

REVIEWS

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THE ROLE OF WILD MAMMALS IN THE MAINTENANCE OF RIFT VALLEY FEVER VIRUS

Marie-Marie Olive,^{1,2,3,6} Steven M. Goodman,⁴ and Jean-Marc Reynes⁵

¹ CIRAD UMR CMAEE, F-97491 Sainte-Clotilde, Ile de La Réunion, France

² Centre de Recherche et de Veille sur les maladies émergentes dans l'Océan Indien (CRVOI), GIP CYROI—2 rue Maxime Rivière, 97490 Sainte-Clotilde, Ile de La Réunion, France

³ Unité de Virologie, Institut Pasteur de Madagascar, BP 1274, Antananarivo 101, Madagascar

⁴ Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605, USA and Association Vahatra, BP 3972, Antananarivo, Madagascar

⁵ Unité de biologie des infections virales émergentes, Institut Pasteur, 21 avenue Tony Garnier, 69 265 Lyon Cedex 07, France

⁶ Corresponding author (email: marie-marie.olive@cirad.fr)

ABSTRACT: Rift Valley fever virus (RVFV) is a zoonotic arbovirus affecting primarily domestic ruminants and humans. Numerous vector species are known or implicated in the transmission of RVFV. The role of mammals in the maintenance of RVFV, and the existence of a wild mammal reservoir in the epidemiologic cycle of RVFV, remain largely unknown. Our objective is to present a detailed review of studies undertaken on RVFV, often associated with wild mammals, with the aim of focusing future research on potential reservoirs of the virus. Natural and experimental infections related to RVFV in several mammalian orders, including Artiodactyla, Chiroptera, Rodentia, Primata (nonhuman), Perissodactyla, Carnivora, Proboscidea, Erinaceomorpha, and Lagomorpha, are reviewed; the first four orders have received the greatest attention. The possible role of wild ruminants, especially African buffalo (*Syncerus caffer*), is also discussed. Conflicting results have been published concerning rodents but, based on the literature, the likely candidate species include the African genera *Arvicanthis* and *Micaelamys* and the widely introduced roof rat (*Rattus rattus*). Members of the orders Chiroptera and Rodentia should receive greater attention associated with new research programs. For the other orders mentioned above, few data are available. We are unaware of any investigation concerning the orders Afrosoricida and Soricomorpha, which are represented in the geographic area of RVFV and can be abundant. As a first step to resolve the question of wild mammals as a reservoir of RVFV, serologic and virologic surveys should be promoted during epizootic periods to document infected wild animals and, in the case of positive results, extended to interepidemic periods to explore the role of wild animals as possible reservoirs.

Key words: Artiodactyla, Chiroptera, infectious disease reservoir, Mammalia, Primata, Rift Valley fever virus, Rodentia.

INTRODUCTION

Rift Valley fever (RVF) is an arthropod-borne zoonotic disease affecting mainly domestic ruminants and humans. Swanepoel and Coetzer (2004) produced a comprehensive review of aspects of this disease. Rift Valley fever virus (RVFV), responsible for the disease, is an enveloped RNA segmented virus in the family *Bunyaviridae*, genus *Phlebovirus*. It was first isolated in 1930 during an outbreak among domestic ruminants near Lake Naivasha in the Kenya Rift Valley (Daubney et al., 1931). Infection in animals may be largely benign, with mild symptoms, or

it may cause necrotic hepatitis and a hemorrhagic state leading to high mortality, particularly among newborns, as well as to spontaneous abortion in pregnant animals. The virus is transmitted between ruminants mainly by the bite of several mosquito genera, in particular *Aedes*; numerous vectors are naturally infected and some have demonstrated vector competence in the laboratory (EFSA, 2005). Humans can be infected by these vectors or via inhalation of aerosols or contact when handling sick or dead infected animals or their fresh tissues. An association between consumption of unprocessed milk and human infection has also been

reported during RVF outbreaks (Swanepoel and Coetzer, 2004). Infection in humans causes influenza-like illness complicated by hemorrhagic fever, encephalitis, ocular damage and, in some cases, death. Outbreaks have been confirmed in 19 countries and the virus probably circulates in 30 countries, including many in continental Africa, Madagascar, and the Arabian Peninsula (Bird et al., 2009; World Organisation for Animal Health [OIE], 2011). Between 2008 and 2011, outbreaks of RVF were documented in Kenya, Tanzania, Somalia, Sudan, South Africa, Madagascar, Union of the Comoros, Mayotte, Swaziland, Saudi Arabia, Namibia, and Botswana (OIE, 2011).

Epidemiology of RVF is complex, with an important link to ecologic and climatic conditions (Linthicum et al., 1987, 1999; Anyamba et al., 2002; Swanepoel and Coetzer, 2004). Outbreaks in southern and eastern Africa have been associated with heavy rainfall at intervals of 5–15 yr or longer (Linthicum et al., 1999; Food and Agriculture Organization, 2000). In eastern Africa, it is believed that RVFV is maintained during interepizootic or interepidemic periods (IEP) through vertical transmission in *Aedes* mosquitoes, as observed in *Aedes (Neomelanimonion) mcintoshi* (Linthicum et al., 1985; Swanepoel and Coetzer, 2004). Outbreaks tend to be correlated with abnormally heavy rainfall that favors the emergence of a large number of adult mosquitoes (Davies, Linthicum, et al., 1985). Following these observations, predictive models, based on satellite-derived information, have been designed (Linthicum et al., 1999, 2007; Anyamba et al., 2009, 2010).

