Crimean-Congo haemorrhagic fever virus in ticks, domestic, and wild animals

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Crimean-Congo haemorrhagic fever virus (CCHFV) poses a significant public health threat due to its potential for causing severe disease in humans and its wide geographic distribution. The virus, primarily transmitted by *Hyalomma* ticks, is prevalent across Africa, Asia, Europe, and the Middle East. Understanding the virus's spread among tick populations is crucial for assessing its transmission dynamics. Vertebrates play a key role in CCHF epidemiology by supporting tick populations and acting as virus carriers during viremia. Livestock, such as cattle, sheep, and goats, amplify the virus and increase tick numbers, posing zoonotic risks. Wildlife, while asymptomatic, can serve as reservoirs. Birds generally do not show signs of the virus but can introduce infected ticks to new regions. This review compiles information on CCHFV's tick vectors and vertebrate hosts, emphasizing their roles in the virus's transmission dynamics. Understanding these dynamics is essential for developing effective control and prevention strategies.

KEYWORDS
Crimean-Congo haemorrhagic fever virus, ticks, livestock, wildlife, zoonotic disease
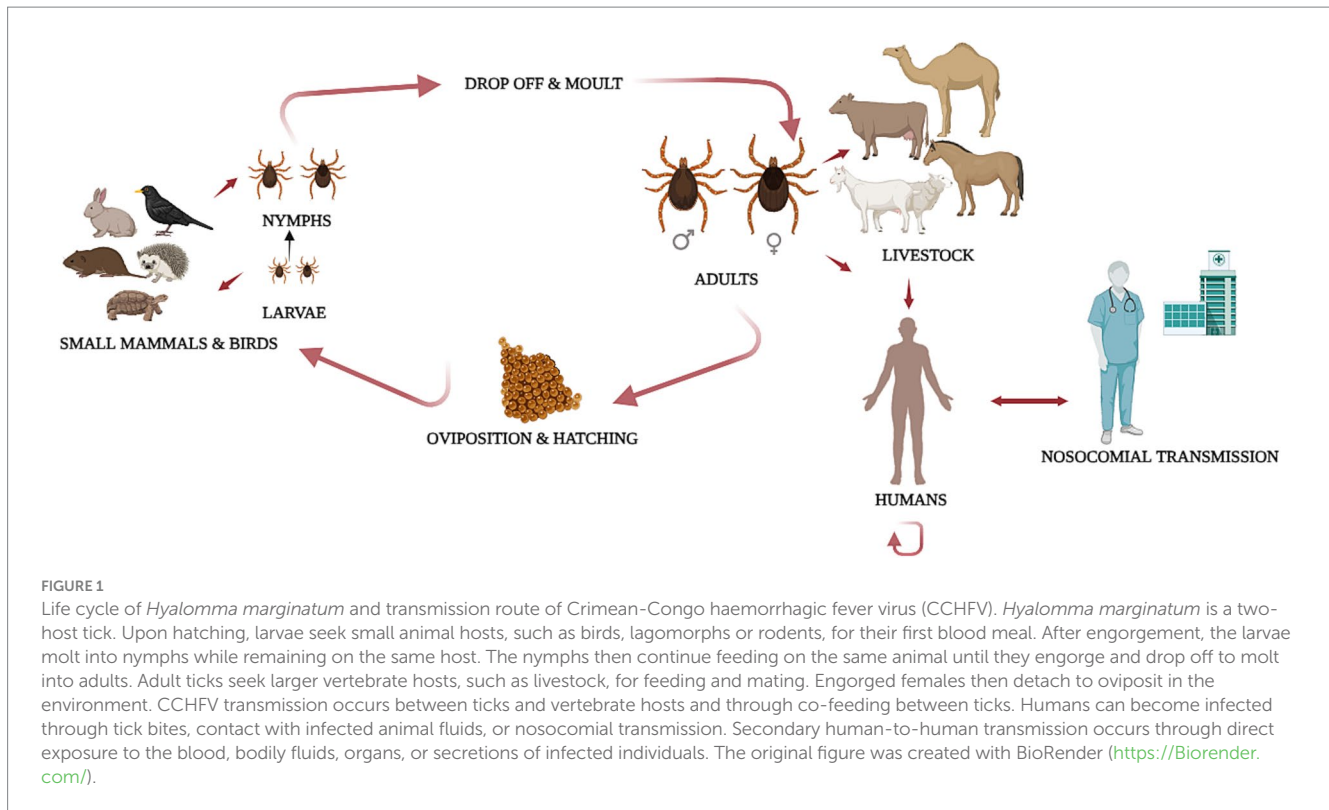
1 Introduction

Crimean-Congo haemorrhagic fever virus (CCHFV) is a lipid-enveloped, single-stranded RNA virus in the *Orthonairovirus* genus (*Nairoviridae* family). It causes Crimean-Congo haemorrhagic fever (CCHF) in humans, a severe disease with significant public health implications due to its widespread prevalence. CCHF is among the most widely distributed tick-borne viral diseases, endemic across Africa, Asia, Eastern and Southern Europe, and the Middle East, with case fatality rates ranging from 5 to 40% (1–3).

Hyalomma ticks, particularly *Hyalomma marginatum*, are the primary vectors for CCHFV. They feed on various domestic ruminants (e.g., sheep, goats, and cattle) and wild animals (e.g., hares, hedgehogs, certain rodents, and ostriches) (4). Ticks play a crucial role in spreading the virus to humans through bites or direct contact with infected animal tissues. Infected vertebrates, although asymptomatic, sustain tick populations and facilitate CCHFV transmission during viremia (5).

Small mammals, such as hares and hedgehogs, amplify immature ticks, while larger domestic animals, including cattle, goats, and sheep, host adult ticks (Figure 1). Although CCHFV has a short viremia in small mammals, their role in CCHFV ecology is significant, as population surges, especially among hares, are linked to disease outbreaks (6, 7). Large domestic mammals inadvertently expose humans to CCHFV, especially during slaughter (8–12). Birds, except for ostriches, generally do not show viremia but may carry infected ticks to new regions (7).

Serological evidence confirms CCHFV exposure in various domestic and wild animals, with experimental infections validating their susceptibility (5). Understanding the virus's

FIGURE 1
Life cycle of *Hyalomma marginatum* and transmission route of Crimean-Congo haemorrhagic fever virus (CCHFV). *Hyalomma marginatum* is a two-host tick. Upon hatching, larvae seek small animal hosts, such as birds, lagomorphs or rodents, for their first blood meal. After engorgement, the larvae molt into nymphs while remaining on the same host. The nymphs then continue feeding on the same animal until they engorge and drop off to molt into adults. Adult ticks seek larger vertebrate hosts, such as livestock, for feeding and mating. Engorged females then detach to oviposit in the environment. CCHFV transmission occurs between ticks and vertebrate hosts and through co-feeding between ticks. Humans can become infected through tick bites, contact with infected animal fluids, or nosocomial transmission. Secondary human-to-human transmission occurs through direct exposure to the blood, bodily fluids, organs, or secretions of infected individuals. The original figure was created with BioRender (https://Biorender.com/).

persistence within tick populations, their role as vectors, and the factors influencing viral transmission is essential for effective control strategies. Examining CCHFV in livestock, which often serve as amplifying hosts, provides insights into the virus's impact on animal health and potential spillover to humans. Additionally, studying CCHFV within wildlife populations is essential for understanding its broader epidemiology.

This review compiles information on CCHFV tick vectors and vertebrate hosts, focusing on their roles in virus transmission and providing a comprehensive resource for understanding CCHFV in animals.

