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STRUCTURAL ANALYSIS OF THE QUESTING BEHAVIOR IN THE DESERT TICK *HYALOMMA ASIATICUM* P. SCH. ET E. SCHL. (IXODIDAE)

СТРУКТУРНЫЙ АНАЛИЗ ПОИСКОВОГО ПОВЕДЕНИЯ ПУСТЫННОГО КЛЕЩА *HYALOMMA ASIATICUM* P. SCH. ET E. SCHL. (IXODIDAE)

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ABSTRACT

The questing behavior of the desert tick *Hyalomma asiaticum* is described in ethological terms. Fundamental similarities in behavior of two tick species with different mode of host attack (*Ixodes persulcatus* and *H. asiaticum*) are shown.

РЕЗЮМЕ

Приведены результаты исследования поведения пустынного клеща *H. asiaticum* при поисках прокормителя, проанализированные с позиций классической этологии. Показано принципиальное этологическое сходство в поисковом поведении двух видов клещей (таежный клещ *Ixodes persulcatus* и пустынный клещ), обладающих внешне различным характером нападения на прокормителя.

INTRODUCTION

Desert ticks *Hyalomma asiaticum* P. Sch. et E. Schl., dwellers of arid deserted biotopes, spend most of their active adult life not on vegetation, but in shelters such as burrows of desert rodents, shadowed areas at roots of desert vegetation, under rhubarb leaves, etc. [Balashov, 1960, 1967; Plekhanov et al., 1977; Leonovich, 1986]. Immature stages of this species are nidicolous. An ability of these ticks to follow any person appearing in a tick-infested area is well known. This behavior of adult ticks clearly differs from the behavior of forest dwellers passively waiting for their possible hosts to approach, which are attacked only during the close contact (see Leonovich [1985, 1989], for detailed description of this kind of behavior).

Desert ticks actively follow their potential hosts using exclusively their eyes. Ticks lacking tarsi (and, correspondingly, the olfactory Haller's organs) are able to follow potential hosts, whereas ticks with painted eyes loose this ability [Plekhanov et al., 1977; Romanenko, 1981; Leonovich, 1986]. Any contrast subject, moving in front of a tick, causes its running in the direction of this subject [Romanenko, 1981]. Running tick can follow its contrast target for rather a long time period. When “tired”, it changes the direction of running toward the nearest contrast object [Romanenko, 1981].

Any comparative analysis of the questing behavior in ticks is hampered by the absence of any sufficient basis for comparison of behavior in accurate scientific terms, for example, related to the morphology of ticks. It is very hard to compare behavior of different species, analyzing papers, where the same event is described as “climbing”, “approaching”, or “reaching” (a host). In one of my previous papers [Leonovich, 1989], the entire behavior of the taiga tick *I. persulcatus* during the period of spring activity was conditionally divided into elementary behavioral acts (EBA) (the terminology by Russel et al., 1954). “Elementary” means that the given act, or element of behavioral activity is performedas a regularly repeated consequence of movements of the body appendages, occurring as a single event. Being started, each EBA lasts to the end (or finishes before it); but no EBA ever found included any unspecific movement of appendages in the given consequence. No “reflector” answers to stimulation released as a simple movement of each or other body appendage(s) were found. So, my observations confirmed the basic principles of classical ethology in relation to tick behavior [Leonovich, 1989]. The author believes that this approach can be very fruitful for a comparative analysis of the behavior of ticks.

Studies of questing behavior in the desert tick *H. asiaticum* P. Sch. et E. Schl., were performed by the author during several expeditions to Central Asia (1977–1984) and in parallel laboratory experiments (1980–1994). Only a brief sketch of these data was published in hardly available “Materials of the Regional Parasitological Conference” (5th Caucasian Conference on Parasitology, Yerevan, Armenia, 1987) [Leonovich, 1987]. In the present paper, the author describes the questing behavior of the desert tick in detail, supplementing it with data on morphology and physiology of sense organs. Many interesting data on behavior of *H. asiaticum* in nature were obtained previously by colleagues from Tomsk State University (V.N. Romanenko, G.F. Plekhanov, V.B. Kupressova) [Plekhanov et al., 1977; Romanenko, 1981, etc.]. Some of these data were used in the present publication after the critical analysis.

