Role of bats in the natural cycle of arboviruses

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Chiropterans constitute the second largest order of mammals in terms of number of species, and are numerically the largest in overall abundance. In India approximately 100 species of bats have been recorded. So far, 31 definite arboviruses and 14 probable arboviruses/antibodies have been isolated from bats from all over the world. Involvement of bats in two important arboviral diseases in India, viz. Japanese encephalitis (JE) and Kyasanur forest disease (KFD), is discussed. It appears that the bats get infected when the virus is active and probably act as 'amplifiers' in conjuction with other hosts.

THE arthropod-borne (arbo) viruses are a group of infectious agents which are biologically transmitted between susceptible vertebrate hosts by haematophagous arthropods. They produce viremia in vertebrate hosts and are picked up through blood by arthropod vectors during feeding. After a variable length of time the vectors become capable of transmitting the virus to fresh hosts. Many species of vertebrates act as hosts for the arthropods and are infected by arboviruses. The effect of the virus on the host may be asymptomatic or symptomatic. Among different groups of mammals, bats (order Chiroptera) have gained considerable importance as hosts that support the multiplication of arboviruses. Chiropterans make up the second largest order of mammals in number of species, and numerically probably the largest in overall abundance. In India there are over 100 species of bats belonging to two groups, viz. insectivorous and frugivorous (H. R. Bhat, personal communication). Their mobility, together with the spectrum of ectoparasites and different species of mosquitoes that feed upon the bats, qualify them as potential amplifiers or reservoirs of arboviruses. This article reviews the information available on the involvement of bats in arboviral infections.

Various types of haematophagous arthropods have been found associated with bats and their habitats. Hiregoudar and Bal[1] reported a variety of ectoparasites of Indian bats. They include 11 species of nycteribiids, 5 species of streblids, 2 species of bugs and 16 species of mites. Bhat *et al.*[2] recorded 16 species of nycteribiids and 8 species of streblids from bats of Malnad area of Karnataka. A variety of ectoparasites including different species of streblids, nycteribiids, mites, soft ticks, etc. have been reported from bats collected from Rajasthan and Gujarat[3]. On a number of occasions soft ticks of the genera *Ornithodoros* and *Argas* have been collected from bat dwellings[4] (NIV unpublished data). Certain mosquito species have been reported exclusively from bat caves[5,6]. O'Gower[7] employed bats to attract mosquitoes into traps. Sulkin *et al.*[8] reported evidence that mosquitoes fed naturally on bats.

So far, 31 arboviruses have been recorded from bats[5,9]. Of these, 8 belong to family Togaviridae, 14 to Flaviviridae and 9 to Bunyaviridae (Table 1). In addition, 14 viruses or antibodies against viruses classified as probable arboviruses and a few unclassified viruses have been detected in bats (Tables 2 and 3). The following are the important arboviral diseases affecting man with which bats are suspected to be involved in the natural cycle of the virus.

Japanese encephalitis (JE)

The virus is generally maintained in a natural cycle involving mosquito vectors and ardeid birds. Pigs act as amplifier hosts. Definite evidence of the involvement of bats in the natural cycle of JE in Japan was obtained between 1952 and 1970 by serological survey and repeated isolation of the virus from bats. Sulkin *et al.*[10] reported the isolation of the virus from *Miniopterus schreibersii* and *Rhinolophus cornutus* collected in Japan. From among 1406 bats of these two species, JE virus was isolated from 16 *M. schreibersii* and 8 *R. cornutus*. Infected bats were found throughout the year. Five hundred and twenty-eight bats of 8 other species were virus-negative. Seasonal incidence of infection varied between about 1% (spring) and 2.73% (autumn). Other than blood, some bats had viruses in brown fat, and one had virus in its kidneys.