2 CCHFV in animals

2.1 CCHFV in ticks

The first documented outbreak of CCHF was reported in the Crimean region of the former Soviet Union in 1944, where 200 military personnel suffered from an acute febrile illness with haemorrhagic symptoms, resulting in a 10% fatality rate (1). Investigating the situation, a team led by Mikhail Chumakov found that tick exposure caused these cases. Collecting over 3,000 blood-sucking arthropods, they observed an abundance of ticks, particularly the *H. marginatum* species, now recognized as the primary CCHFV vector (7). These infections were linked to abandoned cultivated lands during the German occupation, enabling tick host expansion. Subsequently, the virus was independently recognized as the cause of illness in the Congo in 1969, leading to the name Crimean-Congo Haemorrhagic Fever Virus (7). Since then, comprehensive studies have consistently

reaffirmed ticks as the primary transmission source and reservoir for CCHFV in nature.

CCHFV infection persists throughout the tick life cycle without detrimental effects, allowing the virus to survive transstadially and vertically. Although the frequency of transstadial transmission, the percentage of infected eggs, and the number of generations that can sustain the virus are not well understood. However, ticks can survive for extended periods without feeding, which supports the overwintering of CCHFV, allowing them to act as reservoirs even when vertebrate hosts are absent (13).
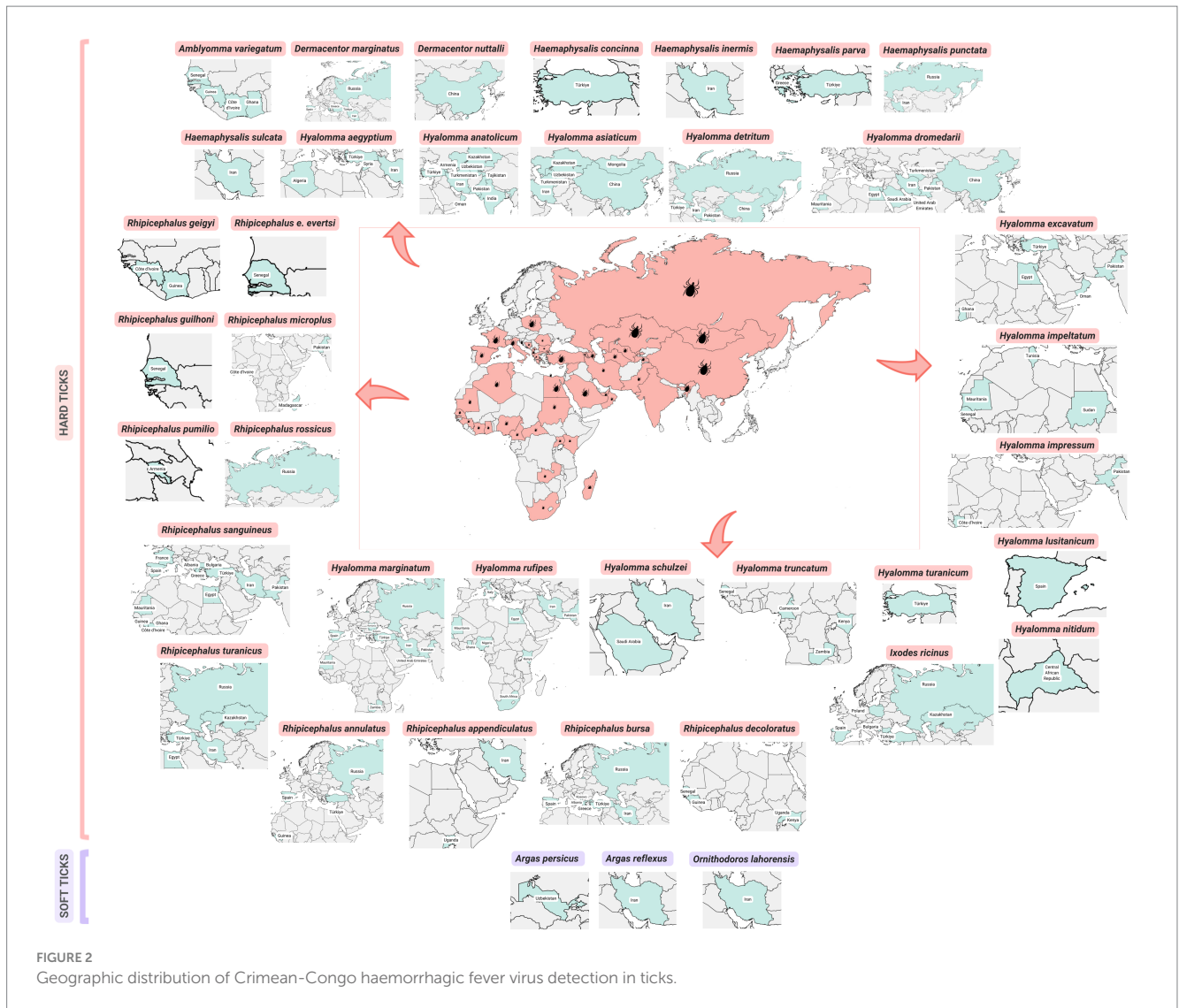
Ticks of the Ixodidae family, especially those of the genus *Hyalomma*, are considered both as reservoirs and vectors for CCHFV. *Hyalomma marginatum* has the most prominent role globally in the natural history of CCHF in the Old World. Dramatic increases in the circulation of CCHFV coincide with significant expansions in *H. marginatum* populations, driven by favorable weather conditions and human-induced ecological alterations (14, 15).

Although the virus is transmitted mainly by tick species in the *Hyalomma* genus, CCHFV has been isolated from other ticks belonging to the genera *Amblyomma*, *Dermacentor*, *Haemaphysalis*, and *Rhipicephalus*. However, there is limited evidence indicating the active circulation of CCHFV among non-*Hyalomma* tick species in natural transmission cycles (16).

CCHFV has been reported in 39 tick species collected from a variety of hosts (13, 16). These include one species from *Amblyomma*, two species from *Dermacentor*, 15 species from *Hyalomma*, five species from *Haemaphysalis*, one species from *Ixodes*, 12 species from *Rhipicephalus*, and three species from the Argasidae family within the genera *Argas* and *Ornithodoros* (Table 1; Figure 2). This wide range of tick species highlights the potential role of numerous ticks in both spreading and maintaining the virus across various regions and host ecosystems.

TABLE 1 List of tick species infected by Crimean-Congo haemorrhagic fever virus.