In western and central Africa, the epidemiology seems different than in the eastern portion of the continent. Here, the virus could be maintained over several years at animal watering sites by horizontal transmission between ruminants and mosquitoes during the rainy season and by vertical transmission in *Aedes* during the dry season (Chevalier et al., 2009). In the Central

African Republic, serologic data suggest permanent circulation of RVFV among humans residing in forested areas (Nakounne et al., 2000). In Gabon, serologic evidence of RVFV in people has also been demonstrated in areas where cattle herds are rare (Pourrut et al., 2010). Finally, RVFV has been isolated from forest-sampled mosquitoes from different portions of the Afro-Malagasy region (Smithburn et al., 1948; Fontenille, 1989). Thus, the hypothesis of an epidemiologic cycle implicating vectors and reservoir hosts of wild vertebrates has been repeatedly proposed.

Because birds were refractory to RVFV during experimental infections, and surveys failed to find the virus among these animals, the class Aves has been largely excluded from research associated with their role in the maintenance of RVFV (Findlay, 1931; Findlay and Daubney, 1931; Gear et al., 1951, 1955; Davies and Addy, 1979; Davies and Linthicum, 1986). We present a detailed review of studies undertaken on RVFV in association with wild mammals of diverse phylogenetic origins and histories, which is a different orientation than previous reviews (e.g., Swanepoel and Coetzer, 2004; Kasari et al., 2008). We also evaluate the role of mammals in the maintenance of RVFV and try to focus future studies on potential reservoirs of RVFV.

Infectious disease reservoirs

Several definitions of an infectious disease reservoir are found in the literature, and these are sometimes contradictory (Haydon et al., 2002). According to the Medical Subject Headings (MeSH) (<http://www.nlm.nih.gov/mesh/>), a disease reservoir is defined as “Animate or inanimate sources which normally harbor disease-causing organisms and thus serve as potential sources of disease outbreaks. Reservoirs are distinguished from vectors (disease vectors) and carriers, which are agents of disease transmission rather than continuing sources of potential disease outbreaks.” This definition rules out vectors

as potential reservoirs of disease and does not take into consideration vertical transmission within the vector population. For example, mosquitoes can function as a pathogen reservoir if vertical transmission is effective and regularly occurring (Rickenbach and Mouchet, 1981; Rodhain, 1998), and such a case has been documented for RVFV in east African *Aedes* (*Neomeaniconion*) *mcintoshi* (Linthicum et al., 1985).

Haydon and collaborators (2002) defined a disease reservoir as “one or more epidemiologically connected populations or environments in which the pathogen can be permanently maintained and from which infection is transmitted to the defined target population”; this definition also includes multiple hosts. However, the perceived notion exists that a pathogen infection will be asymptomatic among the reservoir hosts and, hence, suggests a long-term evolutionary relationship between reservoir host and pathogen; however, there is evidence to the contrary (Peterson et al., 2004). Indisputably, asymptomatic and chronic carriage are efficient maintenance mechanisms as, for example, the epidemiology of hantaviruses and lyssaviruses are closely associated with rodents and bats, respectively (Klein and Calisher, 2007; Tordo and Marianneau, 2009). Nevertheless, to rigorously associate the concept of asymptomatic to reservoir host populations is probably too restrictive epidemiologically. For instance, the maintenance of plague bacillus in certain regions is linked to a balance between asymptomatic and vulnerable species, for which the bacteria is pathogenic, living under natural conditions and in the same habitat (Baltazard et al., 1960).

Finally, in Rodhain’s (1998) arbovirologic definition of a good vertebrate reservoir, several vertebrate species could be involved in the natural cycle of a virus, and these animals would be considered natural hosts. However, the role natural hosts may play in the maintenance of a pathogen can be notably different, ranging from ampli-

fying the virus to spreading the disease, acting as reservoirs, or being a dead-end host. In other words, not all natural hosts are necessarily reservoirs of the pathogen. Rodhain (1998) lists the following characteristics of an effective vertebrate reservoir: 1) The population has the capacity to be infected by a pathogen (susceptible) and exhibit no symptoms of the disease, or only benign ones. Once infected, the reservoir host must not [necessarily] succumb to the pathogen before developing viremia and providing transmission; 2) The viremia has to be effective, that is, sufficiently prolonged and with a high titer; 3) The population has to be actively reproducing and sufficiently common, with a proportion of nonimmune individuals; and 4) The population has to have stable and frequent contact with the vector population.

One of the reasons for this review is to help focus future studies on potential reservoirs of RVFV, rather than being an evaluation (based on current knowledge) of the most important reservoirs. This information is given by taxonomic order.

Order Artiodactyla (even-toed ungulates, including ruminants)

During the 1951 RVF epizootic in South Africa, abortion in pregnant animals, as well as death, was reported among captive wild ruminants and presumed to be associated with RVFV: one wild springbuck (probably *Antidorcas marsupialis*) and one blesbuck (probably *Damaliscus dorcas*) aborted embryos on a farm where RVF domestic ruminant and human cases were observed (Alexander, 1951; Gear et al., 1951). Following these observations, wild ruminants were investigated with regard to RVF epidemiology. Most research on artiodactyls involved the screening for antibodies directed against RVFV (Maurice, 1967; Davies, 1975; Davies and Karstad, 1981; Tessier et al., 1987; Anderson and Rowe, 1998; Evans et al., 2008; LaBeaud et al., 2011). Some of these studies identified RVFV antibodies among wild artiodactyls,

demonstrating that these animals were susceptible to RVFV (Maurice, 1967; Davies, 1975; Davies and Karstad, 1981; Anderson and Rowe, 1998; Evans et al., 2008; LaBeaud et al., 2011; Table 1).