MATERIALS AND METHODS

The methods of examination of the desert tick behavior were described in my previous publications [Leonovich, 1986, 1987], including those for the analysis of the filmed material. All experiments were performed in spring (April-June), mainly at the Repetek Reserve (Turkmen Karakum Desert), during several seasons. Some aspects of behavior were analyzed in the laboratory. In the latter case, the ticks were either collected by the author or provided as a courtesy by Prof. A. Berdyev (National Academy of Sciences, Turkmenistan, Ashgabat). The methods of scanning and transmitting electron microscopy applied can be also found in my previous publications [Leonovich, 1979, 1986, 1999].

RESULTS

By analyzing numerous behavioral events, occurring repeatedly in the various outdoor experiments or during watching the tick behavior, the author has realized that all those events (the behavioral activity) might be represented as a consequence of a limited number of movements or the combinations of these movements, which embrace the elementary behavioral acts (EBA), as in *I. persulcatus* [Leonovich, 1989]. It is necessary to note that the majority of the elementary behavioral acts (EBA) and, what is more significant, their consequences (the behavioral programs), performed by the desert tick in nature, can be watched and examined only in the natural (outdoor) conditions. In my experiments, all attempts to observe most of natural EBAs in the laboratory were not successful. Therefore, I am sure that most of available data on the behavior of ticks obtained in the laboratory are misleading to understand the real outdoor behavior. However, the laboratory experiments do provide very important data on elements of behavioral acts and also can show some mechanisms of their realization.

In order to understand better the outdoor behavior of adult *H. asiaticum*, it is necessary to describe briefly their eyes as the main organs of distant orientation. The sensory organs of the distant reception in the desert tick were discussed by the author earlier in a series of published works [Leonovich, 1978, 1979; Ivanov, Leonovich, 1983].

Adult desert ticks (males and females) possess well-developed eyes. Eye lenses are semispherical, distinct. The fine structure of the eyes is schematically shown in Fig. 1. Main morphological and physiological features of these eyes, which are significant in understanding their role in the behavior, are the following: all photoreceptor neurons of an eye will be stimulated by every light beam that will passthrough the eye lens; only the light beam penetrating a lens from the very top of the convex hemisphere of each eye lens can reach the group of photoreceptor cells. In addition, eyes of the desert tick can detect only the changes between light and darkness and are unable to detect any complicated objects, as it has been shown in the electrophysiolocical experiments [Romanenko, 1981]. Therefore, the direction of the so-called main optical axis, i.e., an axis from which the level of light intensity can be detected by an eye, is very important (Fig. 2). It is interesting that after our first publication on the main optical axes in *H. asiaticum* [Leonovich, 1986], similar axes were distinguished by the methods of electrophysiology in *Hyalomma dromedarii*, possessing similar semispherical eye lenses [Kaltenrider et al., 1989; Kaltenrider, 1990]. The threshold of sensitivity for the eyes of *H. dromedarii* was determined as 5.2×10^6 photons per second [Kaltenrider, 1989]. The maximum sensitivity corresponded to a wave length of 470 nm, whereas the maximum behavioral activity (in the laboratory experiments) corresponded to areas of 380 and 470 nm [Kaltenrider, 1989].

The main EBAs of the desert tick during questing period are listed below. It worthy to note that the author himself understands that this listing is incomplete in some aspects — some EBAs were not yet noticed or not improved statistically (a single event, not observed repeatedly, was not taken into account).

(1). Expectancy Posture. A tick sits under a rhubarb leaf, or in shadowed area of some burrow, sometimes on a piece of concrete (frequently, but not necessary at the border between light and shadow), staying still with its forelegs raised up and spread apart. The ventral side of its body does not touchthe substrate surface. The body is inclined forward. Periodically, a tick produces Scanning Movements (see below). Some authors [Plekhanov et al., 1977] believe that such movements have nothing in common with the olfactory scanning of the environment but make it possible for a tick to find nearby contrast objects by moving the anterior part of the idiosoma with eyes from left to right. I noticed that these movements are observed more frequently in ticks that stayed at open sun for rather a long time (not proved