Several investigations involving experimental infection of bats were carried out by Japanese workers between 1952 and 1960. Specimens of *Pipistrellus abramus* were infected by intracranial inoculation; the animals maintained persistent infection without developing detectable neutralizing antibodies during hibernation[11]. Corristan *et al.*[12,13] and La Motte[14] experimentally infected three species of bats, viz. *Eptesicus fuscus*, *Myotis lucifugus* and *Pipistrellus subfalvus*. The bats developed viremia which lasted for 6 to 12 days. They discovered in one instance that a bat became infected after eating three infected mosquitoes. When certain infected bats were placed in simulated hibernation at 10°C and returned to room temperature after 107 days, no virus was detectable, but three days after being awakened, detectable viremia developed. La Motte[14]

Table 1. Arboviral infections in bats

Virus	Bat species	Evidence of infection: Virus	Evidence of infection: Antibodies	Country	Ref.
Alphavirus					
Chikungunya	*Scotophilus* sp.	Salivary glands	—	Senegal	48
	Hipposideros cafer	—	HI	Senegal	49
Semliki forest	*Tadarida condylura*	—	HI	Uganda	33
Eastern equine encephalitis	*Eptesicus fuscus*	—	N	USA	53, 54
	Artibeus jamaicensis	—	HI	Brazil	5
Western equine encephalitis	*Eptesicus fuscus*	Salivary glands	—	USA	5
Venezuelan equine encephalitis	*Carollia perspicillata*	Liver and spleen	—	Colombia	5
	Artibeus lituratus	—	HI	Panama	55
Nepuyo	*Artibeus lituratus*	Blood	—	Honduras	56
Sindbis	*Hipposideros* sp.	Organ*		Zimbabwe	9
	Rhinolophus sp.	Organ*		Zimbabwe	9
Mucambo	*Carollia perspicillata*	—	HI, N	Panama	5, 51
Flavivirus					
Dengue 1	*Pteropus gouldi*	—	N	Australia	28, 29
	Pteropus giganteus	—	HI	India	30
Dengue 2	*Pteropus gouldi*	—	N	Australia	28, 29
Dengue 2 and/or 4	*Cynopterus brachyotis*	—	HI, N	Malaysia	5
Japanese encephalitis	Many, details given in the text	Blood and spleen	HI, N	Japan, Australia, Taiwan Thailand, Malaysia, Indonesia, India	8-26
Murray valley encephalitis	*Eptesicus pumilus*	—	HI, N	Australia	57
	Pteropus gouldi	—	N	Australia	28, 29
St Louis encephalitis	*Tadarida brasiliensis*	Blood	—	USA	46
	Eptesicus fuscus	—	N	USA	47
	Rhinophylla pumilio	—	HI	Brazil	5
West Nile	*Rousettus leschenaulti*	Spleen	—	India	31
	Pteropus gouldi	—	N	Australia	21
	Eidolon helvum	—	HI	Uganda	33
Yellow fever	*Glossophaga soricina*	—	N	Ethiopia	39
	Eidolon helvum	—	HI, N	Uganda	33
	Epomophorus sp.	Brain	—	Ethiopia	42
Zika	*Tadarida condylura*	—	HI	Uganda	33
Kyasanur forest disease	*Rhinolophus rouxi*	Spleen	—	India	35
	Many, given in the text	—	HI, N	India	38
Hypr	Not given	—	N	USSR	9
Tick-borne encephalitis	*Barbastella barbastellus*	—	HI	Czechoslovakia	58
Wesselsborn	*Cynopterus brachyotis*	—	N	Thailand	9
Uganda S.	Not given	—	HI	Ethiopia	42
Bunyavirus					
Catu	*Molososus obscurus*	Salivary glands	—	Brazil	51
Issyk-Kul	*Vespertilio serotinus*	Blood	—	USSR	9, 59
	Vespertilio pipistrellus	Blood	—	USSR	9, 59
Bunyamwera	*Tadarida condylura*	—	HI	Uganda	33, 40
	Eidolon helvum	—	HI	Uganda	50
Caraparu	*Artibeus lituratus*	—	HI, N	Brazil	5
Guaroa	Not given	—	HI	Brazil	5
Turlock	Not given	—	HI	Brazil	5
Guama	Not given	Organs	—	Brazil	9
Itaporanga	*Artibeus lituratus*	—	HI, N	Brazil	5
Phlebovirus					
Rift valley fever	*Micropterus pusillus*	One isolation*	—	Guinea	60
	Hipposideros abae	One isolation*	—	Guinea	60

*Details not given.
HI, Haemaglutination inhibition antibodies; N, neutralizing antibodies.

