of the course of contacts between the animals, illustrated by photographs. Fights were rarely noted and only between unfamiliar lizards. It is proposed that ritual combat arises from displays of dominance and not from a ritualization of the fight. The behavior of monitors during contacts is highly varied and not stereotypical. Data from observations attests to the existence of a complex, mammal-like social structure in the population. Considered are probable mechanisms of intraspecific communication of monitor lizards.

Key words: social behavior, social relations, Reptilia, Sauria, Varanus griseus

Introduction

In the article at hand we have made an attempt to reveal the communicational function of common behavioral acts of desert monitor. We have made also an attempt to describe some types of interactions between monitors and the role of these interactions in social organization of population. We will not touch upon behavior connected with courtship and mating in the present article.

In 1989, when a program for the study of endangered species of reptiles was developed by us, the principal emphasis was put upon their ecology. When we stumbled onto the fact, that the behavior of the monitor lizard is much more complex than was imagined, we no longer had the opportunity to alter the program of study. Hence, the gathering of ethological material had to be conducted at the same time as the primary tasks. Although we are aware of the incompleteness of our data and the necessarily schematic and fragmentary nature of our description, we do not consider its publication to be in vain. This issue has not only theoretical but practical significance since desert monitor populations arouse serious apprehension in many regions of Middle Asia (Darevsky, Orlov 1988, Khodzhaev 1989)

There exists a vast literature dedicated to the elementary behavioral acts of lizards (see the survey of Carpenter, Ferguson 1977). The behavior of some species of monitor lizards has also been described in some detail (Auffenberg 1981a; 1981b; 1983; 1988; Carter; 1990; Davis et al. 1986; Deraniyagala 1958; Gaulke 1989; Horn et al. 1994; Mertens; 1946). But in the most of herpetological papers the social motives and purposes of behavioral acts are not examined. Behavior of animals during intraspecific contacts is usually considered as a succession of behavioral acts, but not as a social interaction directed at the maintenance of long-term interrelations within a socium. The analysis of behavior is reduced to statistical analysis of the sequence of the behavioral acts of contactants. Generally, the task of the analysis is limited to discovery of the most probable response of a lizard to the acts of another lizard. In analysis one seldom allows for the circumstances, under which the interaction took place. The history of interrelations of contactants, as a rule, is not taken into account at all. Actually, the social interaction is considered as a closed system with internal self-regulation, independent of the structure of the socium.

Viability of the population (the ability for balanced reproduction in particular) is to a considerable extent determined by its social structure. The social structure of many species is rather impressed by environmental conditions and the reptiles are not an exception (Panov, Zykova, 1985; Polynova, Panyushkin 1982; Polynova, 1990; Stamps; 1977). A social response of population to environmental changes is often species-specific (Polynova, 1990) and is not necessarily adaptive (Plyusnin, 1990). Peculiarities of response of socium to the external influences are determined for the most part by two closely interdependent, species-specific systems of animal activity: a) a production of the signals which carry information about the animal and its circumstances; b) a perception, processing and analysis of these signals in conjunction with others external and internal irritants. The principles of organization of these processes may be termed as a "language" and a "mentality" of a species. This issue is closely linked to the problem of management of populations and demands careful study.

The Region of Studies

The studies were conducted in the western area of the sand deserts of Kyzylkum, Uzbekistan. The coordinates of our permanent camp were 40° 40' N and 62° 08' E. The landscape in this region is typical of the Kyzylkum -- sandy ridges, bushy undergrowths (mainly Haloxylon persicum, and Calligonum sp.), and sparse grass (Carex physodes predominates) (Fig. 1). In the region of studies there is a rather high abundance of rodents, for the most part Rhombomys opimus and Spermophylopsis leptodactylus. Both inhabited and abandoned colonies of Rh. opimus -with their complex system of underground passages and location not farther than 150-200 meters from one another -- serve the monitors as refuges and hunting grounds.

Materials and Methods

Observations were conducted from 1990 to 1993 for periods of four to seven months annually. In all, observations were made for a duration of more than 20 months. In the beginning of April, the period in which monitor lizards come out of hibernation, they were caught, measured, weighed, marked, and released at the site of their capture -- usually in the course of a few hours after being caught. A special mark permitted us to identify the animals by their tracks (Tsellarius and Cherlin, 1991). Henceforth, for the greater part of the season of monitor lizard activity we conducted continuous observations of the animals -- following their tracks and observing them visually from camouflaged holes situated in the places where the appearance of monitors was most probable. In order to determine age, we amputated the last phalanx from one of the fingers of a number of the monitor lizards. The specimen was processed by E M. Smirina (Moscow) to whom we owe our sincere gratitude. The region of operations was regularly inspected and all points at which a tracks of the marked animals was apparent were plotted on a chart. As a result, we have at our disposal data on age, the location of home ranges, and the nature of the interrelations between the majority of the mature individuals settled in the region of operations.

Indirect exchange of information predominates in the population (Tsellarius and Men'shikov, 1994). The monitor lizards comparatively rarely enter into direct contacts. A possibility of observations of contacts is all the more rare. Therefore, in order to gather sufficient data, we provoked contacts. To this end, the

monitor lizard was specially caught, usually in the morning hours. In the evening of that same day we attempted to establish from tracks the site where another monitor would spend the night. At dusk we released the monitor captured earlier into a nearby burrow. In the morning, as the monitors emerged from their overnight shelters, encounter was inevitable. It was only possible to perform these operations from time to time so as not to disturb the lizards and disrupt the normal course of their lives. In some instances discussed in this article, data from tracking was also used when it was possible to precisely and fully reconstruct the course of events from the tracks. During observations from hiding, detailed stenographic notes were taken which were deciphered immediately after observations were concluded. Some of the encounters were photographed (from 5 to 16 frames per encounter). Unfortunately, a lack of means prevented us from employing photographic documentation to the extent that was necessary. In all, we observed 37 instances of contact between males, 8 instances of contact between females, and 21 instances of contact between the sexes.

Results

The Spatial Structure of the Population and Annual Dynamics of Activity

Data pertaining to the spatial structure of the population is currently being readied for publication in a separate article. Here, however, it is only necessary to address a few words to this issue. The number of monitor lizards in the region of studies consisted on the average of four adult individuals per square kilometer. The monitors were, however, distributed over the space unevenly: areas of high concentration alternating with thinly populated areas. Areas in which populations were more densely concentrated (settlements) measure nearly 100-150 hectares. The distance between the centers of neighboring settlements ranges from 3-5 kilometers. Each settlement is formed from a group of adult settled individuals consisting of five to six males of various ages and three to four females. In each of two settlements which were under constant surveillance, only one female took part in reproduction. The rest of the females were not impregnated over the entire period of observations although they were in fact courted by the males. The home ranges of all of the animals in a settlement almost fully overlap each other. In the sparsely settled areas between settlements, home ranges may, to a varying degree, either overlap or be located at certain distance from one another. The home ranges of settled animals range from 30 to 200 hectares in size. From time to time, each of the males makes brief, distant excursions beyond the borders of his home range, during which time he may visit the territory of a neighboring settlement. It should be kept in mind that this is a simplified scheme. The real picture is complicated by the presence of stray and nomadic individuals among the settled ones, altering the make-up of the settlements and so forth. The area of a settlement amounts to a kind of "public property" for settled inhabitants of this settlement. It is not specially guarded. We did not observe any territorial behavior either between settlements or within them. The degree of unrest and aggressiveness during encounters with acquaintances was, however, incontrovertibly lower than during encounters with strangers (Tsellarius and Men'shikov 1994) and made the incorporation of newcomers into the settlement difficult. The majority of the animals mentioned in this article were members of one of two adjacent settlements which were under constant surveillance.