Order	Family	Scientific name	Country	References
Ixodida	Ixodidae	*Amblyomma variegatum*	Côte d'Ivoire, Ghana, Guinea, Senegal	(19, 90, 92–94)
		Dermacentor marginatus	Greece, Iran, Russia, Spain, Türkiye	(95–102)
		Dermacentor nuttalli	China	(103)
		Haemaphysalis concinna	Türkiye	(104)
		Haemaphysalis inermis	Iran	(105)
		Haemaphysalis parva	Greece, Türkiye	(102, 106)
		Haemaphysalis punctata	Iran, Russia	(95, 105)
		Haemaphysalis sulcata	Iran	(107)
		Hyalomma aegyptium	Algeria, Iran, Syria, Türkiye	(64, 108–110)
		Hyalomma anatolicum	Armenia, India, Iran, Kazakhstan, Pakistan, Oman, Tajikistan, Türkiye, Turkmenistan, Uzbekistan	(17, 39, 99, 104, 105, 107, 111–125)
		Hyalomma asiaticum	China, Iran, Kazakhstan, Mongolia, Turkmenistan, Uzbekistan	(103, 105, 126–132)
		Hyalomma detritum – (syn. Hyalomma scupense)	China, Iran, Pakistan, Russia, Türkiye	(95, 99, 103–105, 111, 115)
		Hyalomma dromedarii	China, Egypt, Iran, Mauritania, Pakistan, Saudi Arabia, Turkmenistan, United Arab Emirates	(105, 111–114, 128, 129, 133–137)
		Hyalomma excavatum	Egypt, Ghana, Oman, Pakistan, Türkiye	(90, 98, 111, 124, 135)
		Hyalomma impeltatum	Mauritania, Senegal, Sudan, Tunisia	(94, 138–140)
		Hyalomma impressum	Côte d'Ivoire, Pakistan	(93, 113)
		Hyalomma lusitanicum	Spain	(96)
		Hyalomma nitidum	Central African Republic	(141)
		Hyalomma marginatum	Albania, Bosnia, Bulgaria, Iran, Kosovo, Mauritania, Romania, Pakistan, Russia, Spain, Türkiye United Arab Emirates, Zambia	(20, 95, 104, 105, 108, 111, 113, 114, 127, 142–150)
		Hyalomma rufipes	Egypt, Ghana, Iran, Italy, Kenya, Mauritania, Nigeria, Pakistan, Senegal, South Africa	(16, 19, 94, 113, 139, 151–153, 224)
		Hyalomma schulzei	Iran, Saudi Arabia	(105, 108, 134)
		Hyalomma truncatum	Cameroon, Kenya, Senegal, South Africa, Zambia	(94, 144, 151, 154, 224)
		Hyalomma turanicum	Türkiye	(104)
		Ixodes ricinus	Bulgaria, Kazakhstan, Kosovo, Poland, Russia, Spain, Türkiye	(18, 20, 95–97, 99, 130, 155)
		Rhipicephalus (Boophilus) annulatus	Guinea, Russia, Spain, Türkiye	(92, 95, 96, 143)
		Rhipicephalus appendiculatus	Iran, Uganda	(127, 156)
		Rhipicephalus bursa	Albania, Greece, Iran, Kosovo, Russia, Spain, Türkiye	(95, 104, 106, 108, 143)
		Rhipicephalus (Boophilus) decoloratus	Guinea, Kenya, Senegal, Uganda	(92, 94, 157, 158)
		Rhipicephalus e. evertsi	Senegal	(94, 159)
		Rhipicephalus geigyi	Côte d'Ivoire, Guinea	(92, 93)
		Rhipicephalus guilhoni	Senegal	(159)
		Rhipicephalus microplus	Côte d'Ivoire, Madagascar, Pakistan	(93, 113)
		Rhipicephalus pumilio	Armenia	(120)
		Rhipicephalus rossicus	Russia	(95)
		Rhipicephalus sanguineus	Albania, Bulgaria, Côte d'Ivoire, Egypt, France, Greece, Iran, Ghana, Guinea, Mauritania, Pakistan, Spain, Türkiye	(16, 92, 93, 97, 105, 107, 114, 115, 117–119, 125, 139, 147, 160–163)
		Rhipicephalus turanicus	Egypt, Iran, Kazakhstan, Russia, Türkiye	(18, 95, 98–100, 104, 115, 126, 127, 162)
	Argasidae	*Argas persicus*	Uzbekistan	(120)
		Argas reflexus	Iran	(115)
		Ornithodoros lahorensis	Iran	(108)

FIGURE 2
Geographic distribution of Crimean-Congo haemorrhagic fever virus detection in ticks.

Detection of CCHFV in ticks predominantly relies on reverse transcriptase-polymerase chain reaction (RT-PCR) due to its high specificity and sensitivity in amplifying viral RNA. Additionally, a few studies employed immunological methods, including enzyme-linked immunosorbent assay (ELISA) [e.g., studies by (17, 18)], immunofluorescence assay (IFA) (19), and a combination of indirect hemagglutination fluorescence assay (IHFA) with RT-PCR (20).

Hyalomma marginatum is recognized as the primary vector in the Old World. Among the tick species found infected with CCHFV, 15 are confirmed vectors, while 16 are considered potential vectors (16). In addition to *H. marginatum*, confirmed vectors of CCHFV include *Amblyomma* var*iegatum*, *H. aegyptium*, *H. anatolicum*, *H. asiaticum*, *H. asiaticum kozlovi*, *H. detritum*, *H. dromedarii*, *H. excavatum*, *H. impeltatum*, *H. rufipes*, *H. schulzei*, *H. truncatum*, *H. turanicum* and *R. bursa*. This classification is based on documented infection rates, infection records, and observations across over 30 tick species. Potential vectors include *D. marginatus, D. nuttalli, Ha. concinna, Ha. inermis, Ha. parva, Ha. punctata, Ha. sulcata, I. ricinus, R. annulatus, R. appendiculatus, R. decoloratus, R. evertsi evertsi, R. geigyi, R. guilhoni, R. sanguineus,* and *R. turanicus* (16).

Detecting a virus within an arthropod does not necessarily mean it is an active vector (13). Studies on the vector competence of ticks for CCHFV reveal that ixodid (hard) ticks, particularly those in the *Hyalomma* genus, are highly susceptible to infection and can transmit the virus through biting. Conversely, argasid (soft) ticks are generally not efficient CCHFV vectors (13). The evolutionary dynamics of CCHFV are closely constrained by the necessity to maintain high adaptability within both arthropod and vertebrate host environments. To validate a tick species as a vector, several steps are necessary: the ticks must feed on naturally infected hosts without artificial virus exposure, the virus must be detected in the ticks after molting, and the infected ticks must then feed on naïve hosts. The virus should then be found in these hosts and subsequently in the new generation of ticks from the initially infected adults. Strict adherence to these procedures is essential for accurately determining the vectorial abilities of specific tick species. However, these experiments are particularly challenging to perform because CCHFV is a biosafety level 4 (BSL-4) pathogen, requiring high-level containment facilities for safety.

Further studies are needed to evaluate the vector competence of various tick species for CCHFV transmission and to explore factors influencing the spread of the virus. Understanding both vector

competence and vectorial capacity—the extent of transmission—is essential for predicting CCHFV's spread into new areas. Surveillance of the virus in ticks is an effective tool for monitoring the virus's introduction or circulation within vulnerable populations. This surveillance helps assess human exposure risk, identify high-risk areas, and establish early warning systems for potential outbreaks. This surveillance is essential not only for accumulating information about pathogen epidemiology but also for clarifying the role of CCHFV tick vectors in public and veterinary health (16).

2.2 Serological detection of CCHFV in animals

Serological detection of CCHFV in animals provides crucial information about its ecological role. Because CCHFV often causes a short-lived viremia and can be asymptomatic, directly detecting the virus can be difficult. Thus, serological surveys are essential for monitoring the spread of CCHFV in animal populations and assessing spillover risk to humans.

Common serological methods include ELISA, IFA, and neutralization tests. These techniques help identify animals exposed to the virus, even when symptoms are absent or the infection is not active (21).

ELISA is the most frequently used method for detecting anti-CCHFV antibodies across various animal species. This technique typically targets the nucleocapsid protein (NP) of the virus (22). However, because the Hazara virus (HAZV) and CCHFV belong to the same serogroup, their NPs are genetically similar, leading to cross-reactivity in tests. Studies have shown that sera from animals vaccinated with HAZV can weakly cross-react with CCHFV in immunofluorescence and immunoblot assays, although commercial CCHFV ELISAs used in field studies generally do not show this cross-reactivity (23). Similarly, Dugbe orthonairovirus (DUGV), while genetically and antigenically close to CCHFV, can produce false positives in certain CCHFV tests, particularly immunofluorescence assays (24). Therefore, CCHFV prevalence might be overestimated in areas where HAZV and DUGV are present. ELISAs are considered to have the highest specificity, followed by micro-virus neutralization tests (mVNT), indirect immunofluorescence assays (iIFA), and plaque reduction neutralization tests (PRNT) (25).

Virus neutralization assays, known for their high specificity, are rarely used for diagnosing CCHFV due to the requirement of high-containment laboratories (BSL-3/BSL-4) for handling live viruses. The level of containment depends on whether the area is endemic or non-endemic. Alternative methods, such as the pseudovirus neutralization test (pVNT), which uses pseudotyped Vesicular Stomatitis Virus, and the surrogate virus neutralization test (sVNT), can be performed in lower-containment BSL-2 laboratories, making them more accessible for diagnostic purposes (26, 27).