During a 6-yr survey (November 2000–July 2006) in South Africa, seroconversions were detected among 7% of resampled African buffalos (*Syncerus caffer*), demonstrating interepizootic transmission of RVFV among these animals (LaBeaud et al., 2011). Seven of the nine seroconversions observed during the study occurred between mid-2001 and mid-2003 and the two others at 8-mo intervals in 2004 (LaBeaud et al., 2011). Outbreaks of RVF were reported in South Africa in 1999, with six African buffalos and one waterbuck (*Kobus ellipsiprymnus*) in Kruger National Park aborting fetuses (ProMED-mail, 1999); this also occurred among African buffalos on a game farm in 2008 (OIE, 2011). Other studies suggested virus circulation during the 1999–2006 IEP in Kenya among African buffalo (Evans et al., 2008). This species was also affected during the RVFV 2006–07 Kenya outbreak, showing that during epizootics in domestic cattle, the virus circulated among wild animals (Bird et al., 2008).

Few investigators have examined viremia or excretion of RVFV in African buffalo. Daubney and Hudson (1932) studied the susceptibility of a 7-mo-old African buffalo to RVFV inoculation. The animal showed benign symptoms and became healthy 11 days postinoculation; however, these researchers did not investigate viremia and excretion of the virus. Davies and Karstad (1981) inoculated intradermally $10^{7.7}$ tissue culture infectious dose 50% (TCID)₅₀ in five African buffalos, including two pregnant females. Abortion occurred in one female 16 days postinoculation and RVFV was isolated from the liver of the fetus. Viremia persisted at least 48 hr (titers ranged from 3.8 to 5.4 TCID₅₀/ml) in four of the five inoculated buffalos.

Considering the results of these studies and observations during epizootic periods and IEP, RVFV infection seems to cause

similar disease symptoms in wild and domestic ruminants. However, these results do not demonstrate that wild ruminants, especially the African buffalo, act as reservoirs. Although they may participate in the maintenance of the virus, several authors hypothesized that wild ruminants probably play a similar role to domestic ruminants in the cycle of RVFV during IEP (Davies, 1975; Anderson and Rowe, 1998; Swanepoel and Coetzer, 2004; Evans et al., 2008). There is evidence of RVFV circulation in Madagascar during IEP (Zeller et al., 1998; Jeanmaire et al., 2011), yet native Bovidae are not present on the island. Therefore, if we consider RVF an enzootic disease in Madagascar, where wild ruminants do not exist, other animals may have a role in maintaining RVFV.

Other families of even-toed ungulates, including Tayassuidae and Antilocapridae from the New World and Moschidae from Asia, are outside of the RVFV emergence area and are not considered here. Easterday (1965) mentioned a study done by Weinbren and Hewitt (1958), who reported neutralizing antibody against RVFV in hippopotamus (*Hippopotamus amphibius*) serum, although the numbers of positive and tested samples were not specified. To our knowledge, members of the family Cervidae have not been investigated, and the only African member of this family occurs in the Maghreb where RVFV has not been detected. Serologic evidence was found in the giraffe (*Giraffa camelopardalis*, Giraffidae) during an epizootic period (ProMED-mail, 1999; Bird et al., 2008) and an IEP (Evans et al., 2008) as well as in the desert warthog (*Phacochoerus aethiopicus*, Suidae; Evans et al., 2008).

Recently, the possible role of domestic pigs (*Sus scrofa*) as hosts of RVFV was studied during an IEP in Egypt, where 37 (15.1%) of 245 blood samples collected in 2008 were positive by enzyme-linked immunosorbent assay (ELISA) for RVFV antibodies (Bahgat, 2009). Some studies in Nigeria failed to detect RVFV antibodies in pig samples tested by hemagglutination-inhibition, whereas other studies

there produced virologic and serologic evidence of RVFV (Olaleye et al., 1996). During an RVF outbreak at a South African farm, abortion in a domestic pig was mentioned but no test was conducted to isolate the virus (Gear et al., 1951). Experimentally, pigs seem to be clinically resistant to RVF (Easterday et al., 1962; Easterday, 1965; Shimshony and Barzilai, 1983; Swanepoel and Coetzer, 2004). However, Scott (1963) demonstrated that resistance in pigs was dose-dependent: RVFV was detected 2–4 days postinoculation in sera of the animals receiving the highest dose of virus (10^5 – 10^6 Hamster lethal dose 50% [LD_{50}]). In summary, data currently available for wild and domestic Suidae are too few to make any conclusive statement about their potential role in RVFV maintenance during IEP.

Camels have been reported to be resistant to RVFV under clinical conditions, with no apparent infection (Easterday, 1965; Shimshony and Barzilai, 1983; Swanepoel and Coetzer, 2004). However, clinical signs, including fever and abortion in approximately 10% of pregnant females, were observed in free-ranging camel herds during the 2006–2007 outbreaks in Kenya (Munyua et al., 2010). Evidence of RVFV circulation among domestic camels has also been reported (Hoogstraal et al., 1979; Imam et al., 1979; Ezeifeke et al., 1982; Eisa, 1984; Davies, Koros et al., 1985; Mariner et al., 1995; Olaleye et al., 1996; Nabeth et al., 2001; Munyua et al., 2010). In the Camelidae, only *Camelus dromedarius* (one-humped camel) is present in the emergence area of RVFV; it is considered to be native to the Arabian Peninsula, but now extinct in the wild, and as introduced to the African continent (Grubb, 2005). Thus, the role of wild camels in the maintenance of RVFV or as a RVFV reservoir is unlikely.

Order Chiroptera (bats)

Few studies have been undertaken on bats, although in the Republic of Guinea, RVFV strains were isolated in suckling mice from pooled organs of three bat species,

Micropteropus pusillus (Pteropodidae) and *Hipposideros abae* and *Hipposideros caffer* (Hipposideridae; Boiro et al., 1987). However, in another study with seven other bat species, none of 350 organs sampled from 150 individuals trapped in South Africa and Lesotho between 1987 and 1989 (IEP), and tested by ELISA for RVFV antigen, was positive (Oelofsen and Van der Ryst, 1999).