In the region of research the hibernation lasts approximately from the beginning of October to the beginning of April. During 1.5-2.0 months after emergence from hibernation, monitors widely travel within their home ranges and intensively forage. In this period the social activity of monitors is high enough: they readily enter into contacts with conspecifics and show great interest in their tracks, but males do not make any attempts to court the females in this period (Tsellarius and Men'shikov 1994). Mating period continues for a short time, it starts from the first days of June and comes to end till the twentieth of June. Females, which have taken part in mating, dig the nest burrows in the end of June or beginning of July, and diligently protect the clutch during 1-3 months after deposition (Tsellarius and Men'shikov Social activity of other animals rapidly 1995). decreases during 1-2 weeks after the end of mating period. Mobility and activity of the foraging of monitors (females with clutches excluded) also decrease. In the end of July the range, daily inspected by a monitor, is a third or quarter of daily range in May. In addition, in the second part of the summer lizards may, from time to time, spend several days in burrows without emerging to the surface.

The Most Ordinary Behavioral Acts of Desert Monitor

"Confident gait". The animal moves calmly, carrying his body high over the earth (Fig. 2). The monitor lizard holds his head and tail horizontally and sometimes the tip of the tail draws upon the earth while he is in motion. When the monitor examines any object with its tongue (e.g. tracks of other animals, burrow entrances and so forth), the lizard slightly lowers his head.

In ordinary conditions these behavior and body posture were observed during the most part of period of monitor's activity when for example the hunting monitor travels over familiar area. "Confident gait" may be generally characterized as a pose of routine activity. In this time the animal is in a state of psychological comfort. A conflict of motivations is absent or it is possible to realize through the behavioral pattern several motivations simultaneously (e.g. the search for food and a sexual partner in the course of search behavior). The physical state of the animal and its external circumstances do not pose obstacles to the fulfillment of the corresponding type of activity (Ovsyanikov and Badridze, 1989).

The "confident gait" was often observed in course of encounters between monitors (see section "Examples of behavior of monitors...", exs I, 7; fig 14a). This gait probably testifies to the self-confidence and calm of the animal. His contactant evidently interprets it as a threat of attack or the possibility of such threat. In all directly observed instances the approach by "confident gait" provoked an unambiguous response. The approached animal manifests anxiety (see exs 7, 9 and Fig. 14, 16) or displays a peaceableness/submission (ex 1). The latter instances are rare.

Attack. When a monitor attacks a large prey he either immediately rushes on it, abruptly starting a sprint, or sneaks up to it before rushing from a distance of 3-5 m away. The sneaking up monitor walks with a rapid step, creeping along the ground, often uses shrubs and relief of the land as a cover. The act of lowering himself to the ground is also characteristic of the monitor that is avoiding danger (Fig. 3b). When sneaking up and when rushing the monitor holds his head and tail horizontally. During an ordinary hunt all observed actions were directly connected with prey-catching. Any special displays were absent. In general, posture of body of a monitor in assault is the same as in "confident gait".

Attacks on conspecifics were observed only in two situations: a) when a female protects her nest burrow (Tsellarius and Men'shikov 1995); b) when an animal with a lower social status rudely breaks the "rules of etiquette", suddenly appearing, for example, at a distance closer than individual distance (ex 4 and Fig. 12). In such circumstances the emotional state of the attacking monitor may be characterized as anger or rage. Any signals which are expressed through specialized postures and movements during an attack were not recorded. In 1992 we observed how a large monitor, considerably larger than the proprietress of the burrow, returned repeatedly over the course of a few days to the nesting burrow of the female that we had named Biteress and attempted to dig up the burrow in her absence (Tsellarius and Men'shikov 1995). The female, having found the arrival at work, drew close to him with quick dashes from shrub to shrub, slightly lowering herself to the ground, and lunged at him from a distance of 2-5 meters away. Biteress's behavior was, down to the most minute details, similar to the behavior of a monitor stealing up to his prey. In all observed instances attacked animal immediately resorted to flight.

The "threatening gait". The lizard moves in the direction of an adversary at a slow pace. His tail may not touch the ground but may, on certain occasions, leave distinct imprints on both sides of his trail (giving the impression that the lizard is whipping his tail enroute). When walking the monitor "drags his feet", leaving distinct tracks in the sand from the dragging of his fingers and claws. We can say nothing more definite about this pose because it has been noted only in encounters whose course has been reestablished from tracks. The track of "threatening gait", however, is very distinct from all other tracks. The female leaves such a trail when she moves away from her nesting burrow in the direction of an approaching conspecific. Such trails have also been noted a few times on the part of the female who directed it at a male that is pursuing her. The "threatening gait" was recorded in encounters between males when individual distance was abruptly broken (ex 4, Fig. 12). In such a situation the threat was always displayed by animal with higher "social standing"¹. In every instance, the animal to which the threat was addressed sharply changed the direction of his movement and in the majority of cases moved away from the site of events, sometimes taking flight. The lizards did not engage in direct contact.

"Threatening gait" and attack were recorded in very similar circumstances, sometimes "threatening gait" was followed by an attack. The state of the animal in "threatening gait" may be interpreted as anger rather closely linked to size, the duration of residence in a given settlement, and age.

"Sitting dog" posture. Monitor "sits down", lifting forepart of torso and head and looking around (Fig. 6). Very often animal assumes this pose when at great distance away is some disturbing object (observer, for example). "Sitting dog" posture probably is a classic orientation response. This reaction is formed with presence of weak fear (Hinde, 1970).

A monitor often raises his head during contact with subordinate individual when the latter assumes submission posture (exs.1, 3, 5 and Fig. 9). Therefore it may be possible that the "sitting dog" posture (Fig. 6) or very similar pose also has a trace of dominance in it. "Sitting dog" posture was observed in course of conflict between males, when both contactants manifested an unwillingness to yield (ex 9).

"Stooping"". The lizard slightly lowers his head, simultaneously inflating his throat and pressing his tail to the sand (Fig. 15a). This takes place during the encounter of an animal with an unknown object in a familiar area (e.g. a backpack, a shirt hung on a bush), in the event of a careless movement of the observer in hiding when the monitor lizard is not able to precisely identify the character and source of the movement, or during a direct encounter with another monitor that is unknown or whose intentions the animal is not in a position to determine, i.e. during an encounter with an irritant that attests not to an obvious danger but to the possibility of its beginning. In this circumstance the state of the animal may be characterized as a weak degree of fear, unease, lack of self-confidence. This state can even be unmistakably recognized in a lizard's tracks because his tail in these instances leaves a distinct, straight furrow in the sand (Tsellarius and Men'shikov 1994).

Zatir. If the unease is combined with strong excitation, the monitor presses his cloaca and the hind part of his abdomen to the sand and crawls, leaving behind a stripe of flattened sand (Fig. 5). This stripe serves as a signal mark which combines in itself visual and olfactory cues (Tsellarius and Men'shikov 1994). Formerly considering the marking behavior of monitors in a special article (Tsellarius and Men'shikov 1994) we termed this act as "dragging" and mark itself as the "drag". The term is an unfortunate one as it is being used for designation of another type of activity (Carpenter and Ferguson 1977). We propose to use the transliteration of the russian term "zatir".

"Showing of the back". A monitor flattens the torso dorsoventrally and incline laterally in the direction of opponent, showing the back, as it were (Fig. 11, 13d).

¹When speaking of the social status of an individual, we had in mind the "frequency of dominance". In other words, the more the monitors of a given settlement occupy a subordinate position in relation to a given individual, the higher his status. As one would expect, the social status of males turned out to be rather closely linked to size, the duration of residence in a given settlement, and age.

At this time the tail is lowered, but not pressed, to the ground and the throat may be slightly inflated. The monitor always orients himself laterally towards a threat. On certain occasions one may note a tendency of "arching of the back".

We observed "showing of the back" when the monitor encountered retaliatory aggression (active self-defense) on the part of prey and during the hesitant behavior of a human who neither attempted to capture the monitor nor made any sharp movements and yet did not leave the lizard alone. During intraspecific contacts the "showing of the back" was more often observed in situations when, on one hand, it may be suggested that the behavior of the conspecific excites apprehension of the monitor, on the other hand the motivation for present activity is rather strong and monitor refuses to take to flight. The emotional state in such situation may be characterized as alarm.

