Acarina 10 (1): 81–84

THE TYPES OF PATHOGEN TRANSMISSION BY BLOODSUCKING ARTHROPODS: TICKS AS A MOST SPECIFIC VECTORS

ТИПЫ ПЕРЕДАЧИ ВОЗБУДИТЕЛЕЙ КРОВОСОСУЩИМИ ЧЛЕНИСТОНОГИМИ: КЛЕЩИ КАК СПЕЦИФИЧЕСКИЕ ПЕРЕНОСЧИКИ

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Key words: bloodsucking arthropods, ticks, mites, pathogen, transmission
Ключевые слова: кровососущие членистоногие, клещи, возбудители, передача

ABSTRACT

The main types of pathogen transmission by bloodsucking arthropods are surveyed. Transmission to vertebrate hosts and pathogen exchange between vectors inside the population were analyzed as a basis of foci stability.

РЕЗЮМЕ

Рассмотрены основные типы передачи патогенов кровососущими членистоногими позвоночным хозяевам. На примере клещей представлены типы обмена патогенами внутри популяции переносчиков, обеспечивающих стабильность очагов трансмиссивных инфекций.

All arthropods, including ticks, on or inside which pathogenic organisms can survive and whence they can be transferred, are termed as vectors. Parasites transmitted by arthropods range widely from eukaryotes, including helminthes, to prokaryotes and viruses.

One group of prokaryotes (e.g. sporogenic *Anthrax* bacteria) and viruses (e.g. rabbit's myxoplasmosis agent), are capable to contaminate vertebrate host lasting long enough on the mouthparts of relatively small quantity of bloodsucking insects (e.g. horseflies, fleas). Other pathogens being able to survive in the gut of non-bloodsucking insects (e.g. domestic flies, cockroaches), are capable to be dispersed by feces or regurgitation of arthropods. Representatives of both these groups are called contaminators. The efficiency of contamination depends on the ability of pathogenic agents to survive in or on the organism of their temporary vector.

The term specific vector is mainly to be used as regards the large group of vectors, mostly bloodsuckers, whose organism provides not only a pathogen's survival but also its propagation to the level of an invasive stage capable of infecting a vertebrate host. This is quite characteristic of Protozoa or helminthes. The former not only increase their biomass but also develop visibly distinctive invasive forms. The helminthes migrate inside the body of the vector, from gut to mouthparts, molting several times to reach a stage invasive for a vertebrate host.

Specificity of bloodsucking vectors is conditioned by the following criteria [Alekseev, Kondrashova, 1985, with changes]:

1. Any pathogen consumes the energy sources accumulated by its bloodsucking host. The parasite propagates to enhance its chances of transmission.

2. A specific stage in the pathogen's life cycle is developed inside the arthropod host. This developmental stage can be distinguished morphologically (helminthes, Protozoa, agent of plague) or antigenically (bacteriae, viruses).

3. Highly efficient mechanisms of transmission through sting or specific contamination are characteristic.

4. The pathogen transmitted is relatively harmless to the vector either at the individual or the populational level [Kennedy, 1975].

5. Both a pathogen dosage optimal for the vector to be infected or a vertebrate host and the ability of pathogen exchange on an aviremic[1] host while bloodsuckers feed simultaneously on the same ver-

[1]Aviremic hosts are those tolerant to infection or they develop it much later than bloodsuckers are able to exchange the pathogen between infected and naïve specimens.

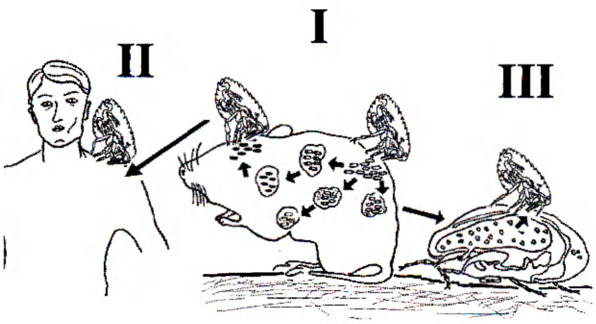

Fig. 1. Plague agent routes of transmission and circulation. I — the system: flea, *Y. pestis* and susceptible rodent; II — transmission of plague to man; III — soft tick *Ornithodoros* as a "living can" of *Y. pestis* for flea.