An experimental study demonstrated that RVFV inoculated intramuscularly into Cape serotines (*Neoromicia capensis*; Vespertilionidae) was still found in brown fat 18 days postinoculation (Oelofsen and Van der Ryst, 1999). In three other clinical tests, *N. capensis* that were inoculated into the wing with 30 μl^a of an RVFV suspension containing 10^6 TCID₅₀/ml, and also Schreiber's long-fingered bat (*Miniopterus schreibersii*; Miniopteridae) and *N. capensis* inoculated orally with 100 μl^1 of the same RVFV suspension, did not develop signs of infection (Oelofsen and Van der Ryst, 1999). However, 4 days postinoculation, RVFV antigens were found in the liver and the urine of *Miniopterus*.

A large number of viruses belonging to several families have been detected or isolated from bats (Calisher et al., 2006). For the last 20 yr, bats have been demonstrated, or suspected, to be the reservoir of several emerging viruses such as lyssaviruses, henipaviruses, filoviruses, and coronaviruses (Calisher et al., 2006). The few positive results associated with bats in relation to RVFV seem to indicate that the virus replicates in these animals and that infection could be asymptomatic. Nevertheless, no study has been undertaken at a large scale on potential viremia and excretion of RVFV from infected bats. Consequently, it is difficult to propose any definitive conclusion about the potential role of bats in the maintenance of RVFV.

^a In the original article, these quantities were mistakenly reported as 30 ml and 100 ml (Dr. Michiel Oelofsen, pers. comm.).

TABLE 1. Summary of research on Artiodactyla (Bovidae, Giraffidae, and Suidae) and Rodentia (Muridae) sera reactive to Rift Valley fever virus. Common names for these animals can be found in Table 3; taxonomy follows Wilson and Reeder (2005).

Family	Species	Percent positive (no. tested)	Laboratory test ^a	Laboratory confirmation test ^a	Location	Period (interepidemic period [IEP] or outbreak and outbreak reference ^b)	Study references
Bovidae	<i>Aepyceros melampus</i>	0.1 (801)	HI	I-ELISA	Zimbabwe	1989-95 IEP (Swanepoel and Coetzer, 2004)	(Anderson and Rowe, 1998)
Bovidae	<i>A. melampus</i>	62.5 (8)	VNT	None	Kenya	1999-05 IEP	(Evans et al., 2008)
Bovidae	<i>Damaliscus korrigum</i>	50.0 (2)	HI	None	Chad	Never officially recognized by WHO and OIE (Ringot et al., 2004)	(Maurice, 1967)
Bovidae	<i>Eudorcas ruffrons</i>	75.0 (4)	HI	None	Chad	Never officially recognized by WHO and OIE (Ringot et al., 2004)	(Maurice, 1967)
Bovidae	<i>Eudorcas thomsonii</i> (syn. <i>Gazella thomsonii</i>)	87.5 (8)	VNT	None	Kenya	1999-05 IEP	(Evans et al., 2008)
Bovidae	<i>Gazella dorcas</i>	50.0 (12)	HI	None	Chad	Never officially recognized by WHO and OIE (Ringot et al., 2004)	(Maurice, 1967)
Bovidae	<i>Hippotragus niger</i>	0.3 (286)	HI	I-ELISA	Zimbabwe	1989-95 IEP (Swanepoel and Coetzer, 2004)	(Anderson and Rowe, 1998)
Bovidae	<i>Kobus ellipsiprymnus</i>	4.5 (179)	HI	I-ELISA	Zimbabwe	1989-95 IEP (Swanepoel and Coetzer, 2004)	(Anderson and Rowe, 1998)
Bovidae	<i>K. ellipsiprymnus</i>	20.0 (10)	VNT	None	Kenya	1999-05 IEP	(Evans et al., 2008)
Bovidae	<i>K. ellipsiprymnus</i>	91.7 (12)	VNT	None	Kenya	2006-07 outbreak (WHO, 2007)	(Evans et al., 2008)
Bovidae	<i>Litocranius walleri</i>	100.0 (5)	VNT	None	Kenya	2006-07 outbreak (WHO, 2007)	(Evans et al., 2008)
Bovidae	<i>Nanger dama</i>	28.6 (7)	HI	None	Chad	Never officially recognized by WHO and OIE (Ringot et al., 2004)	(Maurice, 1967)
Bovidae	<i>Oryx dammah</i> (syn. <i>Oryx algazel</i>)	66.7 (3)	HI	None	Chad	Never officially recognized by WHO and OIE (Ringot et al., 2004)	(Maurice, 1967)
Bovidae	<i>Redunca reclinata</i>	50.0 (2)	HI	None	Chad	Never officially recognized by WHO and OIE (Ringot et al., 2004)	(Maurice, 1967)
Bovidae	<i>Syncerus caffer</i>	100.0 (1)	HI	None	Chad	Never officially recognized by WHO and OIE (Ringot et al., 2004)	(Maurice, 1967)
Bovidae	<i>S. caffer</i>	6.3 (541)	HI	I-ELISA	Zimbabwe	1989-95 IEP (Swanepoel and Coetzer, 2004)	(Anderson and Rowe, 1998)
Bovidae	<i>S. caffer</i>	15.6 (237)	VNT	None	Kenya	1999-05 IEP	(Evans et al., 2008)
Bovidae	<i>S. caffer</i>	21.0 (115)	HI	None	South Africa	2006-07 outbreak (WHO, 2007)	(LaBeaud et al., 2011)
Bovidae	<i>Tragelaphus strepsiceros</i>	50.0 (10)	VNT	None	Kenya	1999-05 IEP	(Evans et al., 2008)
Giraffidae	<i>Giraffa camelopardalis</i>	2.9 (34)	VNT	None	Kenya	2006-07 outbreak (WHO, 2007)	(Evans et al., 2008)
Giraffidae	<i>G. camelopardalis</i>	42.9 (7)	IgG ELISA	None	Kenya	2006-07 outbreak (WHO, 2007)	(Bird et al., 2008)

TABLE 1. Continued.