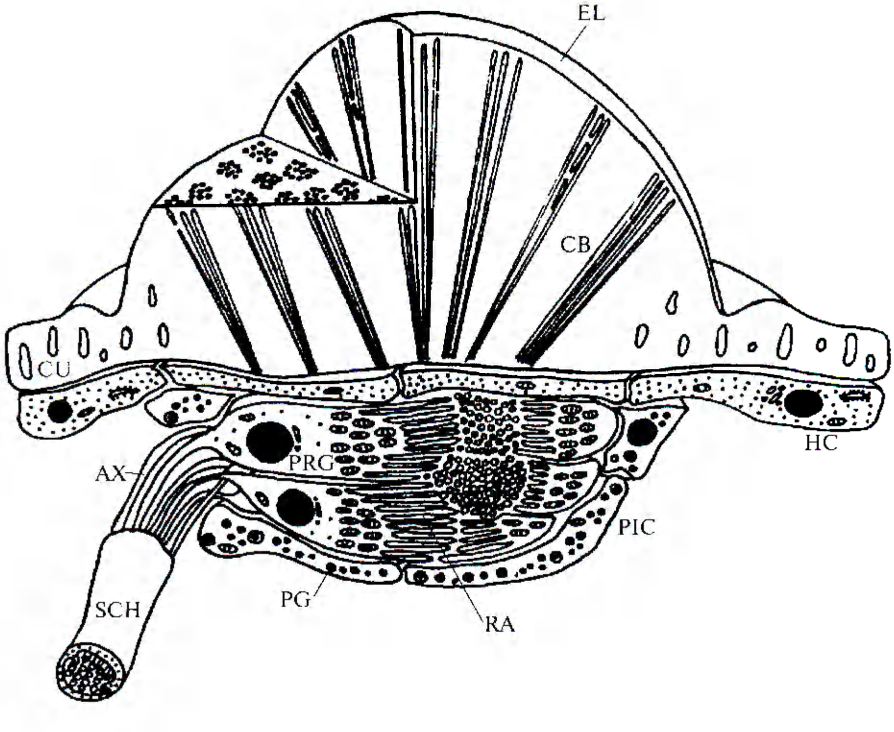

Fig. 1. Fine structure of eyes in the adult *Hyalomma asiaticum* ticks according to electron microscopy data (from Ivanov, Leonovich, 1979, with changes). EL — eye lens; CB — bundles of canals in cuticle of eye lens (maybe these structures make the lens transparent); CU — idiosomal (not transparent) cuticle; AX — axones of unipolar photoreceptor neurons; RA — common rhabdom, composed of rhabdomeres of all photoreceptor neurons (PRC) of the eye (so, any light beam that passed through the lens, will activate all photoreceptor cells of the eye); PG — granules of pigment in pigment cells (PIC), surrounding rhabdom; HC — hypodermal cells.

Рис. 1. Тонкое строение глаз взрослых клещей *Hyalomma asiaticum* по данным электронной микроскопии (из: Ivanov, Leonovich, 1979, с изменениями). EL — глазная линза; CB — пучки кутикулярных каналов линзы (возможно, обеспечивающие ее прозрачность); CU — непрозрачная кутикула идиосомы; AX — аксоны униполярных фоторецепторных нейронов; RA — общий рабдом, сформированный рабдомерами всех фоторецепторных нейронов (PRC) (таким образом, любой пучок света, прошедший через линзу, активирует все фоторецепторные клетки глаза; PG — гранулы пигмента в пигментных клетках (PIC) окружающих рабдом; HC — гиподермальные клетки.

statistically). Any shadowing of the tick in the Expectancy Posture results in a Search Running (see below) (Fig. 3). Sometimes, this posture can turn into Search Running without any distinct stimulation leading to a transition of a tick to some nearby contrast object with a shadow. In the field experiments, ticks can stop this EBA getting into a shadow. The olfactory stimulation from close distances sometimes leads to a kind of irregular, slow walking that is changed by the Search Running after a visual identification of a contrast object. The distance of identification depends on the size of an object and the distance between the object and the tick as well as on the direction of the main optical axes of eyes in relation to the ground surface (Fig. 2). For example, *H. asiaticum* adults can detect a human from the distance of 4.5—5 m, and a camel from 10—12 m [Romanenko, 1981].

(2). Search Running. It is a very specific kind of locomotion that cannot be initiated in the laboratory. A tick runs on three pair of legs, forelegs not scanning or touching the ground; with its body inclined forward at the approximate angle being 10°—20°. When the intensity of light from the direction of the main optical axis (Fig. 2) [Leonovich, 1986] of one or both eyes decreases, a tick starts to run forward; when the light intensity, percepted by eyes from the direction of the main optical axis, changes, the ticks turns in a direction of the previously "darkened" (and now "enlightened") eye. For more detail, see Leonovich [1986]. The cited publication reveals a mechanism of the tick orientation performed during the Search Running.