If another lizard both does not have self-confidence and does not disrupt the contact, the showing back monitor may fall into active self-defence (ex 8). If the opponent does not manifest any symptoms of fear and confidently goes on with approach, the monitor commonly takes to flight. We have never observed that attack or appeasement followed the "showing of the back". However, during contacts with human the "showing of the back" may fall into the "arching of the back". The latter may be followed by attack.

"Arching of the back". In this posture (Fig. 7a) a display of readiness for active self-defense (i.e. the monitor orients himself laterally towards his adversary, the tail is raised for a blow, and the head is turned in the direction of the danger) and elements of passive intimidation (i.e. the animal tries to appear larger than he actually is: the back is arched, the thorax is expanded, the body is raised upon erect front legs, and the throat is inflated) are combined.

Such posture is assumed by a monitor when the danger is serious and paths to retreat are cut off. "Arching of the back" is very common as a response to a threat on the part of human. In such contacts it sometimes follows the "showing of the back". We have never seen this posture in encounters between conspecifics.

If the human does not manifest hostile intentions, the animal slowly retreats (Fig. 7b). In the opposite case the monitor deals a blow with his tail and, after this, either takes flight (if a chance is given) or starts to make a lunge in the direction of the aggressor. When lunging the monitor turns to his adversary breaking the lateral orientation and strongly decreasing the displays of passive intimidation. In the rare cases an infuriated monitor may fall into attack. The state of the animal during "arching the back" is probably very similar to it in "showing the back" but the degree of fear is more high. A fear changes into anger and rage as a degree of threat increases.

"Gape". If the danger is very serious and unexpected, the monitor will display extreme readiness for selfdefense: he opens his mouth wide (Fig. 8a) and lunges in the direction of his adversary. Evidently this display attests to an extreme degree of fear. When a monitor, which is sleeping near entrance of burrow, is being suddenly caught, he often convulsively moves his legs wide apart, and feverishly turns his head with opened mouth in all directions. At this time a "strength" of heartbeat is noticeably increased. The general picture shows strong resemblance to displays of intense fear in man and other mammals (Darwin, 1872; Deryabin, 1974).

The "gape" may be followed by an attack. The animal becomes enraged, the urge for flight is curbed, the monitor chases his adversary and, if he is successful in catching hold of the latter, can be very difficult to deter (Fig. 8b). "Gape" was observed only in encounters of monitors with human.

"Lurking". If during an encounter with danger the monitor thinks that he has gone unnoticed, he will conceal himself by lying down and pressing himself tightly to the ground (Fig. 3a). Furthermore, depending on the circumstances, the lizard will either remain prone or exit stealthily (Fig. 3b).

It is difficult to define the emotional state of a monitor in this situation. Some degree of fear takes place for certain. However, "lurking" is not an involuntary display of fear unlike such reactions as "arching of the back" or "gape". It should be kept in mind that absolutely identical posture is typical of the state of contentment (e.g. basking, resting of replete monitor in the shadow of bush and so forth). This thing should be taken into account when the behavior of a monitor in intraspecific contacts is being interpreted. It may be important for interpretation that in an encounter with danger the monitor's eyes remained open (in every instance of this that we were able to make out) and in state of contentment the lizard very often closes his eyes.

The "lurking" is customary in the social interactions of various species of lizards (Carpenter and Ferguson, 1977) and has traditionally been interpreted as a display of submission. Such behavior is a usual characteristic of the desert monitor also. The female often assumes this posture during the approach of an adult male (ex 1). In this case the "lurking" may truly be a display of submission, but we have never observed such a posture on the part of the subordinate in encounters of males. On the other hand, however, we have observed how it is assumed by the obviously larger and stronger animal in response to a female's or a smaller male's display of readiness for active selfdefense (exs 2, 7 and Fig. 10, 14). We have never observed that "lurking" follows display of fear, unease or alarm during intraspecific contacts. The primary significance of this posture is probably not a display of subordinance as such but a display of a peaceableness. In general, recumbent postures are most characteristic of contacts of a "friendly" type (see below).

Flight. In encounters of a desert monitor with human or another large animal the monitor seldom falls into flight at the first moment. Usually a flight follows "showing of the back", "arching of the back" or "lurking". If a danger arises at a distance more than critical one (the latter is from 4 to 8 m) the animal will lurk as a rule. In opposite cases the animal usually manifests a readiness for active self-defence. In the case when human does not show aggressive intents, the lizard will slowly retreat either stealthily (Fig. 3b) or keeping the posture of readiness for self-defence (Fig. 7b) and falls into flight (if falls) only outside of opponent's sight. The flight is not accompanied by any special displays (Fig. 4).

During encounters between monitors in the majority of cases, a flight is probably an action of ritual nature. Very often flight taken place without any previous symptoms of fear (exs 5, 6 and Fig. 13). No matter how the interaction would turn, in every observed incidence of "sniffing", fighting, and ritual combat, flight on the part of one of the contactants inevitably terminated the contact regardless of the stage to which contact may have progressed. In the event of flight, the "conquered" generally retreated to a distance of 2-3 meters away, more rarely 10-15 meters, resuming his usual pace afterward, with the "victor" generally not displaying intention to pursue (exs 3, 5, 6, 8, 9). Exceptions to this rule are those cases in which one of the contactants immediately sets about an attack (ex 4 and Fig. 12). In this case as well, however, the attacker's rage and the retreatee's fear are certain only in the first moment of encounter. From that point on both flight and pursuit begin to increasingly take on the character of display (Fig. 12 and ex 4). It is symptomatic of this behavior that in not one of the observed incidences did the attacker catch up to his adversary.

Behavior Characteristic of Certain Types of Interrelations

Manifestations of dominance. We were able to closely observe the interrelations of some monitors for a length of 3-4 years. During these years we observed a stable asymmetry of behavior in all encounters between certain individuals. One monitor of two always (or in overwhelming majority of cases) displays relatively more anxiety in contacts with another and another's tracks. We regarded the first animal as a subordinant. Another lizard displays a self-confidence and was regarded as a dominant.

In the case of monitors, the behavioral syndrome of dominance is divided into two groups of "symptoms". On one hand there are distinctive features of behavior which are connected with the social status of an animal and which are manifest in many types of activity. These features are displayed from the first moment of interaction during direct contact between lizards. On other hand there is the "behavior of the victor" which is displayed only in agonistic contacts and only when the "correlation of forces" has been revealed.

The idea was formed that behavior of monitor during contact with conspecific is more strongly impressed by the social status of the animal (i.e. general experience and history of interrelations with conspecifics at all) than by concrete dominance and subordinance. The lizard with low status even during an encounter with his subordinant sometimes displays the most anxiety than high-ranking animal in contact with his dominant. On the whole, the behavior of a high-ranking animal is distinguished by self-confidence: the monitor rarely displays signs of unease or, rarer still, alarm. This is especially apparent in tracking studies (Tsellarius and Men'shikov 1994). Absolutely dominant in one of the settlements, the fourteen year old male named Vasya, boasting a snout-vent length of nearly 600 mm and a weight of 3.5 kg, did not display substantial alarm even upon encountering a human. In Vasya's case we did not observe postures of active self-defence (Fig. 7a) at all. As a rule, the monitor turned sideways towards the human encountering him, lowered his head, and slightly inflated his throat. The "showing of the back" was faintly expressed if expressed at all. In such a position the monitor first drew back a few steps and then moved away only at a slightly quickened pace, periodically sitting and looking back (Fig. 6).

It is highly probable that, during encounters between animals, behavior attesting to states of comfort are devoid of any expression of a conflict of motivations (exs 1, 7 and Fig. 14) and is in itself a display of high rank. We have observed such behavior primarily in males which have high social standing. Females may assume a submissive posture (ex 1) during such an approach by a male but low-ranking males display a great degree of alarm and often resort to flight. The specific "threatening gait" and lifting of the head are also apparently linked to high social status.