2.3 CCHFV in domestic animals

CCHFV circulates silently in an enzootic tick-vertebrate-tick cycle, without manifesting disease in animals. In humans, however, it triggers severe illness. Seroepidemiological surveys have identified CCHFV antibodies in various domestic animals (5) (Table 2; Figure 3).

These surveys are crucial for identifying potential sources of CCHFV that might otherwise remain undetected. Since infected animals show no clinical symptoms, serological investigations are essential for assessing CCHFV exposure in animals and the associated risks for human exposure to infected tickssticks (4).

These surveys, especially in CCHFV-endemic regions, reveal high levels of antibodies in cattle, sheep, goats, horses, camels, and other domestic animals, indicating their significant role in the epidemiology of CCHF. These animals support tick reproduction and facilitate the movement of ticks across large areas, aiding the spread of the virus. Large mammals serve as hosts for the virus during viremia, acting as intermediaries and amplifiers between ticks. Various vertebrate hosts, particularly large ungulates, can transiently increase infection opportunities, enabling the virus to spread to other ticks feeding on these hosts. They can also contribute to CCHFV spread through co-feeding transmission, where ticks acquire the virus from infected ticks nearby, even if the host animal is not viremic (13). The movement of livestock, which may harbor infected ticks, significantly influences the spread of the virus (13). When livestock travel long distances, they can unknowingly transport infected ticks, as these ticks feed for an extended period. Unregulated trade movements of domestic animals could greatly elevate the risk of introducing infected ticks to new areas (28).

The prevalence of CCHFV antibodies among livestock varies based on factors like age and breed, highlighting different levels of susceptibility and exposure. Older animals typically have higher antibody levels due to repeated exposure, while younger animals, such as calves, are more likely to contract the infection while grazing, increasing their chances of encountering infected ticks (29–32). Cross-bred cattle often show higher seropositivity compared to native breeds, possibly due to genetic or environmental factors L (32). Longitudinal studies suggest that animals with existing antibodies and tick infestations may be at risk of reinfection (19). Antibodies against CCHFV can persist in naturally infected livestock for up to 2 months, emphasizing the need for effective surveillance and control strategies (19).

The detection of CCHFV antibodies in domestic animals has been crucial in identifying the presence of the virus and localizing areas with higher risks of human infection. Livestock such as cattle, sheep, camels, and goats commonly become infected with CCHFV through tick bites, often experiencing asymptomatic transient viremia for 7–15 days (33, 34). Other domestic species, including buffaloes, horses, donkeys, dogs, chickens, and ostriches, occasionally show CCHFV seropositivity, though less commonly than livestock.

Buffaloes play an important role in CCHFV epidemiology as definitive hosts for *Hyalomma* and *Rhipicephalus* ticks. In a study examining the sera of 880 buffaloes, using ELISA, 145 were found to have been exposed to the virus (35). Their resistance to tick bites due to thicker hides and mud wallowing habits reduces the likelihood of tick-borne pathogen transmission (36–38). However, in densely populated regions like India, buffaloes may increase the risk of CCHFV transmission to humans (39, 40). In Africa, the coexistence of buffaloes and cattle within integrated wildlife-livestock ranching systems suggests a potential reservoir role for buffaloes in CCHFV transmission. A recent study in Kenya observed higher CCHFV prevalence in buffaloes compared to cattle, indicating that buffaloes could act as a reservoir, potentially transmitting the infection to cattle due to shared habitats and overlapping ranges (41).

TABLE 2 List of seropositive domestic animals infected by Crimean-Congo haemorrhagic fever virus.
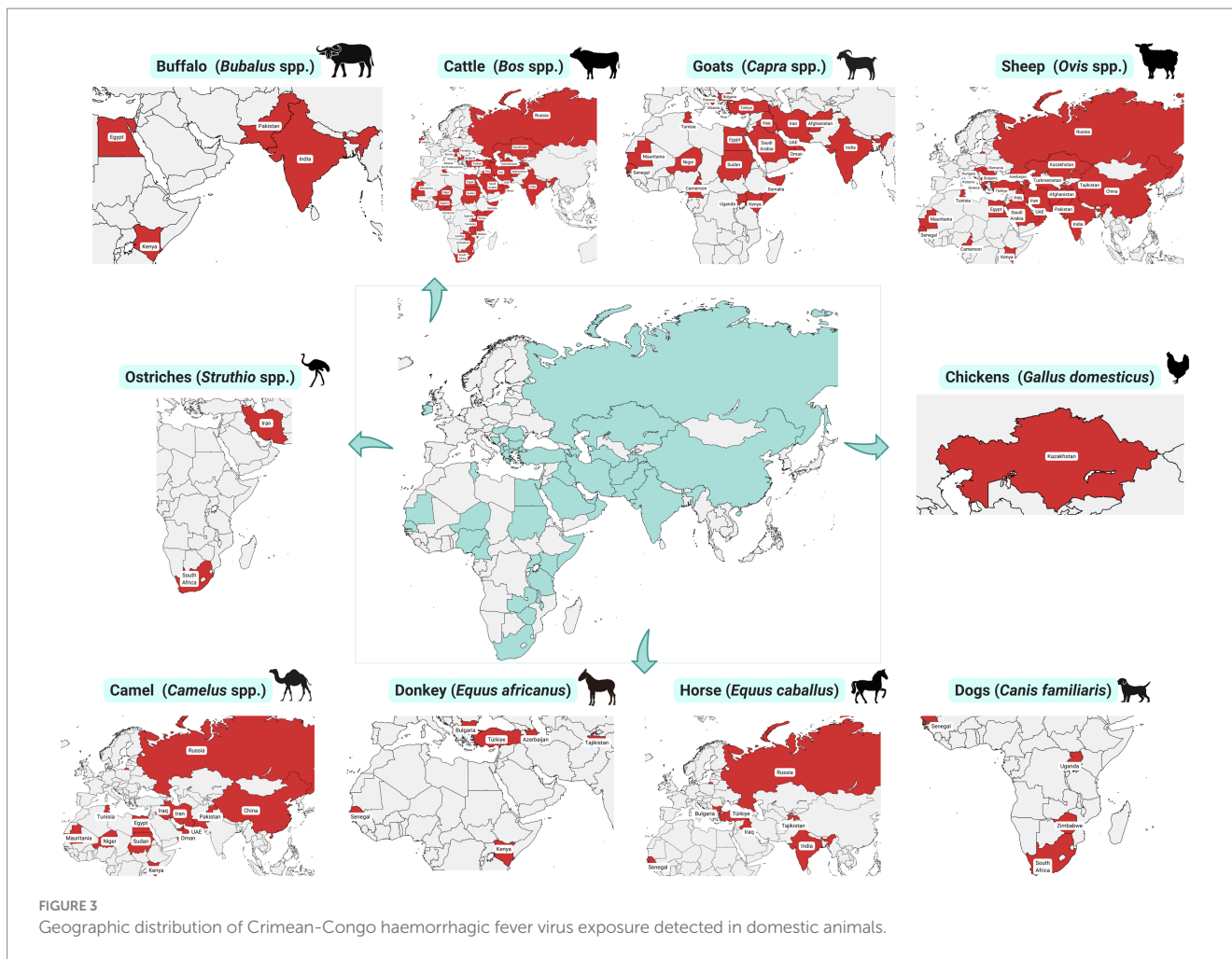
Artiodactyla	Bovidae	Buffalo	*Bubalus* spp.	Egypt, India, Kenya, Pakistan	(39, 41, 60, 164)
		Cattle	*Bos* spp.	Afghanistan, Albania, Armenia, Azerbaijan, Bosnia, Bulgaria, Cameroon, Egypt, Hungary, India, Iran, Iraq, Ireland, Kazakhstan, Kenya, Kosovo, Malawi, Mauritania, Niger, Nigeria, North Macedonia, Oman, Russia, Saudi Arabia, Senegal, Somalia, South Africa, Sudan, Tajikistan, Turkmenistan, Tanzania, Tunisia, Türkiye, United Arab Emirates, Uganda, Zambia, Zimbabwe	(12, 29–32, 39, 41–45, 47, 60, 61, 88, 108, 124, 145, 154, 164–200)
		Goats	*Capra* spp.	Afghanistan, Albania, Bulgaria, Cameroon, Egypt, India, Iran, Iraq, Kenya, Kosovo, Mauritania, Niger, Oman, Saudi Arabia, Senegal, Somalia, Sudan, Tunisia, Türkiye, United Arab Emirates, Uganda	(29, 39, 42–44, 61, 67, 108, 124, 139, 153, 154, 164, 172, 174–176, 178, 180, 186, 189, 190, 192–194, 197–203)
		Sheep	*Ovis* spp.	Afghanistan, Azerbaijan, Bulgaria, Cameroon, China, Egypt, Greece, Hungary, India, Iran, Iraq, Kazakhstan, Kenya, Kosovo, Mauritania, Oman, Pakistan, Romania, Russia, Saudi Arabia, Senegal, Tajikistan, Tunisia, Türkiye, Turkmenistan, United Arab Emirates	(4, 5, 12, 29, 42, 44, 47, 51, 124, 132, 153, 154, 162, 164, 167, 176, 178, 180, 186, 190–194, 196–200, 204–210)
	Camelidae	Camels	*Camelus* spp.	China, Egypt, Iran, Iraq, Kenya, Mauritania, Niger, Oman, Pakistan, Russia, Sudan, Tunisia, United Arab Emirates	(44, 124, 132, 138, 162, 173, 180, 186, 192, 193, 196, 211–216)
Perissodactyla	Equidae	Donkey	*Equus africanus*	Azerbaijan, Bulgaria, Kenya, Senegal, Tajikistan, Türkiye	(29, 42, 47, 48, 52, 167)
		Horses	*Equus caballus*	Bulgaria, India, Iraq, Russia, Senegal, Tajikistan, Türkiye	(42–45, 47, 48, 52, 182)
Carnivora	Canidae	Dogs	*Canis familiaris*	Senegal, South Africa, Uganda, Zimbabwe	(52–54)
Galliformes	Phasianidae	Chickens	*Gallus domesticus*	Kazakhstan	(177)
Struthioniformes	Struthionidae	Ostriches	*Struthio* spp.	Iran, South Africa	(56, 57)