An ability to change rapidly the direction of running by following some contrast subject is one of the main characters of this EBA.

(3). Pursuit Running. This EBA differs from the Search Running in the following: a tick runs using legs of all four pairs, with a body being parallel or only slightly inclined towards the ground surface. The speed of running is the highest (5—7 cm per second) When the position of a target changes, the tick continues to run in the previous direction for a rather long time; when the

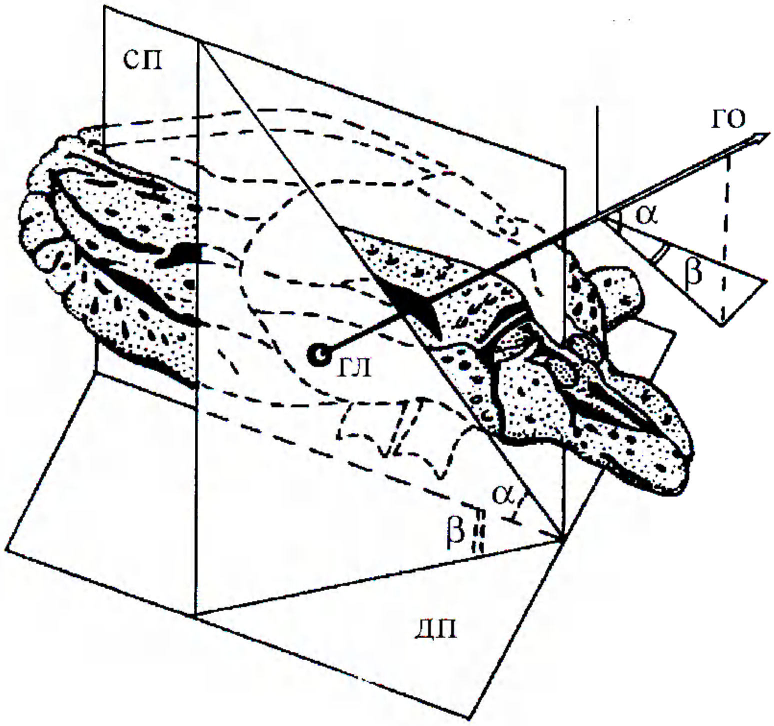

Fig. 2. Position of the main optical axis (*го*)of eye lens (*гл*)in relation to dorso-ventral (*дп*) and sagittal (*сп*) planes and longitudinal axis of the body (*по*) in the tick *Hyalomma asiaticum* (from: Leonovich, 1986).

Рис. 2. Расположение главой оптической оси (*го*) глазной линзы (*гл*) относительно дорзовентральной (*дп*) и сагиттальной (*сп*) плоскостей и продольной оси тела (*по*) клеща *Hyalomma asiaticum* (из: Леонович, 1986).

target is lost, Pursuit Running turns into Shelter Running (see below) or, more frequently, into Search Running from relatively short distances, depending on angular size of a host detected from directions of main optical axes of eyes [Leonovich, 1986].

The main feature of this EBA, together with the specific mode of the locomotion, is an ability to retain the direction of running independently of changing environmental conditions. When a tick in the state of Pursuit Running is transported several meters away, it continues to run in the given direction, although no target now exists in this direction. The same fact was mentioned by Plekhanov et al. [1977], although they paid no attention to differences in modes of running, and mixed them altogether. The same authors assumed that a tick "remembered" the direction of running

(4). Shelter Running. A tick runs on all four legs, with the body inclined forward. No host stimulation affects the tick in this EBA (however, being touched by a researcher, the tick accepts the Death Simulation Posture). Shelter Running usually finishes by accepting a Resting Posture. Most frequently (if at all), this EBA is the only EBA performed by a tick in the laboratory. My numerous attempts to initiate other modes of running (locomotion) in the laboratory failed. It means that the real (natural) behavioral activity is indirectly regulated by a composition of numerous environmental conditions; and it is in most cases impossible to simulate these conditions artificially. Therefore, any laboratory experiments with *H. asiaticum* can reveal only the peculiarities of this EBA (including reactions to light, olfactory stimulation, etc.), and have nothing in common with the real outdoor behavior.