Family	Species	Percent positive (no. tested)	Laboratory test ^a	Laboratory confirmation test ^a	Location	Period (inter-epidemic period [IEP] or outbreak) and outbreak reference ^b	Study references
Suidae	<i>Phacochoerus aethiopicus</i>	2.5 (81)	VNT	None	Kenya	1999–05 IEP	(Evans et al., 2008)
Suidae	<i>P. aethiopicus</i>	14.3 (28)	VNT	None	Kenya	2006–07 outbreak (WHO, 2007)	(Evans et al., 2008)
Muridae	<i>Acomys cahirinus</i>	8.2 (49)	HI	None	Egypt	1977–78 outbreak	(Hoogstraal et al., 1979)
Muridae	<i>Arvicanthus niloticus</i>	21.5 (121)	HI	None	Egypt	1977–78 outbreak	(Hoogstraal et al., 1979)
Muridae	<i>A. niloticus</i>	4.3 (140)	VNT	None	Senegal	1996–98 IEP	(Diop et al., 2000)
Muridae	<i>A. niloticus</i>	2.9 (70)	Not specified	Not specified	Senegal	1993 IEP	(Zeller et al., 1997)
Muridae	<i>Gerbillus</i> sp.	1.9 (53)	HI	0 confirmed by VNT	Egypt	1977–78 outbreak	(Kark et al., 1982)
Muridae	<i>Mastomys erythroleucus</i>	0.75 (268)	IFI	None	Senegal, Mauritania	1980–86 IEP	(Saluzzo et al., 1987)
Muridae	<i>M. erythroleucus</i>	2.4 (84)	VNT	None	Senegal	1996–98 IEP	(Diop et al., 2000)
Muridae	<i>Mastomys huberti</i>	13.3 (15)	VNT	None	Senegal	1996–98 IEP	(Diop et al., 2000)
Muridae	<i>Mastomys natalensis</i>	7.7 (65)	ELISA	1 of 5 confirmed by VNT	South Africa	1986–90 IEP	(Pretorius et al., 1997)
Muridae	<i>M. natalensis</i>	1.63 (736)	HI	0 confirmed by VNT	Zimbabwe	1974–75 IEP	(Swanepoel et al., 1978)
Muridae	<i>Mastomys</i> sp.	3.6 (56)	IFI	0 confirmed by VNT	Central African Republic	1979–82 IEP	(Gonzalez et al., 1983)
Muridae	<i>Meriones crassus</i>	5.0 (20)	HI	0 confirmed by VNT	Egypt	1977–78 outbreak	(Kark et al., 1982)
Muridae	<i>Micaelamys namaquensis</i> (syn. <i>Aethomys namaquensis</i>)	23.1 (312)	ELISA	47 of 72 confirmed by VNT	South Africa	1986–90 IEP	(Pretorius et al., 1997)
Muridae	<i>Rattus rattus</i>	3.1 (161)	HI	None	Egypt	1977–78 outbreak	(Hoogstraal et al., 1979)
Muridae	<i>R. rattus</i>	50.0 (2)	VNT	None	Senegal	1996–98 IEP	(Diop et al., 2000)
Muridae	<i>R. rattus</i>	29.3 (300)	ELISA	ID	Egypt	2000 IEP	(Bahgat and Hadia, 2001)

^a HI = hemagglutination inhibition test (adapted from Clarke and Casals, 1958); I-ELISA = indirect enzyme-linked immunosorbent assay; IgG-ELISA = immunoglobulin G, enzyme-linked immunosorbent assay; VNT = virus neutralization test; ELISA = enzyme-linked immunosorbent assay; IFI = indirect immunofluorescence; ID = immunodiffusion technique.
^b WHO = World Health Organization; OIE = Office International des Epizooties.

Order Primata (primates)

To our knowledge, RVFV has not been isolated from a wild primate. Using a complement fixation test, RVFV antibodies were detected in sera of several monkey species including one *Cercocebus galeritus* (three tested), two *Cercopithecus cephus* (49 tested), two *Cercocebus mona nigripes* (14 tested), four *Cercocebus nictitans* (28 tested), one *Mandrillus* sp. (11 tested), one *Miopithecus talapoin* (two tested), and one *Pan troglodytes* (six tested; Pellissier and Rousselot, 1954). In another study, East African primates held in captivity in Kenya were tested for RVFV antibodies by indirect fluorescent antibody test (Johnson et al., 1982). Six of 464 sera tested were positive including two *Chlorocebus pygerythrus* or *Chlorocebus aethiops*, three *Papio cynocephalus*, and one presumed *C. aethiops*. Other studies failed to detect RVFV antibodies in sera: 72 wild monkeys belonging to nine unspecified species captured before, after, and during RVFV circulation in Uganda using the neutralization antibody test (Smithburn et al., 1948); 1,304 *C. aethiops* trapped in areas close to regions known to be enzootic using the indirect fluorescent antibody method (Davies and Onyango, 1978); and 151 lemurs in Madagascar, including *Eulemur macaco macaco*, *Eulemur fulvus*, and *Lepilemur dorsalis*, using the hemagglutination inhibition test (Fontenille et al., 1988). Nevertheless, seroconversion to RVFV has been shown in several species of nonhuman primates through experimental studies (Findlay, 1932; Smithburn et al., 1948; Davies et al., 1972).

Rift Valley fever virus can persist for several days in the blood of primates after subcutaneous experimental inoculation (0.5 ml of blood from mice that died of RVFV) in several species of monkeys including the New World primates *Callithrix jacchus*, *Callithrix penicillata*, *Cebus albifrons*, and *Cebus paella*, and the African species *Cercocebus atys*, *Chlorocebus sabaeus*, and *Erythrocebus patas* (Findlay, 1932). *Papio anubis* has been shown to develop viremia, lasting 2–4 days

after subcutaneous injection of RVFV inoculums of at least 10^6 mouse LD₅₀ (Davies et al., 1972). Clinical signs were few and benign, consisting mainly of febrile reactions, and all animals survived.