Observers of monitor behavior have described an absolutely unambiguous "victor's pose" that is assumed when the victorious monitor mounts the defeated one (Auffenberg, 1981a; Deraniyagala, 1958; Gaulke, 1989; Horn et al., 1994). A posture of this sort (e.g. topping, riding, straddling) is characteristic of many species of lacertilias and is displayed in the course of both agonistic and sexual interaction (Auffenberg, 1981a; 1983; Carpenter and Ferguson, 1977; Horn et al., 1994; Noble and Bradley, 1933). In the case of the desert monitor, we observed such posturing only during mating attempts but it is impossible to rule out its use as a "victor's pose" as well.

Within a certain context, it is possible that, when one of the contactants assumes the posture of submission, the act of licking the "defeated" plays the role of a "victor's pose" (ex 1). In opinion of Auffenberg (1981a), tongue licking in the case of *Varanus bengalensis* has a signaling function.

Displays of amicability. Informal contacts, founded upon personal attachments, are common to many species of animals and may play a substantial role in the formation of the social structure (Panov, 1983b). A similar sort of connection probably exists in the case of Varanus komodensis (Auffenberg, 1981b), V. bengalensis (Auffenberg, 1983), V. rosenbergi (Green and King 1993) and some other species. In the case of monitors, the basis for this connection probably lies in the habit of neighborhood as a familiar lizard evokes much less unease than a strange one (Tsellarius and Men'shikov, 1994). It may be possible that the personality traits of an animal are of significance as well. Mertens (1946) long ago noted the clearly expressed individual differences in character among monitors. According to our observations, in the case of the desert monitor, individual differences in the degree of excitability, aggressiveness, and the ability to alter behavioral patterns in changed circumstances may be very pronounced.

We only observed friendly contacts between settled monitors whose home ranges were broadly overlapping for a long period of time. The aggressive reaction of animals during such contact may be suppressed to such an extent that the female guarding her nesting burrow will allow another individual to visit it. For example, Mafiozi repeatedly visited the area of Docentess's nesting burrow and even spent the night with her in a single burrow (Tsellarius and Men'shikov 1995). It must be added that sexual contacts between these animals were not observed either that year or later.

Characteristic of friendly contacts are the absence or only very faint display of signs of unease on either individual's part and the mutual display of "submission" (exs 6, 10 and Fig. 17). During such contact the lizards never hold their bodies high over the ground, much as in normal movement or during the "threatening gait". The monitors lie down and either draw together with short, a few steps at a time, crossings or crawl across in each other's direction. Expressions of a peaceful nature do not, however, impede the proposition of ritual combat (exs 5, 6 and Fig. 13).

Common Ceremonies and Their Probable Function

We designate as a ceremony those interdependent actions which occur during contact between two or more individuals and are directed at the maintenance or establishment of certain social relations, and also the rules by which these actions are guided. The social status of the contactants, the dynamics of their motivational and emotional states, and the displays connected with them determine the course of the ceremony and its result for each of the participants but are not linked to the essence (goal) of the ceremony itself.

Mutual "sniffing". Mutual "sniffing" is an almost obligatory act in the encounter of two animals over a definite period of time. Exceptions may include those contacts connected with the protection of a nesting burrow and cases of sudden, involuntary violations of individual distance. In these situations one of the contactants may immediately resort to threat or attack, omitting the "sniffing" procedure. Only in early spring, immediately following the emergence from hibernation, and in the period when all regular activity ceases before hibernation. was the "sniffing" procedure rarely observed in encounters between animals. Monitors encountering one another often (albeit not always) did not engage in contact at all.

During "sniffing" the monitors usually first lick the snout of their conspecific, then his side, the sacrum region, and the base of the tail. Sometimes "sniffing" proceeds without displays of alarm or unease on the part of the contactants for the duration of the ceremony (exs 6, 10 and Fig. 17). More frequently, however, unease or alarm occurs. It is extremely common for animals to display alarm after mutual "sniffing" of the snout and to try to avoid being licked in the sacrum region. In these instances, the monitors "waltz": they circle, as if attempting to catch up with each other's tail (Fig. 13d, 15b). One or both of the animals always "shows the back". If the contactants begin to display alarm at the very start of contact, then they may immediately orient themselves not to the facial but to the sacrum region, which inevitably leads to "waltzing".

The motivation for "sniffing" is, apparently, quite strong. Animals frequently draw together and do not interrupt their contact until each contactant has licked the other, even when the other evokes in each a strong unease (ex 8).

The primary goal of "sniffing" is probably the receipt of certain information about a conspecific. Familiar animals are probably capable of recognizing each other by some external features. In every instance of contact between unacquainted individuals, however, sex and reproductive state were determined only by olfactory means (Tsellarius and Men'shikov 1994). Therefore, it may be possible that the urge to lick one's conspecific has as its basis the urge to receive information about the physiological status of the encountered individual.

Apart from this. however, mutual "sniffing" appears thereby to be a required ceremony in the course of which the social status and the personal interrelations of the contactants are determined (or confirmed). The analogous significance of the ceremony of "sniffing" has been well known for socialized species of carnivorous mammals, canids in particular (Schenkel, 1947; Lorenz 1969).

Fight. We designate as a fight that type of agonistic interaction in which: a) monitors enter into direct contact, b) measures are taken that can lead to the mutilation or death of the contactants, c) on both sides displays of anxiety and readiness for self-defence take place in the course of the interaction. Following Auffenberg (1981a) and other researchers, we treat blows of the tail as measures which can cause mutilation, although, strictly speaking, in the case of monitors they are a ritualized measure, a lesser one, in contrast to bites which are likely to inflict injury on an opponent.

In all, we observed three instances which may be qualify as fights, although with some stretching the point a bit. In each of the three instances unknown or unfamiliar males from various settlements entered into contact. Displays of alarm and unease were clearly expressed by both sides (ex 8, Fig. 15). Following the "sniffing", accompanied by the "showing of the back" and "waltzing", one of the animals, always the one which originally manifested alarm to the greater degree, dealt a blow with his tail which invariably put his adversary to flight. The larger male did not necessarily emerge victorious from the fight. Nor was the victor necessarily a resident of the settlement on whose territory the encounter took place.

The frequency of fights probably depends on a number of circumstances but first of all on the social structure of the population in a given area and at a given time. In other words, it depends on the predominance of a certain type of interrelation. The social structure is not an unchanging, species-specific feature. Although the interrelations between monitors in the region of studies from 1991 to 1993 may be characterized as highly peaceful, in the previous period these relations were, evidentally, of a rather different nature. The majority of monitors caught for marking in 1990, males and females alike, had fresh, deep scars or wounds located primarily in the sacrum region or on the shoulders, rarely on the side. These scars and wounds are reminiscent of the teeth tracks which are left when a monitor takes something in his "mortal grip". In 1991 wounds and fresh scars were a rarity, and from 1992-1993 were noted two times in all.

Ritual combat. Ritual combat is that type of agonistic interaction in which animals enter into direct contact but measures which could lead to the mutilation of an opponent are excluded. Until now, ritual combat in the case of the desert monitor has gone undocumented, although it has been described for many other species of this genus (Green and King 1993; Greer, 1989; Horn et al., 1994).

In every instance, ritual combat is preceded by the ceremony of "sniffing" (exs 5, 6 and Fig. 13). Combat may be broken off at the initiative of one of the participants at any moment and in the majority of cases this took place at the very first stage of combat, the "crossing of necks" (ex 6). We only observed one instance of all-out ritual combat (Fig. 13). Every instance of ritual combat or the attempt to propose it was noted only during contacts between animals from the same settlement.

Ritual combat was recorded only in the case of males. It may be possible, however, that such combat also takes place among females. At the end of June 1993, we observed the tracks of an encounter between two females from the same settlement, Frosya, five years old, and The Fourth, four years old. The trampled patch of sand that remained at the sight of their encounter was somewhat similar to those that are left after ritual combat between males. Frosya followed The Fourth's tracks for nearly 45 m to this patch. The

females were obviously within each other's field of vision and both, probably, "showed their back" from time to time. From the trampled patch the females headed in different directions. Notably, The Fourth ran for nearly 17 m and Frosya moved at an easy pace. In the case of certain varanids, ritual combat has been noted between males, between females, and in contacts between the sexes (Auffenberg,1981a; Gaulke, 1989).