(5). Locomotion to a Zone of Contact. This EBA is not called "running", because a tick moves rather slowly, on all four legs. In nature, this EBA is usually performed during walking of a tick from some resting place (in a burrow of some desert vertebrate, near the stalk of a rhubarb leaf, etc.) finishing in the Expectancy Posture, sometimes at the light-shadow border.

(6). Climbing. This locomotion usually follows Pursuit Running or Search Running, and is, probably, directed by a negative geotaxis. On artificial cardboard models, after Climbing, a tick starts to search a place for possible bloodsucking. In nature, when this EBA is occasionally performed on some desert shrub, the tick, after climbing up the plant, rapidly goes down and takes the Expectancy Posture in shadowed area at roots. So, a tick starts to examine a possible host in relation to its suitability for bloodsucking only after instinctive Climbing.

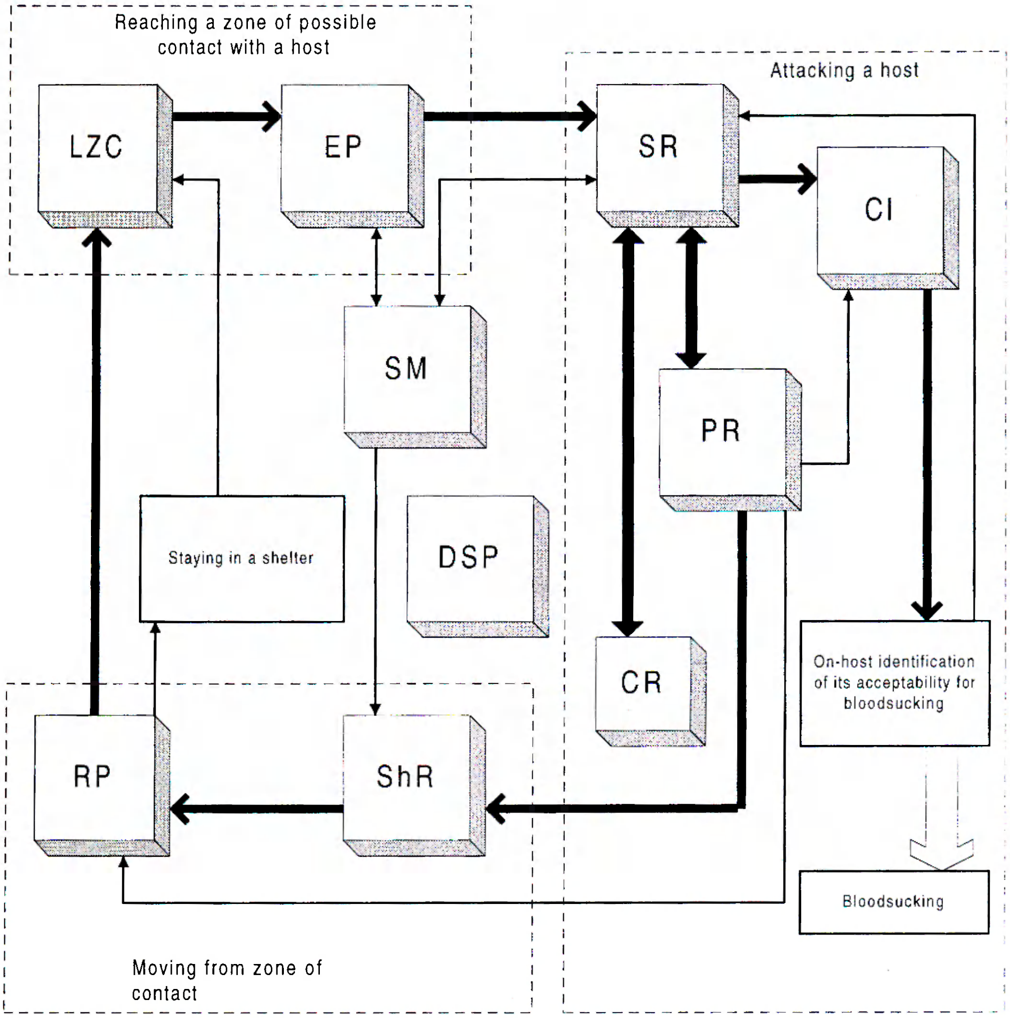

Fig. 3. Basic elementary behavioral acts (in baguette frames) and their consequences in the questing behavior of the Desert tick *Hyalomma asiaticum* (explanations in the text). Locomotions: LZC — locomotion to zone of contact; SR — searching running; PR — pursuit running; ShR — shelter running; CR — circle running; C — climbing. Postures: EP — expectancy posture; RP — resting posture; DSP — death simulation posture. Movements: SM — scanning movement. Dotted lines border main behavioral programs. Thicker arrows indicate more frequent sequences of behavioral acts.

