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THE ROLE OF MAMMALS IN THE CIRCULATION OF ŤAHYŇA VIRUS*)

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Abstract. An analysis is given of the role of mammals in the circulation of Ťahyňa virus on the basis of the results obtained by Czechoslovak, Austrian and Hungarian virologists.

Ťahyňa arbovirus, the first European representative of the California group, was isolated in 1958 in Czechoslovakia (Bárdoš and Danielová 1959). In the years following the isolation great attention was paid to the elucidation of its medical importance and natural cycle. Results of studies undertaken to the elucidation of the medical importance were already summarized and published (Bárdoš 1974). In the present paper the results of studies concerning the role of mammals in the circulation of Ťahyňa virus are evaluated.

The initial stage of the studies concerning the role of vertebrates in the circulation of Ťahyňa virus was influenced by the facts published on the important role of birds in the natural cycle of most mosquito-borne viruses. That is why attention was paid to birds in the beginning of these studies. The results of experimental works have shown, however, that birds of Central Europe are resistant to Ťahyňa virus infection (Šimková 1962).

The attention was focused therefore on mammals living in natural foci of Ťahyňa virus infection. Virus neutralization and heamagglutination tests were used for the detection of antibodies in the sera of wild and domestic mammals. In several European countries serological surveys were undertaken. In this paper, however, the results obtained by Czechoslovak, Austrian and Hungarian virologists only are summarized since there are no great differences in the biocenosis of the natural foci of Ťahyňa virus infections inthese three countries. Table 1 shows that the highest percentage i.e. 36.1 % of virus neutralizing antibodies were detected in the hare. The next is the hedgehog with 3.1%. From Rodentia only 1 specimen of *Citellus citellus* out of 98 and a specimen of *Microtus arvalis* out of 83 tested were positive. The number of tested specimens from foxes, wild boar and roe-deer is too low to draw any conclusion from it.

These results justify the attention paid to the hare and hedgehog and it was decided therefore to elucidate experimentally their possible role in the natural cycle of Ťahyňa virus. Experimental studies were started with the extraneurally passaged strain „236“

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of Ťahyňa virus (Bárdoš et al. 1961). It was previously shown in experimentally infected laboratory mammals that this strain is more suitable for viraemia studies than the neuroadapted (i.e. passaged) variant of the same strain (Bárdoš 1963). Details are seen in Table 2. The titer of virus in the blood of white mice, experimentally infected with the extraneural variant, was higher than with the neuroadapted one and lasted longer. These experiments also revealed that only young mice of 8—9 g and younger react to experimental infection with viraemia and the formation of antibodies. In older mice (20 g) only formation of antibodies was detected.

Table 1. Ťahyňa virus neutralizing antibodies in wild mammals of Central Europe

Order	Species	No. of posit./samples	% posit.	Ref.
Insectivora	*Erinaceus roumanicus*	7/164	3.1	3, 22, 38
	Sorex araneus	0/13		4
	Crocidura leucodon	0/15		
	Crocidura suaveolens	0/2		
Chiroptera	*Myotis myotis*	0/30		39
	Nyctalus noctula	0/112		4
	Pipistrellus nathusii	0/1		
	Plecotus austriacus	0/1		
Lagomorpha	*Lepus europaeus*	163/451	36.1	4, 6, 22, 40
Rodentia	*Citellus citellus*	1/98	1.0	4
	Mus musculus	0/1		4, 22
	Apodemus flavicollis	0/42		6, 22
	Apodemus sylvaticus	0/1		4
	Apodemus microps	0/22		
	Cricetus cricetus	0/40		
	Clethrionomys glareolus	0/53		6, 22
	Pitymys subterraneus	0/2		4
	Microtus arvalis	1/83	1.2	4, 6, 22
Carnivora	*Vulpes vulpes*	2/9	?	4, 22
Artiodactyla	*Sus scrofa*	1/3	?	4
	Cervus elaphus	0/1	?	22
	Capreolus capreolus	4/15	?	4, 6, 22

Table 2. Viraemia in laboratory mammals experimentally infected with Ťahyňa virus