Horses are susceptible to CCHFV infection and can serve as hosts for infected adult ticks, thereby contributing to virus transmission. They can produce antibody levels similar to other animals, but their viremia is too low to infect new naive ticks and sustain transmission through blood feeding (34). Seroprevalence studies have documented CCHFV prevalence in horses across various endemic regions, including Bulgaria (4, 42), India (43), Iraq (44), Russia (45, 46), Tajikistan (47), and Türkiye (48). The role of horses in CCHFV transmission varies depending on environmental conditions, tick prevalence, and the density of horse populations in endemic regions. In regions invaded by *H. marginatum* ticks such as the Czechia (49) and France (50), horses exhibit higher infestation rates compared to other ungulates, likely due to regular ectoparasite checks.

Donkeys play a crucial role in the spread of CCHFV as they frequently encounter ticks during rural activities. Along with mules, they have historically been vital in agriculture and transportation. The high seroprevalence of CCHFV in donkeys is influenced by factors such as climate, animal movement, living conditions, and cohabitation with other livestock, highlighting their role in sustaining the virus within communities. Although donkeys might not directly transmit the virus like viremic livestock, they significantly contribute to its persistence. Spengler et al. (5) reported seroprevalence rates of 18.8% in Azerbaijan, 17.4 and 50% in Bulgaria, and 39.5% in Tajikistan. In Kenya, Omoga et al. (51) found the highest seropositivity in donkeys at 31.4% compared to other livestock species. In Senegal, Mangombi et al. (52) reported a seropositivity rate of 17.2% in donkeys. The highest recorded seroprevalence was in Türkiye, where Saltik (48) reported a rate of 53.48% in donkeys.

Dogs can harbor CCHFV asymptomatically or with mild symptoms when exposed to infected ticks. Studies in Africa have shown varying seroprevalence rates among domestic dogs. Antibodies to CCHFV were found in 6% of dogs (*n* = 1978) in South Africa and Zimbabwe (53). In Senegal, Mangombi et al. (52) found a seropositivity rate of 18.2% in dogs. In Uganda, Atim et al. (54) reported a high seropositivity rate of 56.2% in dogs. While the role of dogs in CCHFV epidemiology is not as well understood as that of livestock, their close association with humans raises concerns about the potential introduction of infected ticks into human environments. Further research into companion animals and their interactions with vector species is essential to better understand their role in the ecology of CCHFV.

FIGURE 3
Geographic distribution of Crimean-Congo haemorrhagic fever virus exposure detected in domestic animals.

While various domestic mammals are susceptible to CCHFV infection, birds generally seem refractory. For example, Spengler et al. (34) stated a seroprevalence of 0.2% in chickens and ducks in Kazakhstan. Interestingly, ostriches demonstrate the presence of both CCHFV antibodies and viremia, unlike most other bird species. Ostriches appear to be the only birds in which there is detectable circulation of the virus in blood comparable to mammals (7). Viremia in ostriches is short, lasting 1–4 days, while the virus persists in visceral organs such as the spleen, liver, and kidneys for up to 5 days (55). Their role in transmitting the virus to humans is uncertain, but instances of notable viremia associated with CCHFV infection in humans have been noted (55–58).

2.4 CCHFV in wild animals

Numerous serological studies across a wide range of wild animals have highlighted the diverse responses observed in populations regarding CCHFV infections. These studies suggest their roles as amplifying hosts, facilitating virus transmission between infected and uninfected ticks during co-feeding or when feeding on a viremic animal.

A comprehensive review of nearly 7,000 samples from over 175 mammalian, avian, and reptilian species revealed varying levels of seroprevalence (Table 3; Figure 4) (5). Certain mammals, such as

hares (3–22%), buffalo (10–75%), and rhinoceroses (40–68%), exhibited considerable seropositivity.