The significance of ritual combat for varanids is unclear (Greer, 1989; Horn et al., 1994) and attempts to link this type of interaction with the struggle for a specific resource (e.g. food, territory, females) have not been successful. In those cases where a few males are competing on account of a female, skirmishes have been observed but ritual combat did not take place (Carter, 1990). Encounters near sources of food may lead to a form of ritual combat but more often proceed otherwise (Auffenberg, 1981b; Gaulke, 1989). Territoriality for the majority of varanids, including the desert monitor, has not been established (Green and King, 1993; Greer, 1989; Tsellarius et al., 1991; Tsellarius, 1994). In the case of the desert monitor it is precisely these skirmishes which, stretching the point a bit, may be regarded as territorial (i.e. the encounter of a settled male with an unknown animal, a female's guarding of her nesting burrow) proceeding more in the form of a fight than ritualized interaction.

If we examine ritual combat in the case of varanids on the whole, then the impression is made that the essence of combat consists in the mutual attempt to knock over the opponent and assume the "victor's pose". The animal throws his front paw (or the front and the hind) over the back of his adversary and tries to stand up over him. This is quite apparent in both our photographs (Fig. 13) and in detailed descriptions of combat among different species of varanids (Auffenberg, 1981a; Davis et al., 1986; Deraniyagala, 1958; Gaulke, 1989; Horn et al., 1994). This grappling, the attempts of each opponent to attain the "victor's pose" while simultaneously trying to frustrate the other, is the essence of the combat. The struggle in a standing position on the hind legs evidentally developed as an attempt to occupy a more favorable position for toppling an adversary. It is significant that a struggle attained to the end has been finished by "victor's pose" (Deraniyagala, 1958; Horn et al., 1994).

If this is true, then ritual combat is most closely linked not with the fight for a specific object but with purely social interaction. Combat is a development of ritual behavior connected primarily with the display of dominance and is not a ritualization of the fight.

In the case of the desert monitor and some other varanids, all-out ritual combat is extremely rare in natural conditions. The reason for this probably lies in the fact that a certain combination of circumstances must be present for ritual combat to occur: uncertainty should exist in the interrelations between animals, their social status should be about equal, and dominance in relation to one another unestablished. In so doing, in the case of an obvious inequality in strength (i.e. in the majority of cases) the question of dominance is resolved by the process of "sniffing" and direct struggle to establish seniority is unnecessary.

In the conditions of a stable settlement, social rearrangements, taking into account the long life expectancy of monitors, are relatively rare: the animals know one another personally and the rank of each is known to all the rest. The need not only for combat but even for the sharp display of dominance rarely arises. In the event that the social structure is destabilized to the point that a large number of lizards appear that are not sufficiently well known to one another, the social rank of an animal is more likely to be established in a series of fights and the conditions for ritual combat rarely take shape.

Examples of Behavior of Monitors During Encounters with Conspecifics.

1. The encounter of a settled male with a female from a neighboring settlement. May 26, 1993. The Contactants: the male Mafiozi, six years old, SVL 475 mm, weight 1.3 kg; the female The Fourth², four years old, SVL 425 mm, weight 1.2 kg. Over the course of two years Mafiozi had encountered The Fourth's tracks but until this moment probably had had no direct contact with her, in this year in any case. The Fourth had been released the previous evening into a burrow located seven meters from Mafiozi's shelter that night and in the morning came to the surface later than he did. On the morning Mafiozi, lying near his burrow, spied the walking female, rose, and, without hesitation or displays of unease, headed for her. The female immediately lay down and Mafiozi, having reached her, licked her head and sacrum region. After this he moved off a few steps to the side, raised his head (Fig. 9) and lay down, turning away from The Fourth. Mafiozi twice more approached the female, with an interval of a few minutes between, and again licked her. Only after this did he move away. When the

²All females mentioned in this section of article did not take part in reproduction for all period of investigations.

male had left, The Fourth, not rising, lifted her head but lowered it again as soon as Mafiozi turned towards her. After every lick of his tongue, Mafiozi lifted his head high and held it this way for some time.

2. The encounter of an adult, nomadic male with a young, settled female. May 14, 1991. The course of events was reestablished from tracks. The Contactants: the male Grigory, seven to eight years old, SVL 505 mm, weight 1.9 kg; the female Frosya, three years old, SVL 425 mm, weight 1.6 kg. Grigory hibernates in this region and in the summer appears here episodically, one or two times a month. Frosya has lived in this area permanently for at least two years. The monitors came into contact while circling a shrub from different sides (Fig. 10). Judging by the tracks, Frosya immediately turned sideways to the male and, probably, "showed her back". Grigory lay down at once. Having taken a few short steps in his direction, Frosya also lay down. After some time Frosya rose and, walking around the male, left in the same direction she had come before the encounter. Grigory followed her tracks for nearly 50 meters, leaving powerful "zatirs", and then also moved in the direction he had kept to before the encounter.

3. The encounter of an adult, but never impregnated. settled female with a settled male. May 22, 1993. The Contactants: the male Es the Ninth, eight years old, SVL 480 mm, weight 2 kg; the female Frosya, five years old, SVL 450 mm, weight 1.2 kg. The animals have belonged to the same settlement for no less than four years and are well acquainted with one another. In 1992, Es the Ninth persistently, but unsuccessfully, courted Frosya. Frosya encountered Es the Ninth on the morning when he was laying, half of his body sticking out of his burrow, and slowly headed for him, lowering her head and slightly inflating her throat. Es the Ninth, obviously disturbed, made a movement in her direction, stooping slightly. Frosya "showed her back" and began to move off sideways, not letting the male draw right up to her (Fig. 11). Then she ran a few meters away and the monitors froze. After a few seconds of immobility, the female slowly moved away, frequently looking back. Es the Ninth remained in place until she was hidden from view, watching her from behind in the "sitting dog" posture. Then he attentively licked her track, left a zatir, and also moved away.

4. A skirmish of two settled males that resulted from the violation of individual distance. June 26, 1991. The course of events was reestablished from tracks. The Contactants: Feodor, nearly 10 years old, SVL 550 mm, weight 3.0 kg; Mafiozi, 4 years old, SVL 430 mm, 1.5 kg. Feodor has the highest status among the males in the given settlement. The animals are members of the same settlement and knew one another well for not less than a year before the encounter. None of the conflicts between them before the one described below, or for a year and a half following it, have been noted. On the morning, Mafiozi, walking around a bush, literally stepped on Feodor, who was basking in the sun after emerging from his night shelter (Fig. 12). The latter jumped on him, apparently without warning, and Mafiozi jumped aside and took to Hight. Evidentally, for the first 15-20 m the monitors ran as fast as they could. For the next 15 m the length of their step decreased. Feodor then shifted to a walk and followed Mafiozi for about 5 m by the "threatening gait". As soon as the young male also shifted to a walk, however, Feodor made a burst of speed, compelling Mafiozi to again take flight. The chase continued in this fashion for more than 200 m. Finally, having startled Mafiozi again in routine order, Feodor shifted to an easy pace and, sharply changing direction, went to one of the nearest colonies of Rhombomys opimus where he began to hunt. Events proceed in like manner when a female is chasing a monitor who has encroached upon her nesting burrow.