Species	Weight in g	Strain e or n*	Passage history (x^{th})	Inoculum s.c. $\log_{10}LD_{50}$†	Viraemia		Ref.
					in days	max. titer in $\log_{10}LD_{50}$	
Mus musculus	20.0	236e	7	4.5	0	0††	8
v. *alba*	8—9.0	236e	7	4.5	4	2.5	
	5.1	236e	7	1.2	6	3.5	
	4.9	236n	9	2.2	5	1.5	
	7.0	236n	9	2.3**	4	0.5	9
	7.4	236e	7	2.0**	4	2.6	
	7.5	236n	9	3.2**	3	2.2	
	7.0	236e	7	3.7**	5	2.0	
Mesocricetus	80.0	236e	4—7	8×1.0	0	0	37
auratus	80.0	236e	4—7	2.7—3×5.3	4—5	2.2—3.5	

† according to i.c. control titration in young mice (0.03), †† tested in 2—3 day-old baby mice (i.c./0.01 ml), *e extraneural, *n neuroadapted, **i.c. inoculation The same symbols apply to Tables 3 and 5.

These findings influenced the approach to the study of experimental infections in wild and domestic mammals in the future. The main points of this approach were formulated as early as 1960 (Bárdoš 1962). Table 3 shows that the young hares weighing 400 g react to an experimental infection with a viraemia of 3—5 days duration with a titer of 2.5—3.2 $\log_{10}LD_{50}$ i.c. (0.03 ml) and with antibodies formation. This viraemia can be considered sufficiently high and long to ensure an infection of the biological vector *Aedes vexans* (Danielová 1966). Thus the young hare may be considered as a host and probable amplifier of Ťahyňa virus in nature awaiting still the decisive proof of his amplifier role, i.e. the transmission of Ťahyňa virus from a viraemic hare to *A. vexans* and the isolation of Ťahyňa virus from the blood of the naturally infected hare.

The possible role of the hedgehogs in the natural cycle of Ťahyňa virus was theoretically very interesting since hedgehogs are hibernating animals. In experimentally infected hedgehogs a high level viraemia (3.0 $\log_{10}LD_{50}$ i.c./0.03 ml) of 6—8 days duration with antibody formation was observed (Table 3). In experiments where hedgehogs were forced to an immediate experimental hibernation after their infection, Ťahyňa virus could be recovered from their blood after 140 days of hibernation (Šimková 1966). Ťahyňa virus could not be isolated from the blood of experimentally infected hedgehogs hibernating in nature after their awakening (Málková et al. 1969). Naturally hibernating hedgehogs obviously do not ensure the survival of Ťahyňa virus over the winter months and their infrequent infection in natural conditions and their low abundance (Aspöck and Kunz 1970) indicate that they cannot be included among important host and probable amplifiers of Ťahyňa virus in nature.

The results of experimental infection of *Citellus citellus* and *Glis glis* (Table 3.) are interesting and the level of viraemia and its duration is considered to be sufficient to

Table 3. Viraemia in wild mammals experimentally infected with Ťahyňa virus

Species	Age or weight	Strain e or n⁺	Passage history (x^{th})	Inoculum s.c. $\log._{10}LD_{50}$†	Viraemia in days	Viraemia max. titer in $\log._{10}LD_{50}$†	Ref.
Erinaceus roumanicus	500 g	236 e	6—7	0.07—0.8	0·	0	38
	500 g	236 e	6—7	2×1.0—2×5.0	6	3.0	
	243—435 g	236 e	9	4.0	8	>2.5††	29
Talpa europaea	?	236 e	9	?	2	TR.††	28
Myotis myotis	juv.	181 n	?	4.0	0	0††	27
Nyctalus noctula	?	236 e	7	1.5—5.5	0	0	39
Lepus europaeus	400 g	236 e	4—7	8×1.0	3	>2.4	37
	400 g	236 e	4—7	4.6—5.8	3—5	2.5—3.2	
Sciurus vulgaris	?	181 n	27	7×2.6	0	0	34
Citellus citellus	3 mo.—1 year	236 e	9	4.0—2×6.2	4—5	2.4—>3.5††	28
Glis glis	110—150 g	236 e	9	6×3.3—5×4.7	4.5	1.7—>3.0††	28
Vulpes vulpes	10 weeks	Cul. 13342n	2	5×4.0††	1··	0.2††	2
	10 weeks	236 e	?	4.0††	2—3	0.4††	
Meles meles	10 weeks	Cul. 13342n	2	5×4.0††	2	1.4††	2
	10 weeks	236 e	?	4.0††	2	TR.††	

· in 1 out of 11 viraemia detected, ·· in 1 out of 2 viraemia detected, TR. = traces.

ensure an infection of *A. vexans* but in wild *Citellus citellus* antibodies were only sporadically detected (Table 1). Data on the frequency of the natural infection in *Glis glis*, are not available.