Рис. 3. Основные элементарные поведенческие акты (в багетных рамках) и их последовательные сочетания в поисковом поведении пустынного клеща *Hyalomma asiaticum* (пояснения в тексте). Локомоции: LZC — перемещение в зону контакта; SR — поисковый бег; PR — бег преследования; ShR — бег в укрытие; CR — бег по кругу; C — напозлание. Позы: EP — поза ожидания; RP — поза отдыха; DSP — поза затаивания. Движения: SM — движение сканирования. Пунктирные линии ограничивают основные программы поведения. Жирные стрелки обозначают более часто встречающиеся последовательности поведенческих актов.

(7). Resting Posture. EBA following Shelter Running. Ventral part of the body is frequently in contact with the surface of substrate. Being stimulated, a tick either shows no reaction, or takes the Death Simulation Posture (see below). In nature, this posture is usually taken by a "tired" tick after a long running, usually in the shadow, under rhubarb leaves, and, frequently, after burying into sand at roots of any desert shrub. Burying just followed continuous Shelter Running stopped by an obstacle.

(8). Death Simulation Posture. This posture is sometimes taken by a disturbed tick (e.g., taking a running or immobile tick from the ground by fingers; touching a running tick with a glass rod or a piece of wood, broken branch, etc.). Morphologically this posture is similar to that in the taiga tick *I. persulcatus* [Leonovich, 1989]. All legs are contracted to the ring-shaped position. No reactions are exhibited upon any stimulation. In contrast to *I. persulcatus*, the mechanically disturbed tick can take this posture from any EBA. However, this is not necessary, and I failed to prove statistically any regularity in starting this EBA. Therefore it is not connected by arrows with any of other EBAs (Fig. 3). It can be mentioned, that some individuals turn into this position easier than others. After the variable period of time the