Рис. 1. Пути передачи и циркуляции возбудителя чумы. I — система: блоха, *Y. pestis* и чувствительный грызун; II — передача чумы человеку; III — аргасовый клещ *Ornithodoros* как "живые консервы" — источник *Y. pestis* для блохи.

tebrate host are developed [Jones et al., 1987; Alekseev, Chunikhin, 1991].

Mechanism lies in pathogen transmission through the sting/bite of a bloodsucker. Pathogens are ejected together with the ectoparasite's saliva. All mites and ticks, mosquitoes, and many other arthropods demonstrate such a mechanism of transmission. Helminthes infest the host during the bite of a fly but not with saliva. They are able to perforate the bloodsucker's soft labium that remains in tight contact with the wound their mouthpart "knife and scissors" would make in the host.

The mouthparts of ectoparasitic mites, ticks and insects are highly varied in construction but invariably well-adapted to blood sucking. The stiff daggers and scissors of a horse-flea's mouthparts are very quick to deplete in spite of the rough skin of the ruminants. The rough, scissor-like tick chelicerae provide a relatively large hole in the host skin, inside which a chippy sword of the hypostome is inserted to ensure tick attachment. Very often, a special kind of saliva, which hardens in contact with air and is thus termed cement, anchors the tick mouthparts in the skin. This is necessary to fix a hard tick whose feeding takes several days. Bloodsucking arthropods' saliva is justly called a pharmacological laboratory [Ribeiro, 1995], as it either permits to irritate the host skin (lice) or to anaesthesize the place of bite (triatomid bugs, ticks and mites), or to dilate host blood vessels and suppress blood clotting. Tick saliva is perhaps the most multifunctional in suppressing not only blood clotting but also host immune reactions. The more elaborate the study of bloodsuckers' saliva, the more diverse the features disclosed. The presence of specific insect- or tick-borne pathogens not only alters arthropod host behavior (e.g. tick-borne encephalitis virus enhances the vector's locomotor activity) but also its saliva.

Vertebrate host blood consumption is absolutely prerequisite to bloodsucking arthropod survival. Yet blood is the main but not the only pathway of pathogen transmission. Devouring the blood gut content of the previously fed stages is relatively common among bloodsuckers.

Often enough, soft tick subadults suck the gut content of fed older specimens, thus engulfing relapsing tick fever pathogens (e.g. *Borrelia duttoni*). Likewise, pathways of transmission and circulation, e.g. donor rodent—flea—recipient rodent, are more than one in the plague agent *Yersenia pestis* transmitted through a flea bite (Fig. 1). It can also be acquired by direct contact of a healthy man with an ill one in case of a pulmonary form of the disease or carried from a sucked-up, infected, soft tick to a hungry flea (Fig. 1, III). At present a telluric way of plague agent maintenance is in debate. *Yersenia pestis* pathogens appear preservable and are capable of re-entering the animal—flea circle at a later time. *Anthrax* bacilli in the spore form can remain conserved in the soil for decades and then infect wild animals or livestock. *Anthrax* kills vertebrate host while horse-flies feeding on the dying or freshly dead animals may disseminate this agent as contaminators. Horse-flies carry about the spores on their mouthparts. Even such a typical vector-borne pathogen as the malaria agent can circulate being transmitted from an infected mother to a child or from an infected man to a healthy one by blood transfusion. In these cases, asexual forms of parasite are transmitted.

The pathways of tick-borne pathogen transmission seem the most complex (Fig. 2). The best studied examples concern tick-borne encephalitis virus, an agent the most dangerous to man [Alekseev, 1993].