In wild mammals belonging to the order of Carnivora and Artiodactyla, experimental infection with properly chosen strains of Ťahyňa virus was undertaken only in the species *Vulpes vulpes* and *Meles meles* (Table 3). A low level viraemia of 2 days duration with formation of specific antibodies was detected in both species. Only the experiments simulating natural conditions may answer the question if the detected viraemia is sufficient to ensure infection of *A. vexans*.

Now let us consider the experiments in mammals with negative results when viraemia was not detected after experimental infection. Bats *Nyctalus noctula* can be exluded from the list of hosts since neither antibodies in specimens caught in nature nor viraemia were detected after their experimental infection with the extraneural strain „236“. In the case of wild young *Myotis myotis* no antibodies were detected. Experimental infection of these species provoked no viraemia but formation of antibodies only. No definite conclusion can be drawn from these experiments since a neuroadapted strain was used (Table 3).

Wild *Sciurus vulgaris* has not been up to now tested for Ťahyňa virus antibodies. The experimental infection was done with a high passaged (27th) neuroadapted strain. No viraemia but formation of antibodies only were detected. Conclusions cannot be drawn likewise from the results of these studies. The role of these species in the natural cycle of Ťahyňa virus ought to be investigated in the future.

Table 4. Ťahyňa virus antibodies in domestic animals of Central Europe

Order	Species	No. of posit./samples	% posit.	Test	Ref.
Lagomorpha	*Oryctolagus cuniculus*	17/181	9.0	NT	40
Carnivora	*Canis familiaris*	3/9	?	NT	12
	Felis domestica	0/2	?	NT	
Artiodactyla	*Sus scrofa*	93/195	47.6	NT	4, 12, 22
	Sus scrofa	60/109	55.0	HI	25
	Bos taurus	97/895	10.8	NT	5, 12, 22
	Bos taurus	68/624	10.8	HI	25, 32, 33
Perissodactyla	*Equus caballus*	65/103	63.1	NT	4, 12, 25
	Equus caballus	21/61	34.0	HI	

A critical approach to the results of experimental infections with the high passaged neuroadapted strain has been justified not only by the facts mentioned above (Table 2) but also by the results of experimental studies published. As early as 1965 it was anticipated that the invasiveness of the neuroadapted strain of Ťahyňa virus is minimal (Bárdoš 1965b). This fact was later clearly demonstrated in experimentally infected suckling and young white mice (Danielová et al. 1970, Wallnerová 1973).

On the basis of the results obtained in serological surveys and experimental infections it can be concluded that the young hare occupies the first place on the list of wild mammal hosts of Ťahyňa virus considered as a probable amplifier of Ťahyňa virus in nature. Placing the hare on the top of the list is justified since this mammal meets the requirements of the criteria published earlier (Bárdoš 1965). The hare is a very numerous wild mammal in Central European biotopes of Ťahyňa virus infections. There are about 120—130 hares per 100 hectares. They have a numerous progeny 3—4 times during the summer months. Since only 36.1% of adult hares posses antibodies, there is a large annual population of non-immune young hares in nature. After birth the young are lying on the ground freely exposed to mosquito bites. Being intensively hunted 80% of the hare population consists of animals below 1 year of age (Mohr 1954). All other species of wild mammals under consideration according to the results of serological surveys and experimental infections are of less importance, since they are less numerous and have a less numerous progeny.

Besides wild mammals, domestic animals are also frequently attacked by mosquitoes. The results of serological surveys are presented in Table 4. The highest percentage of antibodies was detected in horses (63.1 resp. 34.0%) and in pigs (47.6 resp. 55.0%). In cattle and domestic rabbits the percentage was lower (10.8 resp. 9.0 %).