Available data are inconclusive regarding the possible role of wild primates in the maintenance of RVFV. No study has examined potential vectorial transmission of RVFV between monkeys and excretion of the virus, study which is fundamental to determining if a mechanism exists to maintain the virus in wild primate populations.

Order Rodentia (rodents)

Since RVFV was described in 1931, rodents of the family Muridae have been suspected of being involved in the epidemiologic cycle of the virus. During the first outbreaks of RVFV reported in Kenya, high mortality was noted among wild (*Arvicanthis abyssinicus*) and introduced (*Rattus rattus*) rodents at a farm where a large number of sheep died (Daubney and Hudson, 1932). Laboratory examination revealed that the rodents did not die of plague. Subsequently, several authors suggested that rodents may act as reservoirs of RVFV, which led to rodents being the most-investigated group in relation to RVFV.

Serologic investigations demonstrated RVFV antibodies in several rodent species using a variety of techniques (Table 1), confirming the association between rodents and RVFV (Swanepoel et al., 1978; Hoogstraal et al., 1979; Kark et al., 1982; Gonzalez et al., 1983; Saluzzo et al., 1987; Pretorius et al., 1997; Zeller et al., 1997; Diop et al., 2000; Bahgat and Hadia, 2001). Positive virologic studies of a wide variety of other wild rodents tended to corroborate positive results of the serologic surveys. During the 1977–1978 epizootic in Egypt, RVFV was isolated from the brain of one of eight tested *R. rattus* that were obtained on a farm where ruminants died or aborted fetuses, and RVFV was isolated from serum of one of two

sampled sheep from the farm (Imam et al., 1979). Nearly 20 yr later, RVFV was detected in Egypt by reverse transcription-PCR in 9.6% of 300 sera from *Rattus* sampled during an IEP (Bahgat and Hadia, 2002).

The first experimental inoculation of RVFV in rodents demonstrated that several wild species were highly susceptible to RVFV infection, including four species not occurring in RVFV endemic areas: *Apodemus sylvaticus*, *Microtus agrestis*, *Muscardinus avellanarius*, and *Mesocricetus auratus* (Findlay, 1931; Findlay and Daubney, 1931). Within the RVFV geographic area, several other taxa were moderately susceptible: *A. abyssinicus*, *R. rattus*, *Mastomys coucha*, and nonnative *Sciurus carolinensis*. Among certain species, death occurred a few days after inoculation (Findlay, 1931). Increased body temperature was usually observed before death and also among surviving inoculated animals. Later, several experimental infections demonstrated viremia in surviving inoculated rodents. Cases of high viremia compatible with transmission by mosquito bites were observed in *Micaelamys namaquensis* (Pretorius et al., 1997) and *Arvicanthis niloticus* (Diop et al., 2000). Other cases of viremia, based on lower titer and shorter infection time, which are less compatible with infection by mosquitoes, were observed in *A. abyssinicus* (Weinbren and Mason, 1957), *Myodomys albicaudatus*, *Mastomys natalensis*, *Aethomys chrysophilus*, and *A. niloticus* (Hoogstraal et al., 1979; Diop et al., 2000), *R. rattus* (Hoogstraal et al., 1979; Diop et al., 2000) and *Saccostomus campestris* (McIntosh, 1961; Table 2). The jird, *Meriones unguiculatus*, was also experimentally tested with a subcutaneous inoculation of 10^7 plaque-forming units of the RVFV ZH501 strain, leading to encephalitis in young animals but apparent resistance in adults (Anderson et al., 1988). Overall, results from experimental inoculations on rodents were age and dose dependent. In contemporary investigations, inbred rodent species such as lab

mice, rats, and hamsters are commonly used as experimental animals for RVFV infection, leading to rapid and intense hepatitis, encephalitis, or both (Flick and Bouloy, 2005; Smith et al., 2010).

Despite many studies pointing to a rodent-RVFV association, some results do not appear epidemiologically significant owing to low antibody prevalence (Swanepoel et al., 1978; Imam et al., 1979; Kark et al., 1982; Gonzalez et al., 1983; Saluzzo et al., 1987; Swanepoel and Coetzer, 2004) or lack of confirmation using other techniques (Swanepoel et al., 1978; Kark et al., 1982; Gonzalez et al., 1983), and false positives cannot be excluded. Finally, several studies failed to support the serologic or virologic results reported above (Gear et al., 1951, 1955; Davis, 1957; Scott and Heisch, 1959; Woodall and Williams, 1960 cited by Davies, 1975; Henderson et al., 1972; Faghmi et al., 1973 cited by Kark et al., 1982; Davies, 1975; Taylor and Swanepoel, 1980; Saluzzo et al., 1985, 1987). For example, no evidence of RVFV was found in spleen samples collected from 110 wild rodents trapped near the site of the 1931 RVFV outbreak (Davies, 1975). In western Africa, only two of 1,478 rodents trapped in an area that experienced an RVFV outbreak had detectable antibody, and no virus was isolated from these animals (Saluzzo et al., 1987). At a farm in the South African Orange Free State where an outbreak occurred with confirmed cases in ruminants and humans, RVFV was not isolated from an unspecified number of samples of *M. natalensis* organs or blood, and complement fixation test results were negative for the tested sera (Gear et al., 1951). During this outbreak, serum samples of two spring-hares (*Pedetes capensis*, family Pedetidae) were also RVFV-negative by the complement fixation method. Later, in 1968, human cases of RVFV were detected in Uganda, yet a survey of rodents near the outbreak area and the nearby Lunyo Forest showed that none of 281 analyzed sera

TABLE 2. Experimental infection of Rodentia (Muridae and Nesomyidae) with Rift Valley fever virus. Common names for these animals can be found in Table 3; taxonomy follows Wilson and Reeder (2005).