Rodents and lagomorphs are crucial in CCHFV epidemiology (4, 7, 59). Several rodent and lagomorph species, including the European hare (*Lepus europaeus*), scrub hare (*Lepus saxatilis*), Cape hare (*Lepus capensis*), bushveld gerbil (*Gerbilliscus leucogaster*), four-striped grass mouse (*Rhabdomys pumilio*), and multimammate mouse (*Mastomys* spp.), act as amplifying hosts, facilitating virus replication and transmission to ticks during their feeding (7). Infected rodents contribute significantly to the spread of CCHFV by transmitting the virus to ticks, thereby influencing its presence in the environment. Understanding the role of rodents in CCHFV transmission is important for developing effective surveillance and control strategies. Various rodent species such as the Cape porcupine (*Hystrix africaeaustralis*) (53), black rat (*Rattus rattus*) (60), brown rat (*R. norvegicus*) (60), bushveld gerbil (*G. leucogaster*) (53), four-striped grass mouse (*R. pumilio*) (53), Highveld gerbil (*Tatera brantsii*) (53), Indian desert jird (*Meriones hurrianae*) (60), Indian gerbil (*T. indica*) (60), multimammate mouse (*Mastomys* spp.) (53), Namaqua rock rat (*Aethomys namaquensis*) (53), Sundevall's jird (*M. crassus*) (61), South African springhare (*Pedetes capensis*) (53), and Cape ground squirrel (*Xerus inauris*) (53) have displayed seropositivity to CCHFV in different regions, indicating their potential involvement in the virus's transmission cycle.
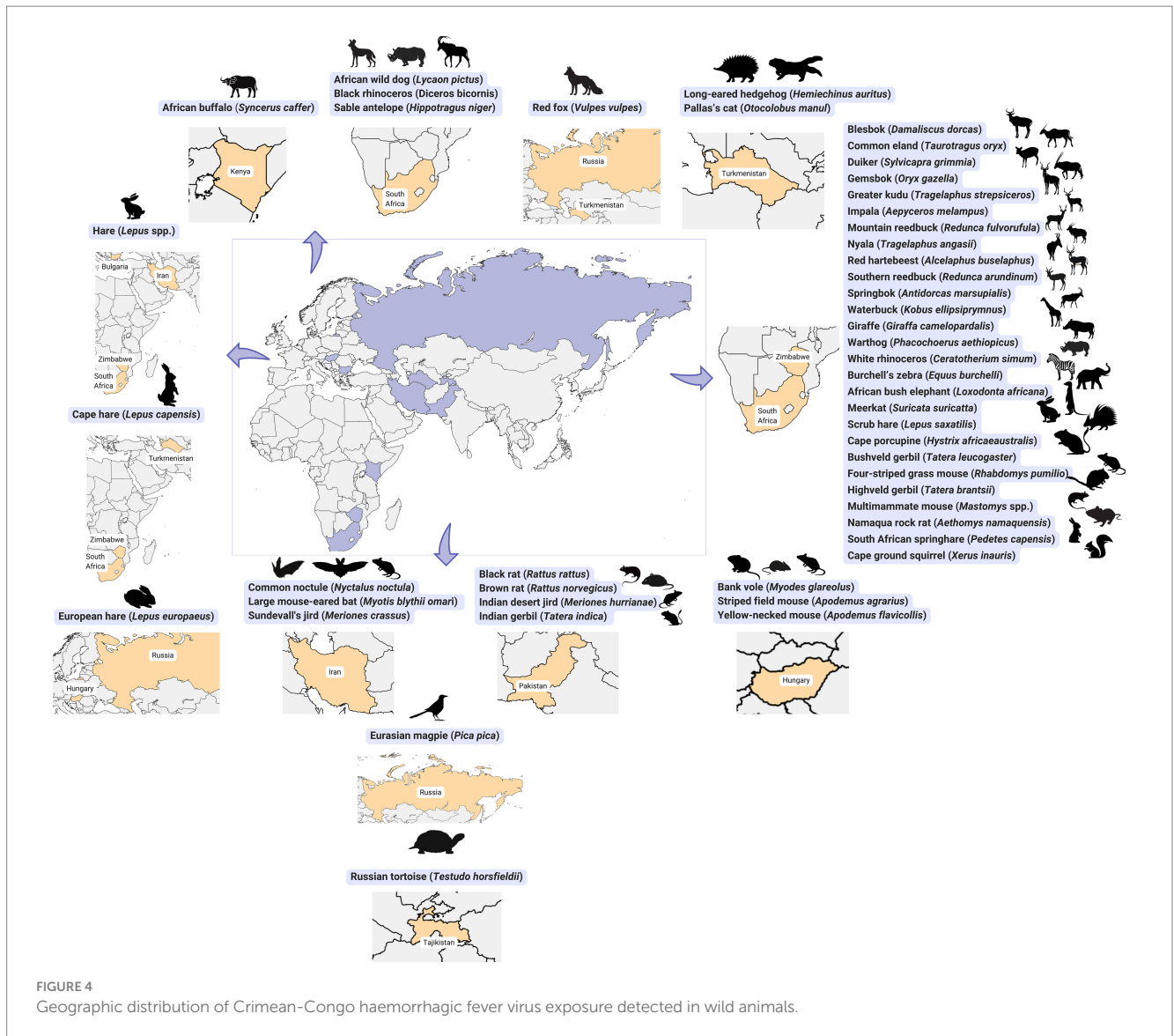
TABLE 3 List of seropositive wild animals infected by Crimean-Congo haemorrhagic fever virus.

Class	Order	Family	Common name	Scientific name	Country	References
Mammals	Artiodactyla	Bovidae	African buffalo	*Syncerus caffer*	Kenya	(41)
			Blesbok	*Damaliscus dorcas*	South Africa, Zimbabwe	(53)
			Common eland	*Taurotragus oryx*	South Africa, Zimbabwe	(53)
			Duiker	*Sylvicapra grimmia*	South Africa, Zimbabwe	(53)
			Gemsbok	*Oryx gazella*	South Africa, Zimbabwe	(53)
			Greater kudu	*Tragelaphus strepsiceros*	South Africa, Zimbabwe	(53, 62)
			Impala	*Aepyceros melampus*	South Africa, Zimbabwe	(53, 62)
			Mountain reedbuck	*Redunca fulvorufula*	South Africa, Zimbabwe	(53)
			Nyala	*Tragelaphus angasii*	South Africa, Zimbabwe	(53)
			Red hartebeest	*Alcelaphus buselaphus*	South Africa, Zimbabwe	(53)
			Sable antelope	*Hippotragus niger*	South Africa	(53, 62)
			Southern reedbuck	*Redunca arundinum*	South Africa, Zimbabwe	(53)
			Springbok	*Antidorcas marsupialis*	South Africa, Zimbabwe	(53)
			Waterbuck	*Kobus ellipsiprymnus*	South Africa, Zimbabwe	(53)
		Giraffidae	Giraffe	*Giraffa camelopardalis*	South Africa, Zimbabwe	(53, 62)
		Suidae	Warthog	*Phacochoerus aethiopicus*	South Africa, Zimbabwe	(53)
	Perissodactyla	Rhinocerotidae	White rhinoceros	*Ceratotherium simum*	South Africa, Zimbabwe	(53, 62)
			Black rhinoceros	*Diceros bicornis*	South Africa	(53, 62)
		Equidae	Burchell's zebra	*Equus burchelli*	South Africa, Zimbabwe	(53)
	Proboscidea	Elephantidae	African bush elephant	*Loxodonta africana*	South Africa, Zimbabwe	(53)
	Carnivora	Canidae	African wild dog	*Lycaon pictus*	South Africa	(62)
			Red fox	*Vulpes vulpes*	Russia, Turkmenistan	(217, 218)
		Felidae	Pallas's cat	*Otocolobus manul*	Turkmenistan	(218)
		Herpestidae	Meerkat	*Suricata suricatta*	South Africa, Zimbabwe	(53)
	Chiroptera	Vespertilionidae	Common noctule	*Nyctalus noctula*	Iran	(61)
			Large mouse-eared bat	*Myotis blythii omari*	Iran	(61)

(Continued)

TABLE 3 (Continued)

Class	Order	Family	Common name	Scientific name	Country	References
	Lagomorpha	Leporidae	Cape hare	*Lepus capensis*	South Africa, Turkmenistan, Zimbabwe	(4, 53)
			Hare	*Lepus* spp.	Bulgaria, Iran, South Africa, Zimbabwe	(4, 42, 53, 219)
			European hare	*Lepus europaeus*	Russia, Hungary	(4, 217, 220)
			Scrub hare	*Lepus saxatilis*	South Africa, Zimbabwe	(53)
	Eulipotyphla	Erinaceidae	Long-eared hedgehog	*Hemiechinus auritus*	Turkmenistan	(4, 221)
		Cricetidae	Bank vole	*Myodes glareolus*	Hungary	(222)
	Rodentia	Hystricidae	Cape porcupine	*Hystrix africaeaustralis*	South Africa, Zimbabwe	(53)
		Muridae	Black rat	*Rattus rattus*	Pakistan	(60)
		Muridae	Brown rat	*Rattus norvegicus*	Pakistan	(60)
		Muridae	Bushveld gerbil	*Gerbilliscus leucogaster*	South Africa, Zimbabwe	(53)
		Muridae	Four-striped grass mouse	*Rhabdomys pumilio*	South Africa, Zimbabwe	(53)
		Muridae	Highveld gerbil	*Tatera brantsii*	South Africa, Zimbabwe	(53)
		Muridae	Indian desert jird	*Meriones hurrianae*	Pakistan	(60)
		Muridae	Indian gerbil	*Tatera indica*	Pakistan	(60)
		Muridae	Multimammate mouse	*Mastomys* spp. *(coucha, natalensis)*	South Africa, Zimbabwe	(53)
		Muridae	Namaqua rock rat	*Aethomys namaquensis*	South Africa, Zimbabwe	(53)
		Muridae	Striped field mouse	*Apodemus agrarius*	Hungary	(222)
		Muridae	Sundevall's jird	*Meriones crassus*	Iran	(61)
		Muridae	Yellow-necked mouse	*Apodemus flavicollis*	Hungary	(222)
		Pedetidae	South African springhare	*Pedetes capensis*	South Africa, Zimbabwe	(53)
		Sciuridae	Cape ground squirrel	*Xerus inauris*	South Africa, Zimbabwe	(53)
Aves	Passeriformes	Corvidae	Eurasian magpie	*Pica pica*	Russia	(217)
Reptilia	Testudines	Testudinidae	Russian tortoise	*Testudo horsfieldii*	Tajikistan	(223)

FIGURE 4
Geographic distribution of Crimean-Congo haemorrhagic fever virus exposure detected in wild animals.