Table 2. Probable* arboviral infections in bats

Virus	Bat species	Evidence of infection: Virus	Evidence of infection: Antibodies	Country	Ref.
Flavivirus					
Tembusu	*Pteropus vampyrus*	—	N	Malaysia	5
Usutu	*Eidolon helvum*	—	HI	Uganda	50
Ntaya	*Eidolon helvum*	—	HI	Uganda	50
Jugra	*Cynopterus brachyotis*	Blood	—	Malaysia	9
Carey Island	*Cynopterus brachyotis*	Salivary gland	—	Malaysia	9
	Macroglossus lagochilus	Two isolations†		Malaysia	9
Sokuluk	*Vespertilio pipistrellus*	Brain, liver, spleen and kidney pool	—	USSR	9
Bunyavirus					
Utinga	*Artibeus lituratus*	—	HI	Brazil	5
Bangui	Not given	Salivary gland	—	Central African Republic	61
Tacaiuma	*Artibeus jamaicensis*	—	HI, N	Brazil	5
Keterah	*Scotophilus temmincki*	Blood	—	Malaysia	9
Mojui Dos Campos	Not given	—	HI	Brazil	9
Coronavirus					
Bocas	*Myotis lucifugus*	One isolation†	—	USA	9
Vesiculovirus					
Jurona	*Artibeus lituratus*	—	HI, N	Brazil	5, 9
Orbivirus					
Japanaut	*Syconycteris crassa*	Blood	—	New Guinea	9

*Includes viruses for which supportive data are too meagre for their inclusion as definite arboviruses.
†Details not given.

Table 3. Recent isolations of viruses from bats

Virus	Bat species	Country	Ref.
Kasokero*	*Rousettus aegyptiacus*	Uganda	62
Rio Bravo	Not given	—	63
Fomede	*Nycteris nana*	Guinea	64

*Unclassified virus.

suggested a mosquito–bat–mosquito cycle as a possible overwintering mechanism for JE virus and interpreted the oral route of infection to mean that foraging bats might become infected in nature by feeding on infected mosquitoes. It was shown that the infected mosquitoes can transmit the virus from and to bats under the laboratory conditions. Sulkin and coworkers[15–19] carried out experimental viremia studies on three species of bats, viz. *Epstesicus fuscus*, *Myotis lucifugus* and *Tadarida brasiliensis*, by inoculating the virus subcutaneously. Viremia lasted for 15 to 30 days and neutralizing antibodies appeared as the viremia declined. They could isolate the virus from the bats during the period of viremia from brains, kidneys and brown fat. The transplacental passage of the virus to the offspring was also demonstrated in *Tadarida* species.

A number of serological surveys from different parts of the world have indicated the presence of haemagglutination inhibition (HI) and neutralizing (N) antibodies to JE. Miura *et al.*[20] showed that about 7% of bat sera from 10 different species collected in Japan had N antibodies to JE virus. Neutralizing antibodies were also detected in *Pteropus gouldi* from Australia[21], *Hipposideros* sp. from Taiwan[22], *Cynopterus brachyotis* from Thailand and *P. vampyrus* from Malaysia[5].

In India, the involvement of bats was suspected ever since Carey *et al.*[23] detected HI antibodies in *Pteropus giganteus* from Vellore, South India. Kaul *et al.*[24] reported the presence of HI antibodies to JE virus in two bat sera, one each from *Megaderma lyra* and *Cynopterus sphinx*. In a laboratory study *Rousettus leschenaulti* (a frugivorous bat) were infected with JE virus[25]. Viremia was detected up to day 8 post-inoculation (PI). Virus could not be detected in organs such as spleen, liver and brain at the termination of the experiment or from dying bats during experiment. Experimental infection of *C. sphinx*, another species of frugivorous bat, has shown development of viremia which persisted up to day 9 PI. Transmission of the virus from viremic bats by *Culex bitaeniorhynchus* mosquitoes to bats and chicks was also demonstrated[26]. All animals developed neutralizing antibodies.

A serological survey of bats in the JE endemic areas of Kolar and Mandya districts, Karnataka state, was carried out[27]. Of 626 sera collected, 46 (7.3%) sera from five species of bats, viz. *Hipposideros pomona*, *H. speoris*, *H.*, *bicolor*, *H. cineraceus* and *Rhinolophus rouxi*, were positive for N antibodies to JE virus.

Studies conducted in Japan indicated that the incidence of antibodies in bats correlated fairly well with the incidence of JE in man[10]. Banerjee *et al.*[27]

observed a correlation between the seropositivity of bats and human epidemics in 1983 and 1985 in Kolar district. A similar correlation was observed in 1986 in Mandya district by the same authors.