Family	Species	Inoculation route ^a	Inoculated dose ^b	Maximum virus titer in blood, plasma, or serum; day postinoculation ^b	Reference
Muridae	<i>Acomys cahirinus</i>	SC	2,000 MICLD ₅₀	10 ² MICLD ₅₀ /ml; day not specified	(Hoogstraal et al., 1979)
Muridae	<i>Aethomys chrysophilus</i>	IC or IP	10 ^{1.9} MICLD ₅₀	10 ^{2.1} MICLD ₅₀ /ml; day 2	(McIntosh, 1961)
Muridae	<i>Arvicanthis abyssinicus</i>	IC	10 ^{2.3} MICLD ₅₀	10 ^{2.5} MICLD ₅₀ /ml; day 1	(Weinbren and Mason, 1957)
Muridae	<i>A. abyssinicus</i>	IC	10 ^{3.3} MICLD ₅₀	10 ^{3.1} MICLD ₅₀ /ml; day 5	(Weinbren and Mason, 1957)
Muridae	<i>A. abyssinicus</i>	IC	10 ^{4.3} MICLD ₅₀	10 ^{3.7} MICLD ₅₀ /ml; day 3	(Weinbren and Mason, 1957)
Muridae	<i>A. abyssinicus</i>	IC	10 ^{5.3} MICLD ₅₀	10 ⁵ MICLD ₅₀ /ml; day 3	(Weinbren and Mason, 1957)
Muridae	<i>A. abyssinicus</i>	IC	10 ^{5.3} MICLD ₅₀	10 ⁴ MICLD ₅₀ /ml; day 3	(Weinbren and Mason, 1957)
Muridae	<i>Arvicanthis niloticus</i>	SC	2,000 MICLD ₅₀	10 ² MICLD ₅₀ /ml; day not specified	(Hoogstraal et al., 1979)
Muridae	<i>A. niloticus</i>	IP	250 µl (±100 µl) of 1/10 dilution virus stock	10 ^{5.7} MICLD ₅₀ /ml; day 3	(Diop et al., 2000)
Muridae	<i>Mastomys natalensis</i>	IC or IP	101.9 MICLD ₅₀	10 ^{1.7} MICLD ₅₀ /ml; day 4	(McIntosh, 1961)
Muridae	<i>Micaelamys namaquensis</i> (syn. <i>Aethomys namaquensis</i>)	SC	103 TCID ₅₀	10 ^{6.5} to 10 ^{8.5} TCID ₅₀ /ml; day 2	(Pretorius et al., 1997)
Muridae	<i>Rattus rattus</i>	SC	2,000 MICLD ₅₀	10 ³ MICLD ₅₀ /ml; day not specified	(Hoogstraal et al., 1979)
Nesomyidae	<i>Mystromys albicaudatus</i>	IC or IP	103.2 MICLD ₅₀	10 ² MICLD ₅₀ /ml; day 2	(McIntosh, 1961)
Nesomyidae	<i>Saccostomus campestris</i>	IC or IP	10 ^{1.9} MICLD ₅₀	10 ^{2.3} MICLD ₅₀ /ml; day 4	(McIntosh, 1961)

^a SC subcutaneous; IC intracerebral; IP intraperitoneal.

^b MICLD₅₀ mouse intracerebral lethal dose 50%; TCID₅₀ = tissue culture infectious dose 50%.

neutralized RVFV (Henderson et al., 1972).

Regarding data currently available for sub-Saharan Africa, the most likely rodent candidates for maintenance of RVFV are *A. niloticus*, *M. namaquensis*, and *R. rattus*. *Arvicanthis niloticus* is widespread in Africa and is documented to be antibody-positive with an effective viremia following inoculation (Diop et al., 2000). *Micaelamys namaquensis*, distributed across the southern portion of the continent, has been found antibody-positive in nature and viremia has been induced experimentally (Pretorius et al., 1997). Finally, *R. rattus* is a good candidate because of near worldwide distribution, and antibody-positive and viremic individuals have been found in nature (Bahgat and Hadia, 2001, 2002).

Despite evidence in favor of rodents acting in the maintenance of RVFV, this role is incompletely demonstrated and published data are conflicting. Mims (1956) concluded that RVFV was unstable in Swiss lab mice (*Mus musculus*) urine and little, if any, virus could be found in urine and milk or isolated in nasal mucosa of infected animals. Few other viable data are available on RVFV excretion in rodents. In most cases, the context is restricted and this is a clear area for future studies. Another critical area of needed research is RVFV transmission between rodents, such as direct transmission involving excretion of RVFV through feces or urine in the absence of vector mosquitoes.

The “neglected” mammalian orders

The class Mammalia contains 29 orders (Wilson and Reeder, 2005). Mammals in 15 orders can be excluded from consideration as candidates for RVFV reservoirs because their distributions do not coincide with known distributions of the virus or because of aquatic distribution: Cetacea, Cingulata, Dasyuromorphia, Dermoptera, Didelphimorphia, Diprotodontia, Hyrocoidea, Microbiotheria, Monotremata,

Notoryctemorphia, Paucituberculata, Peramelemorphia, Pilosa, Scandentia, and Sirenia. The remaining 14 candidate orders, four of which have been discussed in the previous sections of this review, are listed in Table 3.

Five of these, Afrosoricida, Hyracoidea, Macroscelidea, Soricomorpha, and Tubulidentata, have never been studied with respect to RVFV. However, taxa from these five orders occur in known RVF areas, namely continental Africa, the Arabian Peninsula, and Madagascar (Table 3). Because some species, particularly in the Afrosoricida in Madagascar and in the Soricomorpha in Africa, are common in known areas of RVF, and their role in the maintenance of RVFV needs to be examined.