5. Ritual combat between two settled males. June 1, 1993. The Contactants: Mafiozi and Edik, both 6 years old, measure SVL 475 mm, and weigh 1.3 kg. The animals know each other well and have been members of the same settlement for at least four years. At the end of 1992, the leader of the settlement, the old male nicknamed Feodor, disappeared. Among the remaining males Mafiozi is one of the largest and most energetic. He is active over the entire space of the settlement and regularly goes far beyond its borders. Edik's primary region of activity lays on the northeastern edge of this settlement and he visits its central area only episodically. The encounter took place on the morning. The monitors spent the night in the same colony of Rhombomys opinus and emerged from their burrows almost simultaneously. It is highly probable that the animals had made contact in the burrow. The lizards lay for a few minutes near the exit from the burrows and then Mafiozi moved toward Edik who, in his turn, took a few steps in his direction. Meeting, the monitors lay down and, lying down, licked one another first on the snout and then on the side and sacrum (Fig. 13a). Next, they crossed their necks, each attempting to deflect the neck of his opponent to the side while simultaneously trying to seize with his paw the supporting foreleg of rival (Fig. 13b). Until this moment neither of the monitors had displayed any alarm or substantial unease. Then, Mafiozi succeeded in budging his opponent (Fig. 13c) and the monitors began to "waltz" (Fig. 13d) at which time Edik (left) "showed his back", displaying obvious alarm. At some moment the monitors were side to side and their heads were directed in the same way. Mafiozi immediately threw his front paw over Edik's shoulders. The latter did the exact same thing at once. The lizards made attempts to overturn each other, slipping their heads under their opponent's neck. One time that Mafiozi succeeded in doing this, the monitors rolled over on their backs and ended up in their previous position. The lizards gradually shifted to the "face to face" position (Fig. 13e) and, continuing the struggle, began to rise on their hindlegs. Having assumed a vertical position and closed their front paws on each other's backs (Fig. 13f), the males continued their vigorous attempts to topple their opponent. The males fell down together a few times, breaking their grip in the process (Fig. 13g), but immediately jumped up and seized one another anew. The entire skirmish was conducted very energetically and the positions of the opponents changed rapidly. Edik suddenly ran to the side for 3-4 m and the monitors watched one another motionlessly for nearly 30 seconds. Edik then slowly moved away, describing a zigzag and frequently looking back. Mafiozi, remaining in place, watched him from behind, raising his head. The entire struggle, from the moment the adversaries crossed necks, lasted no longer than two minutes. The entire encounter, from the moment the monitors emerged from their burrows, lasted 14 minutes.

6. Encounter and ritual combat between two settled males. June 2, 1993. The Contactants: Rhombik, 5 years old, SVL 445 mm, weight 1.2 kg. Mafiozi is older and larger (see ex 5 for his description). The monitors belong to the same settlement and have known each other well since at least 1991. On the evening of June 1, 1993, without our interference, the monitors spent the night in the same colony of Rhombomys opimus which that day, in the morning, a young female from a neighboring settlement, The Fourth, had repeatedly visited. Emerging from their burrows the next morning, the monitors lay for a long time near each other, basking in the sun and yawning in turn. Their behavior was not unlike the usual behavior of monitor that have emerged from his night shelters. After approximately 30 minutes the animals crawled together and the procedure of mutual "sniffing" lasted for nearly 10 minutes. It was not accompanied by any apparent displays of unease. Mafiozi then crossed necks with Rhombik and attempted to press him to the ground. Rhombik very calmly freed himself, ran a few meters off, switched to an easy pace, and left. Mafiozi licked his tracks and went off in a different direction.

7. The encounter between a settled male and a nomad. May 24, 1993. The Contactants: Alitet, 5 years old, SVL 470 mm, weight 1.4 kg; Shot Glass, 10-11 years old, SVL 560 mm, weight 1.8 kg. Alitet is a settled resident of the settlement on whose territory the encounter took place. Shot Glas has spent the winter within the borders of this settlement for at least three years but about a month after coming out of hibernation goes far east and appears here only episodically, for two to three days, until the end of the season of activity. As far as we know, these monitors had not had direct contact this year, although they regularly came across one another's tracks. The encounter took place on the morning. The monitors saw each other practically simultaneously, at a distance of nearly 15 meters, and froze motionless for some time. Then, Shot Glass decisively headed toward Alitet (Fig. 14a) who, having allowed him to approach within 1.5-2.0 m, inflated his throat and "showed his back". Shot Glass immediately lay down (Fig. 14b) and Alitet, stepping slowly, walked around the recumbent monitor from the side and, looking back from time to time, went away. About a minute later, Shot Glass rose and, pressing his tail to the ground, licked Alitet's tracks (Fig. 14c), left a zatir, and followed the trail of his conspecific. Having followed the tracks for nearly 34 m, he "sniffed" Alitet's excrement and peacefully went away, sharply changed direction.

8. An encounter between two unfamiliar males which ended in a fight. May 31, 1993. The Contactants: The Tip, 6-7 years old, SVL 460 mm, weight 1.4 kg; Dusty, 12 years old, 590 mm, weight 2.2 kg. The Tip is a settled resident of the settlement on whose territory the encounter took place. For at least three years, Dusty has spent the winter near the borders of this settlement but immediately after coming out of hibernation has traveled to places located several kilometers to the southeast. In 1993 he remained in the region of hibernation for the summer for the first time. The encounter took place early in the day. Having noticed The Tip at a distance of about eight meters, Dusty lay for a few seconds and then headed for The Tip who immediately turned sideways to him. The Tip displayed greater and greater alarm as Dusty approached and the "showing of the back" became more and more apparent (15a). Dusty's lowered head, inflated throat, and tail pressed to the ground appear threatening but actually attest to his unease and lack of self-confidence. After the mutual "sniffing" of the snout, Dusty attempted to "sniff" The Tip's sacrum but the latter drew back, "showing his back" (15b). As a result, the monitors described a few circles in place. Suddenly, The Tip dealt a blow of his tail and Dusty quickly scurried aside. Having moved about six meters away, he stopped and the monitors watched each other for some time. Then Dusty slowly moved away, barely looking back. After one or two minutes The Tip also left, not even having been interested by his opponent's tracks.

9. An encounter between two unfamiliar males. June 18, 1993. The Contactants: The Tip, 6-7 years old; C-59, approximately the same age as The Tip but a bit larger, his SVL is 480 mm and he weighs 1.5 kg. C-59's home range is situated in a zone little settled by monitors between two settlements located far from one another. Hence, he periodically makes excursions far beyond the borders of his range. The previous evening C-59 was released into a burrow not far from The Tip's night shelter in almost the center of the latter's settlement. C-59 was caught nearly a day before this. Over the previous three and a half years he had appeared in the given region not more than two or three times. Emerging from his night shelter in the early morning, C-59 walked for some time about the colony of Rhombomys opimus and, finding the burrow where The Tip had spent the night, hid in it. About 10 minutes later the monitor again appeared on the surface from a different opening, having traveled nearly three meters underground. Emerging from the burrow, C-59 looked around, licked the sand, yawned, and, having moved a few meters away, lay under a bush, head raised. The Tip emerged from his own burrow a few minutes later and headed confidently for C-59 who remained in the very same posture but kept an eye on The Tip, turning his head to follow the latter's movements. The Tip made a circle, having drawn close to C-59 who at that moment rose halfway, inflated his throat, and "showed his back" (Fig. 16a). Later, The Tip made yet another circle and again returned to C-59. Both monitors assumed the "sitting dog" posture (Fig. 16b) and remained motionless for some time, located at a distance of about two meters from one another. Then The Tip again began to make a circle, at the same time inspecting the burrows of Rh. opimus as if not noticing the newcomer. When he came near to C-59 the latter jumped up and turned in his direction, having lowered his head, inflated his throat, and flattened his trunk dorsoventrally. The Tip did the same and the monitors simultaneously lunged at one another. Each having struck the sacrum of his opponent with his nose, and each "showing his back" (Fig. 16c), they made a full revolution after which The Tip jumped aside, ran 9-10

meters off, shifted to a walk and after 25-30 m entered a burrow of *Rh. opimus*. C-59 immediately assumed a normal position and, once The Tip was hidden from view, walked about the site of the encounter, inspecting burrows, and then peacefully went away.