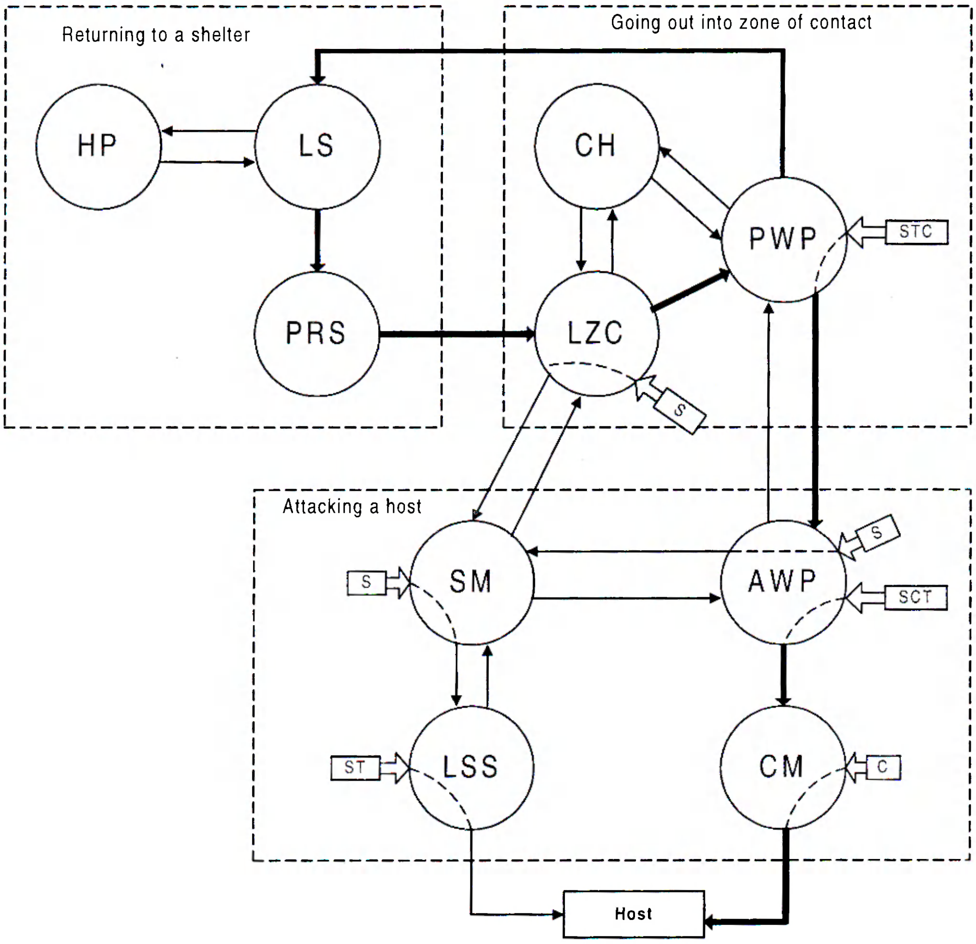

Fig. 4. Sequence of elementary behavioral acts in behavior of the Taiga tick *Ixodes persulcatus* in a period of spring activity (from: Leonovich, 1989).
Postures: AWP — active waiting posture; HP — hiding posture; PRS — posture of resting in a shelter; PWP — passive waiting posture. Locomotions: LS — locomotion to a shelter; LSS — locomotion to a source of (olfactory) stimulation; LZC – locomotion to a zone of contact. Movements: CH — cleaning of Haller's organs; CM — climbing movement; SM — scanning movement. Modes of host-produced stimuli: S — smell (olfactory stimulus); C — contact (tactile) stimulus; T — temperature stimulation.

Рис. 4. Сочетание элементарных поведенческих актов в период весенней активности у таежного клеща *Ixodes persulcatus* (по: Леонович, 1989). Позы: AWP — поза активного ожидания; HP — поза затаивания; PRS — поза отдыха в укрытии; PWP — поза пассивного ожидания; локомоции: LS — локомоция в укрытие; LSS — локомоция к источнику (запаховой) стимуляции; LZC — локомоция в зону контакта; движения: CH — чистка органов Галлера; CM – движение прицепления; SM — движение сканирования. Модальности продуцируемых хозяином стимулов: S — запах (обонятельный стимул); C — контактный (тактильный) стимул; T — температура (температурный стимул).

undisturbed tick stops simulation of death, performing any type of running.

(9). Scanning Movements. A tick moves its raised forelegs with Haller's olfactory organs [Leonovich, 1978] as if scanning the air. The behavior can be performed in Expectancy Posture or during Search Running (Fig. 3). In the latter case, a tick frequently stops to perform this EBA. It highly resembles the scanning movements of ticks of the genus *Ixodes* [Leonovich, 1989].

(10). Circle Running. Sometimes an undisturbed tick, without any stimulation, starts to run, making widening circles on ground surface. A tick moves on all four legs, sometimes stopping to perform Scanning Movements. Usually this EBA turns into Search Running. Frequently, when a tick looses a host during Search Running, it performs Circle Running in order to find the lost contrast object, and when successful, continues to follow the host (Fig. 3).

Some aspects of behavioral activity of ticks were not included into the scheme (Fig.3), because they were observed in nature only occasionally, or were observed mainly in the laboratory conditions. Therefore, the placing of these EBAs in the patterns of the questing behavior remains questionable. They include the cleaning of legs (similar to cleaning of Haller's organs, found in the taiga tick [Leonovich, 1989]), that was observed only in the laboratory (or in the glass tubes, but not in the nature); climbing down from an object insufficient for feeding after some period of staying on it; postures or locomotion in a shelter.

DISCUSSION

In general, the entire behavioral activity of the adult desert ticks (males or females) during the questing period may be conditionally divided into three main behavioral programs, which are similar to those described previously in the taiga tick: (1) reaching a zone of possible contact with a host; (2) attacking a host; and (3) moving from a zone of contact (Fig. 3). In the taiga tick, one can distinguish (1) going out into a zone of contact; (2) attacking a host; and (3) returning to a shelter (Fig. 4).