Additionally, other animals, including many large herbivorous mammals within the Artiodactyla and Perissodactyla orders, such as the African buffalo (*Syncerus caffer*), blesbok (*Damaliscus dorcas*) (53), common eland (*Taurotragus oryx*) (53), duiker (*Sylvicapra grimmia*) (53), gemsbok (*Oryx gazella*) (53), greater kudu (*Tragelaphus strepsiceros*) (53, 62), impala (*Aepyceros melampus*) (53, 62), mountain reedbuck (*Redunca fulvorufula*) (53), nyala (*Tragelaphus angasii*) (53, 62), red hartebeest (*Alcelaphus buselaphus*) (53), sable antelope (*Hippotragus niger*), southern reedbuck (*Redunca arundinum*) (53), springbok (*Antidorcas marsupialis*) (53), waterbuck (*Kobus ellipsiprymnus*) (53), giraffe (*Giraffa camelopardalis*) (53), warthog (*Phacochoerus aethiopicus*) (53), white rhinoceros (*Ceratotherium simum*) (53, 62), black rhinoceros (*Diceros bicornis*) (53, 62), and Burchell's zebra (*Equus burchelli*) (53), as well as the African bush elephant (*Loxodonta africana*) (53, 62) in South Africa and Zimbabwe, have demonstrated seropositivity to CCHFV.

Certain members of the Carnivora order also exhibited seropositivity in specific regions, including the African wild dog (*Lycaon pictus*) (62) in South Africa, red fox (*Vulpes vulpes*) in Russia and Turkmenistan (4), and Pallas's cat (*Otocolobus manul*) in Turkmenistan (4).

Bats, such as the common noctule (*Nyctalus noctula*) and large mouse-eared bat (*Myotis blythii omari*) in Iran (61), also displayed seropositivity to CCHFV.

The potential involvement of birds in transmitting and maintaining CCHFV poses a significant concern in disease ecology. Migratory birds, traveling long distances through various habitats, carry a range of ectoparasites like ticks, mites, fleas, and lice. Their movements, especially between Africa and Europe, coincide with environmental changes that may affect the spread of tick-borne diseases. Studies show migratory birds can transport *H. marginatum* ticks from Africa to Europe, with certain Passerine bird species (e.g., *Acrocephalus arundinaceus*, *A. scirpaceus*, *A. palustris*, *A. schoenobaenus*, *Locustella luscinioides*, and *Luscinia megarhynchos*) facilitating the dispersion of infected ticks along their migratory routes (59). Although avian species may be refractory to CCHFV infection (5, 34, 56, 63), they can serve as blood sources for immature *H. marginatum* ticks, potentially contributing to disease spread. While most wild birds do not show evidence of CCHFV infection, exceptions like magpies (*Pica pica*), which have displayed CCHFV antibodies, suggest a more complex situation (7). Ostriches, however, show unique susceptibility to CCHFV, displaying both antibodies and

viremia, unlike other birds (7). Further research is crucial to understand how different bird species contribute to CCHFV transmission.

Among reptiles, only one species—the Horsfield's tortoise (*Testudo horsfieldii*) in Tajikistan—has been reported as seropositive for CCHFV (4). Notably, the tick species *H. aegyptium*, which is closely associated with tortoises and often linked to CCHFV transmission (64, 70), primarily infests hosts within the *Testudo* genus. This suggests a possible role of tortoises in virus transmission. However, the overall susceptibility of reptiles to CCHFV remains unclear, despite evidence pointing to potential transmission through tortoise-associated ticks.

2.5 Molecular detection of CCHFV in animals

Despite evidence of seropositivity among domestic and wild animals, isolating CCHFV directly from these hosts has proven challenging and direct CCHFV isolation from animals is scarce (5). Documented instances of direct CCHFV isolation from animals remain scarce, with notable cases including a febrile cow in Kenya (43), cattle and a goat from a Nigerian abattoir (90), a sentinel goat in Senegal (4, 43), European hares in Crimea (67), and a hedgehog in Nigeria (90). These sporadic cases highlight the difficulties in identifying and isolating the virus due to the typically short viremic period in infected animals and the absence or mildness of clinical symptoms (7). As a result, most successful isolations come from ticks or human cases, where the virus is more prominent.

Molecular detection of CCHFV infection relies on both real-time and end-point PCR techniques (68). These methods amplify specific segments of the viral RNA, such as the S segment encoding the nucleoprotein, enabling precise detection and quantification of the virus. In resource-limited settings, loop-mediated isothermal amplification (RT-LAMP) offers a cost-effective alternative, amplifying viral RNA under isothermal conditions without the need for advanced equipment (69).

Enhanced molecular detection methods, longitudinal studies, and comprehensive monitoring programs are essential for fully understanding the role of various animal species in the ecology of CCHFV. This knowledge is important for mitigating potential transmission risks to humans and preventing outbreaks of this serious zoonotic disease.

2.6 Experimental CCHFV infections in animals

Experimental studies investigating CCHFV infections across various animal species have provided valuable insights into susceptibility patterns, infection dynamics, and immune responses.

Small mammals, despite displaying short viremic periods of 2 to 15 days followed by antibody development, are not considered long-term reservoirs for CCHFV (34). Nonetheless, population surges in species like hares have been linked to disease outbreaks, implying their ecological significance in CCHFV transmission (7, 34). Studies on small African wild mammals and laboratory animals showed diverse

responses to CCHFV, with some species showing viremia and antibody responses, while others did not. South African hedgehogs, for instance, display resistance but develop neutralizing antibodies (71). Furthermore, the virus was recovered from the blood of experimentally infected long-eared hedgehogs (*Hemiechinus auritus*) (4), while European hedgehogs (*Erinaceus europaeus*) did not exhibit similar susceptibility (72). The varying outcomes among hedgehog species indicate that susceptibility to CCHFV and infection dynamics may vary even within closely related species.

Experimental studies have shown that various rodent and lagomorph species respond differently to CCHFV infection. European hares (*Lepus europaeus*), for example, showed varying viremic intervals (2, 4, 5, 9 dpi) and generated an antibody response by day 7, which was maintained throughout the study (34). Similarly, scrub hares (*Lepus saxatilis*) and bushveld gerbils (*G. leucogaster*) exhibited viremia within the first week after infection, along with the production of antibodies (71). However, some species like the Cape ground squirrel (*Xerus inauris*) and the four-striped grass mouse (*Rhabdomys pumilio*) showed limited or no viremia and inconsistent antibody responses (71). On the other hand, the Southern multimammate mouse (*Mastomys coucha*), white-tailed rat (*Uromys caudimaculatus*), and red veld rat (*Aethomys chrysophilus*) demonstrated viremia (ranging from 1 to 6 dpi) and produced antibodies, indicating different responses to CCHFV among rodent species (71). Guinea pigs displayed low-level viremia accompanied by elevated temperatures. The onset of viremia correlated with the route of infection (71). The varied responses among small mammals highlight the complexity of CCHFV interactions, emphasizing the need for species-specific understanding in ecological dynamics. For a more comprehensive list, we encourage referring to the detailed experimental infection data of various small mammals infected with CCHFV, as thoroughly discussed in these studies (7, 34).