The prolonged viremia, though at low titres after 5–6 days PI, experimental transmission through mosquitoes to and from bats, and serological evidence of natural infection give credence to the role of bats in the epidemiology of JE. However, unlike in Japan, in India the bats may not be acting as overwintering hosts for JE virus as they do not generally hibernate. It is therefore possible that the bats may act as amplifying hosts of JE virus in conjuction with other hosts such as birds and pigs.

Dengue

The virus is transmitted from man to man by mosquitoes. No extra-human reservoirs are usually involved. Neutralizing antibodies against dengue types 1 and 2 have been shown in *Pteropus gouldi* in Australia[28,29]. In Malaysia HI and N antibodies to dengue types 2 and/or 4 have been detected in *Cynopterus brachyotis*. In India, N antibodies against dengue viruses have been demonstrated in *Pteropus giganteus*[30]. In experimental transmission studies, no viremia could be demonstrated in *Myotis lucifugus* with dengue type 1 virus. Shah and Daniel[30] could not demonstrate any viremia with DEN-2 in *P. giganteus*. They also could not detect any antibody in 43 sera from this species collected at the edge of Calcutta city after an outbreak of dengue. Apparently, bats seem to have no significant role in the epidemiology of dengue, which is mostly an urban disease.

West Nile

In India, West Nile virus has been isolated from the spleen of one frugivorous bat, *Rousettus leschenaulti*[31]. Neutralizing and HI antibodies have been reported from different bat species, viz. *Pteropus gouldi* in Australia[28], *R. aegyptiacus* in Israel[32], and *Eidolon helvum* in Uganda[33].

Kyasanur forest disease (KFD)

The involvement of bats in the natural cycle of KFD virus was first suspected when HI and N antibodies to this virus were detected in a frugivorous bat, *Rousettus leschenaulti*, collected at Manjri near Pune[34]. Subsequently, four isolations of KFD virus were made from the spleen of naturally infected *Rhinolophus rouxi* and one from a pool of ticks, *Ornithodoros chiropterphila*, collected from the habitat of the same bats in the KFD area in Karnataka[35]. Further studies have shown that in *Rous. leschenaulti*, *Cynopterus sphinx* and *Rhin. rouxi*[36,37], the level of virus in blood ranged from traces of virus on days 1 and 2 PI to 3.0 to 4.0 dex/0.03 ml on days 3 and 4. KFD virus was recovered from spleen, lung and brain on day 2 PI. The duration of viremia varied between 2 and 6 days PI in *R. leschenaulti*. Virus could be recovered from spleen and brain. In one bat, the virus was isolated from the brain 30 days after the infection. The studies showed that 11 out of 14 bats circulated the virus and subsequently 10 of the infected bats showed N antibodies.

In an intensive serological study of bats in the area of occurrence of KFD and the neighbourhood, 727 sera were collected from 17 species of bats and tested for antibodies[38]. One hundred and thirty-eight sera from 7 species of bats, viz. *Rous. leschenaulti*, *Eonycteris spelaea*, *C. sphinx*, *Rhin. rouxi*, *Hipposideros speoris*, *H. lankadiva* and *Miniopterus schreibersi*, showed N antibodies. Of the 49 sera tested for HI antibodies 31 sera from *R. leschenaulti* and 17 from *E. spelaea* were positive. Paradoxically, *R. leschenaulti* collected in the KFD epizootic-epidemic area in Shimoga district had the lowest incidence of antibodies.

Yellow fever

Though no definite role of bats in the natural cycle of the virus has been established, antibodies have been demonstrated in different species, viz. *Glossophaga sorcina* from Brazil[39], *Eidolom helvum*[40] and, *Rousettus* sp.[41] from Uganda, and *Epomophorus* sp. from Ehiopia[42]. *Epomophorus* sp. has been suspected to have some role in the spread of the disease because of its migratory behaviour[42]. Studies have shown that *Eptesicus fuscus*, *Eidolon helvum* and *Myotis lucifugus* circulate the virus after experimental infection[43,44]. *Desmodus rotundus* (a species of vampire bat) has been reported to have transmitted the virus between monkeys while feeding upon them[45].

St Louis encephalitis

This virus is known in the United States, Jamaica and Trinidad. Birds and mosquitoes have been incriminated in the natural cycle. Sulkin *et al.*[46] reported an isolation of this virus from the blood of *Tadarida brasiliensis*. Serum specimens from 12 of 127 *Eptesicus fuscus* also showed N antibodies[47]. Infrequent transplacental passage of the virus has been demonstrated in *Myotis lucifugus*[15,16].