Behavioral program of reaching a zone of a possible contact with a host includes two EBAs: Expectancy Posture and Locomotion to a Zone of Contact (Fig. 3). The latter probably corresponds to the Locomotionto Zone of Contact in the taiga tick [Leonovich, 1989]. During the daytime adult desert ticks spend rather a long period in shelters (in burrows of *Rhombomys*, under rhubarb leaves, in the litter under saxaul shrubs), and only after moving from these shelters to the open place or to the border between the light and shadow they take the Expectancy Posture and are ready to attack a host. According to Balashov [1967], *H. asiaticum* possesses a regular alternation of periods of activity lasting for 10–20 days and periods of staying in shelters with a high level of the relative humidity, lasting for 2–4 days. The Expectancy Posture resembles very much the Passive Waiting Posture of the taiga tick (Fig. 4), with forelegs being raised and set apart. However, while *I. persulcatus* uses this position of forelegs to indicate the appearance of a host from the long distances by means of olfaction [Leonovich, 1989], it is rather meaningless in the desert tick. I assume that this is a kind of the "behavioral rudiment", demonstrating together with other features (see below) shared sources of the questing behavior in the aforementioned species. It is interesting that Cleaning of Haller's Organs, typical of the behavior of the taiga tick [Leonovich, 1989], was repeatedly observed in the laboratory in *H. asiaticum*.

The behavioral program of attacking a host includes four kinds of locomotion (three kinds of running and one climbing locomotion). So, an active mode of the host attack is really typical of the desert tick. Expectancy Posture, after shadowing of one or both eyes from the direction of the main optical axes of their eye lenses turns into Search Running. During this EBA a tick can follow a moving host for rather long distances (up to 72 m in my experiments). The successfulSearch Running finishes by Climbing and the following bloodsucking (Fig. 3). The orientation mechanism regulating this EBA (Search Running) probably developed on the basis of a reaction of negative phototaxis, supplemented with a transformation of the eyelenses. In laboratory, *H. dromedarii* ticks demonstrated a distinct reaction of scototaxis [Kaltenrider, 1990]. The immature desert ticks are burrow dwellers (living mainly in the burrows of *Rhombomys opimus*). So, a reaction of negative phototaxis, typical of all burrow dwellers, could be evolutionary transformed in adults into such a way, that a tick, demonstrating fundamentally scototaxic behavior, in reality approaches a contrast subject, that in the desert is in most cases a host or, at least, a shelter [Leonovich, 1986].

When the first visual stimulation gets no further confirmation, e.g., a contrast object is rather far and, therefore, lost because of the tick getting into some fold or depression on the ground surface, Search Running turns into Pursuit Running (Fig. 3), allowing the tick to retain the direction of running and making it possible to return to Search Running being more closely to the host (Fig. 3). When Pursuit Running appears to be unsuccessful and the tick is overheated, the latter EBA turns into Shelter Running, finishing by Resting Posture (Fig. 3).

When the host is completely lost, the mechanism of orientation provokes running to any contrast subject (usually, to some desert shrub), thus helping the tick to survive for some more time before meeting the another prospective host [Leonovich, 1986].

As it was mentioned above, when a contrast object is reached, a tick climbs up on it, irrespective of the nature of the object offered, for example, humans, sheep, cardboard boxes of various sizes moving or staying still. Many times ticks were observed climbing the saxaul shrubs. It confirms a previous assumption [Romanenko, 1981] that the vision plays a major role in the host finding, whereas the examination of acceptability of this "host" for bloodsucking takes place only on this host itself.

In the taiga tick, the main role in attacking a host belongs to the climbing movement following the active waiting posture, after stimulation with the olfactory, temperature, or tactile stimuli [Leonovich,1989], whereas the locomotion to a source of stimulation is less significant (Fig. 4).

However, many other very similar EBAs, including the aforementioned ones, can be found in questing behavior of both species: Resting Posture and posture of resting in ashelter, Scanning Movement (in both species), Death Simulation Posture and hiding posture, Climbing and climbing movement, in *I. persulcatus* and *H. asiaticum*, respectively. One can assume, that both modes of questing behavior developed on the same fundamental basis, retaining many relics in behavior of both species and demonstrating how evolutionary development of some EBAs together with changing of their sequences can form such different modes of behavior, belonging to the same type: questing behavior in pastures.

A detailed analysis of the evolution of the tick behavior will be a subject for a special publication. In conclusion, it is necessary to underline that the described above method of analysis could be very fruitful in a computer analysis and modeling of the behavior of ticks and mites.

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