The first, "classical" pathway (Fig. 2, I) implies infected blood consumption by an adult female tick feeding on a vertebrate showing viremia (high concentrations of the virus in host blood). For a long time this pathway was believed the main one.

It includes:

(a) TRANSOVARIAL transmission, implying infected blood consumption and pathogen transmission to the egg (beginning of the F1 progeny, Fig. 2, I). Transovarial virus transmission has also been proved for Diptera, i.e. mosquitoes as vectors

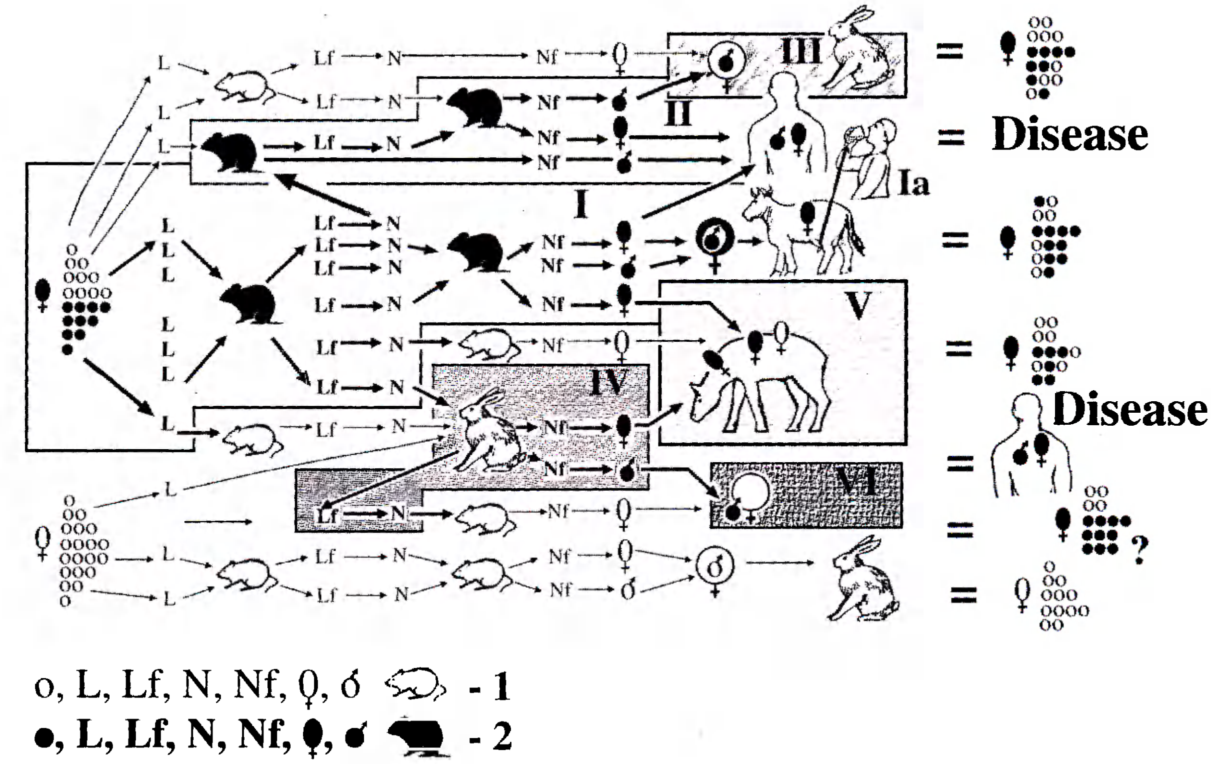

Fig. 2. Tick-borne encephalitis virus routes of transmission. I — "classical"(transmissive) route from egg to egg by feeding on the susceptible animals with threshold quantity of virus in the blood; Ia — man infection by virus containing goat or cow milk; II — transphasic transmission: naive larva gets virus on infected susceptible animal; III — sexual transmission: infected male transmits virus to naive female during copulation; IV — virus exchange between infected nymphs and naive larvae cofeeding not near each other on the animal without viremia (distant transmission); V — virus exchange between specimens cofeeding near each other on aviremic (not susceptible to the virus) animal (transsalival transmission); VI cannibalistic route of transmission: infected male consumes hemolymph from naive female and injected virus infected saliva in her body; 1 — naive tick and animal: o — ova, L — larva, Lf — fed larva, N — nymph, Nf — fed nymph, ♀ — female, ♂ — male; 2 — same: infected ticks and animals.