10. A friendly encounter between an old male and a young male. May 12, 1993. The Contactants: Chuck Norris, not less than 10 years old, SVL 520 mm, weight 1.8 kg; Egghead, 4 years old, 425 mm, weight 1.2 kg. The home ranges of both monitors broadly overlap but lay beyond the boundaries of the region where regular observations were conducted and their status and the history of their interrelations is unknown. Having caught sight of each other, both monitors lay down and for a long time crawled around each other, "sniffing" their partner's snout, side, and base of the tail, displaying virtually no signs of unease. From time to time the animals would break off their activity and for 10-15 minutes lie near to each other, occasionally closing their eyes (Fig. 17). After this the "sniffing" was resumed. At the end of the encounter the young male began to make "zatirs" (signal marks), crawling across Chuck's back and neck in doing so, after which he left. The old male immediately entered a burrow. Contact lasted for 47 minutes in all.

Discussion

On a certain stage of investigation of social structure of population the researcher will inevitably clash with necessity of a studying of mechanisms of the social reciprocal influences, that is the problem of intraspecific communication.

In classic ethology the concept of animal communication is based on the three postulates: a) it is proposed that behavioral acts, that carry socially important information, must be rather exotic, in order that a perceiving animal will be able to correctly single a communicative signal out of series of non combehavioral municative. routine acts; b) а communicative act must be very stereotyped, in order that a monosemantic interpretation will be provided; c) a set of responses to certain act must be strictly limited to provide its adequacy and coordination of interactions. Thus, a communicative system is being considered as the system of discrete, ritualized behavioral acts with fixed significance (Hinde, 1970; Mac-Farland, 1985). A process of communication is being regarded as the stereotyped succession of acts, which is founded on either innate or learned automatism of responding.

These three principles are formulated by Tinbergen and his followers in course of investigations of behavior of invertebrate animals, pisces and aves. It should be noted that behavior connected with reproduction (courtship, mating, parental care) was mainly examined. This behavior is directed at the reaching of limited set of strictly specific aims. An investigations of "everyday" social behavior (especially in mammals) led to accumulation of facts which poorly harmonize with basic principles (for survey see Panov, 1983a). Evidently, it should be admitted that development of communication on the base of other princior on the base of several principles ples simultaneously is possible.

A contradistinction of exotic behavioral acts of the desert monitor and non-exotic ones is very relative and quite useless both for ascertaining of communicative significance of these acts and for analysis of their forming and origin. In the point of view of a researcher, who observes the monitors during all periods of their activity, the "confident gait" is an element of common, routine behavior, and the "showing of the back" is a bright, exotic posture. But in monitor's point of view the "showing of the back" or "stooping" are far more usual acts than "confident gait", since monitor observed his conspecifics during contacts only. Only the monitor's "point of view" is important for formation and evolution of his communicative system. A coincidence of researcher's and monitor's "points" about exoticness of the posture should be possible only in the case if a monitor would be aware of his behavior and identify his own behavior with that of a conspecific. As far as we can judge by behavior of monitors during contacts, all features of behavior, exotic and non-exotic, are equally important for communication.

A large majority of behavioral acts of desert monitors may be expressed in varying degrees: they may be very distinctive or hardly noticeable. Many different acts may smoothly turn one into another. Some signaling elements of behavior, inflating of the throat for example, take part in many displays, which have distinctly different significance. It was noticed in many species (Auffenberg,1981a; Panov and Zykova, 1986; Hikida, 1989) and, evidently, it is not an exception, but a rule.

The data from our observations conforms poorly to the widespread perception of lizards as animals that display relatively primitive behavior based upon simple stereotypical reactions. A behavior of the monitor during encounter with conspecific is definitely not an automatic response to the behavior of partner. Behavior is conditioned by many circumstances, among them the most important ones are such interdependent factors as a) initial emotional state of contactants; b) a history of interrelations of given animals; c) a social status of animal, i.e. personal experience of previous intercourse with conspecifics.

When a problem of decoding of any system of signals arises, it should be useful to formulate a supposition of what a kind of information is transmitted by this system. It should be quite correct to use an analysis of nonverbal communication of our own species for solution of this problem. A majority of nonverbal behavioral signals of Man carry information about the emotional and/or motivational state of an individual. Direct information about the intents of an individual or his external circumstances is not contained in the majority of behavioral acts. Nonverbal behavioral signals carry information about circumstances and/or the intentions of given individual so far as a particular external circumstance frequently provokes a particular emotional state and this emotional state is, in a particular situation, a base of a particular action. A human's response to behavioral signal may be very diverse and depends upon the situation, his emotional state and his personal experience. It is evident that communicative systems of other mammals is organized in a similar way (Schenkel, 1947; Ladygyna-Kots, 1958; Lorenz, 1969). We have not any reasons to expect some things of a fundamentally different nature in other higher vertebrates.

It is strictly imagined that the majority of behavioral acts of the desert monitor clearly reflect the emotional state of an animal and are in this regard perfectly unambiguous. But displays of even diametrically opposed states may contain identical behavioral elements. In addition, the intensity of every emotional state may be various and, accordingly, the intensity of display may be various too. Emotional states are not discrete and, between them, there exist an entire gamut of transitions. It concerns the manifestation of these states also.

It seems to us that, without an understanding of the dynamics of the motivational and emotional states of animals engaged in social interaction, a correct interpretation of the course of these interactions and their result is often complicated or altogether impossible.

A human perceives the behavior of a conspecific as a stream of integrated mental pictures. Separate elementary behavioral acts, as a rule, are not perceived individually. This stream of nonverbal signals first of all influence the emotional state of the perceiver, and do not act upon behavior immediately. Adjustment of behavior is being realized by indirect way through a change of subjective feeling of situation and emotional estimation of it. It is quite probable that the mechanism of the animal's perception of conspecific's behavior is the same. If this suggestion is right, we arrive at a picture of nonverbal communication as a "process of tuning each of communicants into the behavior of its partner" (Panov, 1983a). A mechanism of this tuning is influence of animals the emotional and motivational state of each other through the exchange of information about the alteration of these states. Communication of this sort asks for analogy to our own highly developed systems of nonverbal communication, such as music, dance, etc.

During many decades amidst ethologists it was considering as an indisputable tenet that animal's subjective feelings (including emotions) are unable to be subject of scientific analysis. Actually it meant that existence of subjective feelings in animals is denied since a veto upon the use of this idea for explanation of mechanisms of behavior was imposed. But till now no one succeeded in creating a general theory of behavior within the bounds of behavioral approach.

Psychologists and neurophysiologists, having looked at the matter the other way round, propose a concept of evolution of the psyche of vertebrate animals and influence of psyche on their behavior. This concept well conforms to facts (Anokhin, 1968; Delgado, 1969; Shepherd, 1987; Vartanyan and Petrov, 1989). Using a concept of emotion, one generally managed to obtain the harmonic, economical explanation of observed behavior. Suppositions were warily declared that not only emotions, but also the higher kinds of psychological processes, those are termed a "mind" in respect to Man, are characteristic of animals (Gallup, 1985; MacFarland, 1985; Sevastyanov, 1989). The existence of emotions is not called to question in respect to mammals with a developed brain. The analogy of basic and some secondary emotions of Man and other mammals is not refused also. But in respect to reptiles, a use of the concept of emotion is unusual for the majority of zoologists. However, if we denied the existence of a sharp border between the psyche of Man and that of other mammals, we find ourselves before the necessity to seriously warrant a placing of such boundary-line in any other case.

Emotions are an internal regulator of psychological activity and behavior, and are a universal measure of values that have a great adaptive importance. Under the shortage of prognostic information or absence of possibility of processing of it the emotional estimate of situation allows one to quickly find one's bearings and to make one's choice (Anokhin ,1968; Simonov, 1970). Probably emotions are a very ancient mechanism of estimating the influence of internal and external irritants, which developed long before arising of new cortex. Morphological and neurophysiological ground for forming of emotions probably arose as long ago as the anamnia arose (MacLean, 1949; Dethier and Stellar 1967). A presence of afferent tone is the indispensable component of conditioning reaction, without it a forming of feedback mechanism is impossible (Wiener, 1958).