Experimental studies have investigated how CCHFV infects livestock, focusing on ruminants like sheep, cattle, horses and donkeys. Similar to small mammals, these ruminants experienced a brief period of viremia and developed antibodies about a week after inoculation (34). In sheep, maternal transfer of these antibodies was demonstrated, indicating a form of passive immunity (73). Additionally, experiments on West African sheep highlighted diverse clinical manifestations following infection (73). Some infected sheep developed moderate fever, hepatic dysfunction, and abnormal blood cell counts, including marked neutrophilia, that persisted for weeks. These observations highlight the potential impacts of CCHFV infection in livestock, particularly in sheep, affecting their health and possibly contributing to the virus's circulation in nature. Calves have also been subjects of experimental infections, showing varying responses based on their age at the time of infection (74). When infected, 2-month-old calves displayed mild illness, with the virus detected in their blood. In contrast, 6-month-old calves did not show signs of viremia. However, only the younger calves, with detectable viremia, would be significant for the virus's circulation, despite both age groups exhibiting high levels of antibodies against CCHFV. Horses and donkeys showed different responses: donkeys exhibited low-level viremia (75), while horses displayed minimal or no viremia but developed strong virus-neutralizing antibodies for up to 3 months (76). This highlights horses as valuable sources of serum for diagnostic and therapeutic purposes due to the stability of their virus-neutralizing antibodies.

It is important to note that these experimental studies were conducted in the 1970s. These studies revealed low viremia levels and asymptomatic cases in many animals, yet some could still transmit the virus to ticks during feeding. These results emphasize the need for updated research to better understand current CCHFV dynamics in livestock and improve prevention strategies. On the other hand, performing such research would be very complicated or even impossible nowadays as CCHFV is classified as BSL-4 pathogen.

Efforts to establish animal models for CCHF have faced challenges, with limited success achieved so far. Newborn mice are the only animals besides humans that display symptoms of the disease, providing a basis for research. (7). Additionally, genetically modified adult mice and hamsters, deficient in specific immune components, mimic human disease and exhibit uncontrolled viral replication, inflammatory immune reactions, liver pathology, and mortality (77–81). Non-human primate models, such as cynomolgus macaques, reflect varied disease outcomes similar to humans, aiding in preclinical assessments of therapeutics and vaccines (82). In experimental infections with African green monkeys (*Chlorocebus sabaeus*), the majority of subjects exhibited either limited symptoms or remained asymptomatic, although one monkey developed fever post-infection, with some monkeys showing detectable antibodies against the virus (83). In a separate study, Patas monkeys (*Erythrocebus patas*) and a Guinea baboon (*Papio papio*) displayed low-level viremia following inoculation, ultimately leading to the development of neutralizing antibodies in the baboon (84).

Studies investigating CCHFV infection in birds suggest that avian species, both wild and domestic, are generally refractory to the virus. Early experiments found that birds remained healthy after CCHFV inoculation, displaying no signs of viremia or detectable antibody responses (87). However, several studies showed that ground-feeding birds may therefore contribute to the virus's ecological dynamics by facilitating viremic, non-viremic transmission or cofeeding (7, 56, 85, 87). Ostriches, however, appear to be significant hosts for CCHFV, showing detectable viremia and epidemiologically linked to human infections (85). In controlled experiments, infected ostriches developed viremia and subsequently produced antibodies against CCHFV (88). Other bird species, for example the red-billed hornbill (*Tockus erythrorhynchus*), demonstrated replication of CCHFV without viremia but were able to infect immature naive ticks (85). Other birds, for example helmeted guineafowl (*Numida meleagris*), exhibited low-level viremia followed by a transient antibody response starting 5–6 dpi (56). Additionally, birds like the glossy starling (*Lamprotornis* spp.), did not display viremia but generated an antibody response (85). Further research is needed to clarify the role of birds in CCHFV transmission and its ecological implications.

3 Prevention and control of CCHFV in animals

Preventing and controlling the transmission of CCHFV in animals is crucial not only for animal health but also for preventing the virus from spreading to humans, where it poses a significant health risk. These measures aim to minimize the risk of virus transmission to humans and prevent CCHFV from reaching non-endemic regions.

The primary strategy to control CCHFV in animals involves managing tick populations, the main vectors for the virus. Using acaricides and other tick control methods is the most practical approach, although complete prevention of tick bites is unlikely (86). Efforts often focus on periods surrounding slaughter, when exposure of slaughterhouse workers to CCHFV in animal blood or tissues is most likely. Additional practices to reduce tick exposure include environmental adjustments, treating animals with tick repellents, maintaining clean pastures, establishing quarantine measures for new animals, and improving animal housing (86). Preventing or controlling CCHF infection in animals and ticks is complex due to the typically unnoticed tick-animal-tick-CCHFV life cycle and the often asymptomatic nature of the infection in most animals. The widespread presence of tick vectors further complicates control efforts, making acaricide-based tick control feasible only in well-managed livestock facilities.

Surveillance systems play a crucial role in early detection and response to CCHFV outbreaks in animals. Regular monitoring of animal populations in endemic areas for the presence of CCHFV antibodies or viral RNA could help identify potential reservoirs and understand disease dynamics. Timely detection enables prompt interventions to prevent further spread.

Finally, implementing biosecurity measures in farms, slaughterhouses, and veterinary facilities is essential to prevent CCHFV transmission between animals and humans as these facilities have been identified as major risk areas for human infection (8, 90, 224, 225).

Control strategies for CCHF infection in animals also extend to human protection. These strategies include avoiding tick bites through the use of repellents and employing adequate protection when handling or slaughtering animals (226). Preventing the movement of naive animals into endemic areas is crucial, as it minimizes the risk of vertebrate amplification of the virus, reducing occupational risks for workers involved in animal processing. Educating livestock owners, veterinarians, and the general public about CCHFV transmission, symptoms in animals, and preventive measures is vital. Raising awareness about the disease's impact, emphasizing the importance of early reporting of suspected cases, and promoting proper biosecurity measures are key components of effective disease control efforts.

4 Conclusion

CCHFV, a highly virulent virus transmitted by *Hyalomma* ticks, poses a significant global health threat by causing severe haemorrhagic fever in humans. Its widespread presence across Africa, Asia, and Europe highlights the urgent need to understand its behavior within tick vectors and animal hosts.

Both wild and domestic animals, acting as asymptomatic carriers, play critical roles in maintaining tick populations and transmitting the virus, thereby potentially spreading the disease. Further, small mammals like hares and hedgehogs support immature tick populations, while larger domestic animals such as cattle, goats, and sheep can inadvertently expose humans to CCHFV during handling and slaughter. The complex interplay between the virus, ticks, and vertebrate hosts presents significant challenges in controlling CCHFV transmission. Despite often lacking visible symptoms, animals play a crucial role in the maintenance and spread of the virus, highlighting the necessity for rigorous surveillance, serological screening, and a deeper understanding of their roles in CCHFV ecology. Experimental infections confirm that various animal species are susceptible to CCHFV, emphasizing the need for ongoing research and monitoring.

Control strategies mainly focus on managing tick populations through the use of acaricides and improving hygiene in animal habitats. However, the virus's elusive nature within animals and the difficulties in identifying infected hosts continue to pose significant challenges to disease control. Continued research and a deeper understanding of CCHFV in animal populations are essential for developing more effective control strategies, mitigating zoonotic risks, and protecting the health of both animals and humans.

Author contributions

SS: Conceptualization, Data curation, Formal analysis, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. JI: Formal analysis, Methodology, Writing – original draft, Writing – review & editing. AT: Formal analysis, Methodology, Validation, Writing – review & editing. JČ: Conceptualization, Funding acquisition, Supervision, Writing – review & editing.

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