Chikungunya

Chikungunya is another arboviral disease in which no extra-human hosts are believed to have any major role in the natural cycle. Subcutaneous inoculation of virus produced transient viremia in one of the four bats (*Pteropus giganteus*) studied[30]. Neutralizing antibodies persisted through the observation period of 14 to 27 weeks in 3 of the 4 bats. Antibodies to chikungunya virus were not demonstrated in 43 bat sera collected in the vicinity of Calcutta where there was an outbreak of chikungunya two years before the sera were collected. Antibodies to chikungunya virus were detected in one of the *Megaderma lyra* specimens collected at Vellore[25].

Isolations of chikungunya virus have been reported from the salivary glands of *Scotophilus* sp. from Senegal[48]. HI antibodies have been reported in *Hipposideros cafer* from Senegal and Uganda[49]. *Rousettus angolensis* and *Eidolon helvum* did not circulate the virus on experimental infection[36,50].

Venezuelan equine encephalitis

It is a disease of horses but occasionally affects man in the western hemisphere. The virus has been isolated from mosquitoes, rodents, bats and birds. The virus was isolated from 4 out of 176 *Carollia perspicillata* bats collected in Colombia[5]. Experimental transmission of the virus was demonstrated from bats to bats (*Eptesicus fuscus*) through mosquitoes[13].

Western equine encephalitis

It is a disease transmitted by mosquitoes to horses and occasionally to man in North and South America. The virus was isolated from the salivary glands of a bat, *Eptesicus fuscus*, in New Jersey[5].

Catu

The virus is known only from Brazil, where it has been reported from man and rodents. Isolation of the virus from the salivary glands of a Brazilian bat, *Molossus obscurus*, has been reported[5]. HI antibodies to the virus have been found in the bat species *Artibeus fulginosus*[51].

Vertebrate hosts of arboviruses are usually mammals or birds that are susceptible to a virus and are able to circulate it in titres high enough to infect vectors. The most effective vertebrate hosts are those that themselves remain healthy but circulate the virus in sufficient titres and duration to infect a large number of competent vectors. A large number of susceptible small vertebrates or a small number of large mammals may produce similar effects[52]. The work done so far on bats in connection with arboviral diseases indicates that bats fulfil the above requirements. Definite involvement of bats in the natural cycle of certain arboviral diseases has been obtained on the basis of virological and serological studies. However, the paucity of studies on vector competence of arthropods infesting bats and their habitats is the major lacuna in this field.

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A novel mechanism for the decay of neutron star magnetic fields

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If the generally accepted picture that the neutrons and protons in the core of a neutron star will be in a (vortex) superfluid state is correct, then the Onsager–Feynman vortices in the neutron superfluid and the Abrikosov vortices in the proton superfluid may be strongly interpinned. We argue that because of this the evolution of the magnetic field will be intimately related to the rotational history of the star. Based on this hypothesis we present a model for the decay of the magnetic fields of neutron stars.

We point out that our model is able to explain for the first time, at least qualitatively, many of the outstanding questions such as (i) the exponential decay of the field in young pulsars, (ii) preponderance of binaries among low-field pulsars, (iii) why very old ($>10^9$ yr) neutron stars retain substantial residual fields and what determines this residual value, etc.

Soon after pulsars were discovered Gunn and Ostriker[1] conjectured that their magnetic fields may be decaying exponentially with a time constant of a few million years. This was motivated by the need to explain the secular decrease in the spin-down torque acting on the pulsar (over and above that due to period lengthening). This idea did not gain immediate credence because it was difficult to reconcile such a rapid decay of the magnetic field with the expected superconducting properties of the interior[2]. In principle, as Gunn and Ostriker themselves pointed out, the decay of the torque acting on the pulsar could also be due to a tendency of the magnetic and rotation axes to align, although they did not favour it. Recent measurements of the obliqueness angle for about 150 pulsars now seem to rule out this possibility[3,4]. Thus, despite the theoretical difficulty in understanding the decay it now appears that the distribution of the measured periods and derived magnetic fields of nearly 500 pulsars is best explained by the hypothesis that the magnetic fields of the population of normal pulsars decay rather rapidly.

There is also circumstantial evidence that this decay may continue for sufficiently long for the magnetic field to decrease to a value of the order of 5×10^8 G. This

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