Essential resemblance of the behavior of lizards and mammals (MacLean, 1978; Regal, 1978; Tsellarius and Men'shikov 1994), unstereotyped course of interactions, universality and non-discrete nature of the majority of lizard's signals (Auffenberg, 1981a; 1981b; 1983; Carpenter and Ferguson 1977; Gaulk, 1989; Panov and Zykova, 1986), rather high ability for education (Brattstrom, 1978; Krushinsky, 1977) make quite permissible the supposition that reptiles have rather developed forms of psychological activity.

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Appendix I

Figures 1-17



Figure 1. Landscape of the region of operations. (photo by Yu. G. Men'shikov)



Figure 2. The carriage of a peacefully moving monitor. (photo by A.Yu.Tsellarius)

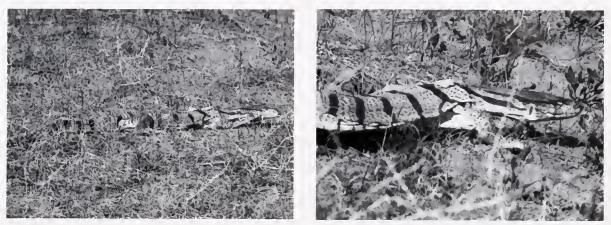


Figure 3. Concealing himself, the monitor presses his body tightly to the ground (3a, above left) and remains motionless. The animal's eyes remained open in every instance of this that we were able to make out. Convinced that he has not been noticed, the monitor moves away from the site of the encounter after a short time, creeping along the ground such that his elbows and knees frequently rise higher than the level of his back (3b, above right). The animal moving away from the observer in this fashion uses shrubs and elements of relief so skillfully as cover



Figure 4. The carriage of the monitor in flight. The animal is fleeing the observer. (photo by Yu. G. Men'shikov)



Figure 5. The male drags his body along the ground, flattening the substratum in his wake (signaling marks, below transliterated from the Russian as "zatirs") in the area which a female from his settlement (The Fourth) and males from a neighboring settlement (Rhombik and Mafiozi) had visited not long before. This took place on June 5, 1993 in a region where the borders of neighboring settlements touch and animals from both settlements visit. (photo by A.Yu.Tsellarius)



Figure 6. The "sitting dog" posture. When the monitor is moving away from a site where he had encountered danger, the more frequent display of the reference reaction "What's going on?" is quite apparent. The lizard periodically -- sometimes every few steps -- sharply "falls" on his rear, raises his head and the frontal section of his body on erect forelegs, and looks around. (photo by A.Yu.Tsellarius)



Figure 7. The display of readiness for active selfdefense characteristic of the monitor lizard facing a threat from a human or another large animal (7a, at left, top). If an opponent does not start an active operations the monitor, continuing the display of readiness for defence, slowly retreats (7b, at left, bottom). (photo by A.Yu.Tsellarius)







Figure 8. Finding himself in an unavoidable position, the monitor opens his mouth widely in the direction of the danger (8a, above left). An attack very frequently follows this and the monitor seizes his enemy in a "mortal grip" (8b, above right). (photo by A.Yu.Tsellarius)



Figure 9. The male lifts a head moving away from the female which assumes the posture of submission (for detail see description of encounter in section "Examples of behavior...", ex 1). (photo by A.Yu.Tsellarius)

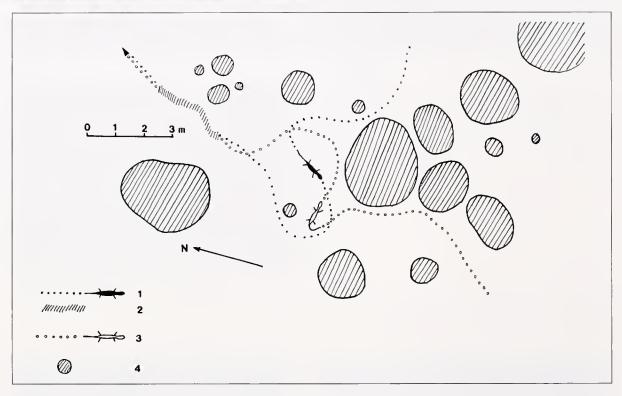


Figure 10. Diagram of trails of encounter between male and female (for detail see ex 2). 1 - male's trail and place of lying; 2 - zatir of mail; 3 - female's trail and place of lying, 4 - shrub.

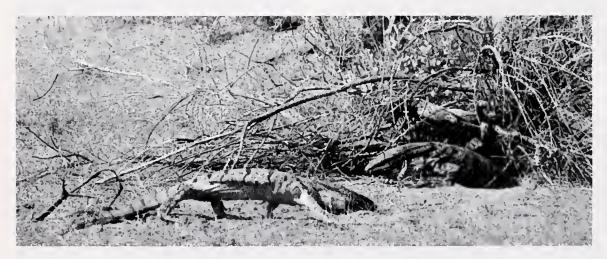


Figure 11. Female "shows the back" to familiar male which goes out of burrow (see ex 3). (photo by A.Yu.Tsellarius)

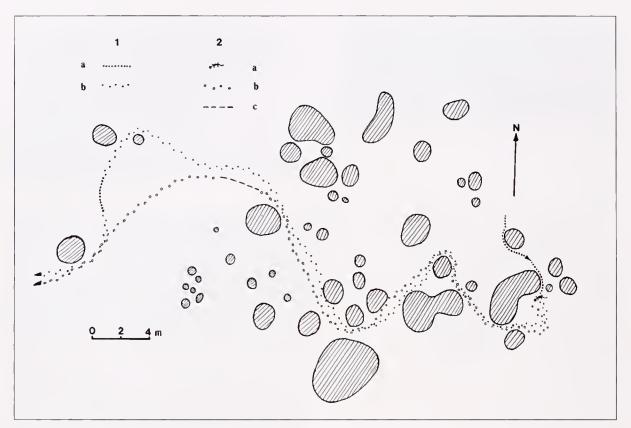


Figure 12. Diagram of trails of encounter between two males (see ex 4). 1 - trail of young male (a - the step, b - the run); 2 - trail of old male (a - place of basking, b - the run, c - "threatening gait").



Figure 13a



Figure 13b



Figure 13c



Figure 13d



Figure 13e



Figure 13f

Figure 13 (a-g). Ritual combat between males (for detail see ex 5). a - mutual "sniffing'; b, c - wrestling by necks; d - "waltz" with "showing of the backs"; e - transition to standing position on the hind legs; f - wrestling in vertical position; g - loss of equilibrium. (photo by A.Yu.Tsellarius)



Figure 13g



Figure 14a





Figure 14c



Figure 14b

Figure 14. The encounter of a settled male with a nomad (see ex 7). a - the nomad heads for the settler by "confident gait"; b - the nomad assumed a posture of appeasement; c - the nomad "sniffs" the track of the settler. (photo by A.Yu.Tsellarius)



Figure 15a

Figure 15b

Figure 15. The encounter of a settled male with a new settler (see ex 8). a - stooping new settler approaches to the "host"; b - new settler (above right) attempts to "sniff" the sacrum of "host". (photo by A.Yu.Tsellarius)

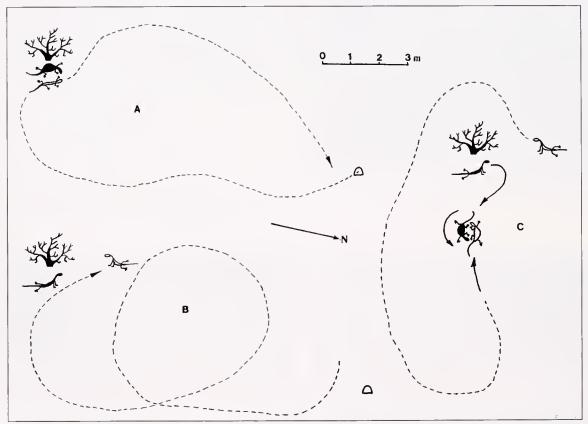


Figure 16. Diagram of encounter between two unfamiliar males (see ex 9). A, B, C - the succession of events. The resident is designated by light figure, the stranger by black.



Figure 17. Mutual amicable "sniffing" of an old male (left) and a young male (for detail see ex 10). (photo by A.Yu.Tsellarius)