Table 5. Viraemia in domestic mammals experimentally infected with Ťahyňa virus

Species	Age or weight	Strain e or n*	Passage history (x^{th})	Inoculum s.c. $\log_{10}LD_{50}$†	Viraemia		Ref.
					in days	max. titer in $\log_{10}LD_{50}$	
Oryctolagus	400 g	236 e	4—7	4 × 1.0	3·	>3.4	37
cuniculus	400 g	236 n	4—7	2.7—6 × 4.0	3—4	2.9	
	1.5—2.2 kg	181 n	2	3 × 3.6—5 × 3.0††	3—4	TR.††	30
Sus	1.8—2.0 kg	236 e	11	2.5—4.5	4—5	2.5	6, 14, 17
scrofa	3.4—5.8 kg	236 e	11	3.5	3	TR.†††	
	27.0—30.0 kg	236 e	11	6.4 !	3	TR.††	
	27.0—30.0 kg	236 e	11	7.4	3—4	TR.††	
Bos taurus	2—5 days	236 e	11	4.1	4	TR.††	6, 13
Equus	3—17 days	236 e	7	2.5—3.5	3—5	1,5	6
caballus	1 year	236 e	?	4.7	4	TR.††	
	3 years	92 n	?	5.9	0	0††	

· in 3 out of 4 viraemia detected, ! intracutaneous inoculation, *** in 2 out of 3 viraemia detected; TR. = traces.

Table 6. Ťahyňa virus neutralizing antibodies and viraemia in „sentinel" rabbits

Country	No. detected reactors/exposed	% reactors	Viraemia detected in	Viraemia detected in reactors in %	Ref.
Czechoslovakia	4/22		1		21,26
USSR	4/20		0		18
Austria	25/91		2		1
Total	33/133	24.8	3	9.0	

The results of experimental infections with the extraneural strain "236" have demonstrated that the highest viraemia is detectable in suckling pigs weighing 1.8-2.0 kg (Table 5). A low level viraemia was also detected in 3—17 day-old foals. On the basis of these results of experimental infections all above mentioned species should be considered as hosts and probable amplifiers of Ťahyňa virus. More experiments should be undertaken, however, to prove that viraemia in pigs and foals is sufficient to ensure the infection of mosquitoes and further attempts should be made to isolate Ťahyňa virus from the blood of the naturally infected pigs and foals.

Different, however, is the situation with the domestic rabbits. Table 6. shows that "sentinel" rabbits are frequently infected if exposed in natural conditions to mosquito bites (24.8 %) thus approaching almost the frequency of infections in wild hare. And moreover, it is also notable that Ťahyňa virus was isolated from the blood of "sentinel" rabbits. Preparing the list of priorities among domestic animals in regard to their role as host-amplifiers of Ťahyňa virus it seems necessary to take into consideration the following facts. In spite of the evidence that rabbits react to experimental infections with a satisfactory viraemia and that Ťahyňa virus was isolated from the blood of naturally infected rabbits (thus they can be labeled as host-amplifiers), they are rarely infected in natural conditions when housed in cages protected against mosquitoes with a wire netting which prevents the access of mosquitoes.

In Central European conditions pigs might play an important role as hosts and supplementary amplifiers of Ťahyňa virus, since numerous large breeding pigsties are built with thousands of suckling pigs annually. In spite of the anticipated large percentage of suckling pigs with maternal antibodies there are many others without these antibodies which can serve as supplementary amplifiers for Ťahyňa virus.

Foals are much less numerous in Central European conditions and since in half of them maternal antibodies can be anticipated their importance will lag far behing that of suckling pigs.

Summarizing the facts already gathered it may be stated that in conditions of Central Europe the young hares and suckling pigs should be considered as the most important host and probable amplifiers of Ťahyňa virus in nature.

There is plenty of work still to be done for the reasons mentioned above. Conditions typical of Central European biotopes cannot be applied to other countries of Europe, Asia and Africa, since studies done in other areas, for instance in France, Uzbekistan (U.S.S.R.) and Finland indicate that the host-amplifiers of Ťahyňa virus (resp. Inkoo virus) might be other mammals (Hannoun et al. 1969, Yakubov et al. 1971, Brummer-Korvenkontio 1973).

РОЛЬ МЛЕКОПИТАЮЩИХ В ЦИРКУЛЯЦИИ ВИРУСА ТЯГИНЯ

В. Бардош

Резюме. Дан анализ роли млекопитающих в циркуляции вируса Тягиня на основе результатов полученных чехословацкими, австрийскими и венгерскими вирусологами.

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