Рис. 2. Пути передачи вируса клещевого энцефалита. I — "классический" (трансмиссивный) путь: от яйца до яйца с питанием на чувствительном животном с надпороговой вирусемией; Ia — заражение человека молоком козы или коровы; II — трансфазовая передача: незараженная личинка получает вирус, питаясь на чувствительном животном; III — половая передача: от зараженного самца самке при копуляции; IV — обмен вирусом между зараженными нимфами и незараженными личинками при совместном питании вдали друг от друга на животном без вирусемии (дистантная передача); V — обмен вирусом между незараженными и зараженными клещами, питающимися из одного очага воспаления на животном без вирусемии (чрезслюнной обмен вирусом); VI — омовампирический обмен вирусом при питании зараженного самца на голодной незараженной самке: поглощение гемолимфы и выделение зараженной слюны; 1 — незараженные клещи и животные: о — яйцо, L — личинка, Lf — напитавшаяся личинка, N — нимфа, Nf — напитавшаяся нимфа, ♀ — самка, ♂ — самец; 2 — тоже зараженные клещи и животные.

of yellow and Denge fevers, and sand-flies as vectors of phleboviruses (e.g. papattasi fever).

(b) TRANSPHASIC transmission (Fig. 2, II) must include at least one of the following steps: transmission of a pathogen from fed and infected larvae to nymphs; survival of the pathogen in hungry and fed nymphs and its transmission to adults following the nymph's moult. Adults can transmit the virus to man and an animal. Transphasic transmission is also typical of *Rickettsia* and *Borrelia*, of the relapsing tick fever agent transmitted by soft ticks, and of the Lyme disease agent transmitted by hard ticks of the genus *Ixodes*.

The ability of SEXUAL transmission of tick-borne encephalitis (TBE) virus, *Rickettsia* and Lyme disease agents from males to females has been proved as well (Fig. 2, III).

A CANNIBALISTIC type of pathogen exchange cannot be excluded as, e.g., *Ixodes* tick males sometimes feed not only on fed females but also on hungry specimens (Fig. 2, VI).

At present the classical pathway of pathogen transmission (Fig. 2, I) is no longer considered as the main one. Pathogen exchanges between cofeeding vector specimens (Fig. 2, IV) belonging to various age groups, e.g. nymphs and larvae of ticks or, ipso facto, different generations, is most probably the most efficient way of obtaining the viruses and other pathogens by uninfected specimens from infected ones. Ticks issuing saliva near each other may transfer pathogen regurgitated by infected specimens in the common focus of inflammation in the host skin. Such a type of transmission is called TRANSSALIVAL (Fig. 2, V) and may come about both on a viraemic and an aviraemic vertebrate host.

Similar exchanges of pathogens, not only of viruses but of borreliae and many others as well, can take place when ticks feed on infected and aviraemic animals apart. Such a type of transmission is termed infection on an aviraemic host, or DISTANT (Fig. 2, IV) infection. The mechanism of such an exchange is fit out by the host immune cells, which transfer absorbed pathogens from one focus of inflammation to another.

The manifoldness of the described types of pathogen transmission secures stability in time and space of the foci of infection transmitted by bloodsucking insects, mites or ticks.

ACKNOWLEDGEMENTS

Vice-President of PENSOFT Publishers Mr. Sergei Golovatch was kind enough as to correct the English of an advanced draft. The research described in this publication was made possible in part by Grant 02-04-48654 from the Russian Basic Research Foundation.

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