Species in five other orders have been too superficially investigated to assess their role in the maintenance of RVFV: Perissodactyla (Anderson and Rowe, 1998; Fischer-Tenhagen et al., 2000; Evans et al., 2008), Carnivora (Findlay, 1931; Francis and Magill, 1935; House et al., 1996), Proboscidea (Evans et al., 2008), Erinaceomorpha (Easterday, 1965), and Lagomorpha (Findlay, 1931; Findlay and Daubney, 1931; Gear et al., 1951; Easterday, 1965).

Among the Perissodactyla, domestic horses seem to be resistant to RVFV (Swanepoel and Coetzer, 2004), and experimental infections failed to lead to symptoms or viremia (Daubney et al., 1931). However, in the lower Nile Valley, RVFV or RVFV antibodies have been detected in horses and donkeys sampled during IEP and during or immediately after epizootics (Hoogstraal et al., 1979; Imam et al., 1979; Meegan et al., 1979; Eisa, 1984). Moreover, in Nigeria, RVFV antibodies were detected in horses using a complement fixation test (Olaleye et al., 1989, 1996). In this same country, the virus was isolated from sheep around 1959, but this was not associated with an epizootic event (Adeyeye et al., 2011). Negative serologic results obtained from zebras (*Equus burchelli*) led to the conclusion

TABLE 3. Published studies associated with the role of mammal orders in the epidemiology of Rift Valley fever. Taxonomy and distribution follows Wilson and Reeder (2005). Backslashes "/" are used in cases when the taxon was not explicitly stated associated with a study and the genus, species and associated geographical range cannot be inferred.

Order	Family	Species	Common name	Studies	Current distribution (Wilson and Reeder, 2005)
Tubulidentata	Not investigated				Continental Africa
Afrosoricida	Not investigated				Continental Africa and islands in the western Indian Ocean
Macroscelidea	Not investigated				Numerous species present on continental Africa
Hyrocoidea	Not investigated				Several species present on continental Africa and the Arabian Peninsula
Proboscidea	Elephantidae	<i>Loxodonta africana</i>	African bush elephant	Field studies (Evans et al., 2008)	Disjunct distribution in sub-Saharan Africa
Primata	Cebidae	<i>Cebus albifrons</i> (syn. <i>Cebus chrysomus</i>)	White-fronted capuchin	Experimental studies (Findlay, 1932)	Outside the emergence area (South America)
Primata	Cebidae	<i>Cebus apella</i> (syn. <i>Cebus fatuellus</i>)	Tufted capuchin	Experimental studies (Findlay, 1932)	Outside the emergence area (South America)
Primata	Cebidae	<i>Callithrix jacchus</i> (syn. <i>Hapale jacchus</i>)	Common marmoset	Experimental studies (Findlay, 1932)	Outside the emergence area (South America)
Primata	Cebidae	<i>Callithrix penicillata</i>	Black-tufted marmoset	Experimental studies (Findlay, 1932)	Outside the emergence area (South America)
Primata	Cercopitheciidae	<i>Cercocebus atys</i> (syn. <i>Cercocebus fuliginosus</i>)	Sooty mangabey	Experimental studies (Findlay, 1932)	Coastal areas from Senegal to Ghana
Primata	Cercopitheciidae	<i>Cercocebus galeritus</i>	Tana River mangabey	Field study (Pellissier and Rousset, 1954)	Lower Tana River, Kenya
Primata	Cercopitheciidae	<i>Cercopithecus cephus</i>	Moustached guenon	Field study (Pellissier and Rousset, 1954)	Southern Cameroon south to portions of the Congo Basin
Primata	Cercopitheciidae	<i>Cercopithecus mona</i>	Mona monkey	Field study (Pellissier and Rousset, 1954)	Ghana to Cameroon
Primata	Cercopitheciidae	<i>Cercopithecus nictitans</i>	Greater spot-nosed monkey	Field study (Pellissier and Rousset, 1954)	Nigeria to Republic of Congo through Central African Republic
Primata	Cercopitheciidae	<i>Chlorocebus sabaeus</i>	Green monkey	Experimental studies (Findlay, 1932)	Senegal to Mali until Ghana to Sierra Leone
Primata	Cercopitheciidae	<i>Erythrocebus patas</i>	Patas monkey	Experimental studies (Findlay, 1932)	West Africa to Ethiopia, Kenya, and Tanzania
Primata	Cercopitheciidae	<i>Mandrillus</i> sp.	Drill	Field study (Pellissier and Rousset, 1954)	Southeastern Nigeria to Cameroon

TABLE 3. Continued.

Order	Family	Species	Common name	Studies	Current distribution (Wilson and Reeder, 2005)
Primata	Cercopitheciidae	<i>Miopithecus talapoin</i>	Angolan talapoin	Field study (Pellissier and Roussetol, 1954)	Angola to southwestern Democratic Republic of the Congo
Primata	Cercopitheciidae	<i>Papio anubis</i>	Olive baboon	Experimental studies (Davies et al., 1972)	West Africa to Ethiopia, Kenya, and Tanzania
Primata	Hominidae	<i>Pan troglodytes</i>	Common chimpanzee	Field study (Pellissier and Roussetol, 1954)	Disjunct distribution in western and central Africa
Rodentia	Muridae	<i>Acomys cahirinus</i>	Spiny mouse	Field studies (Hoogstraal et al., 1979)	Northeastern Africa, Sinai Peninsula, northern Sudan, Ethiopia, and Djibouti
Rodentia	Muridae	<i>Aethomys chrysophilus</i>	Red rock rat	Experimental studies (McIntosh, 1961; Taylor and Swanepoel, 1980)	Angola, Mozambique, and northeastern South Africa
Rodentia	Muridae	<i>Arvicanthus niloticus</i>	African arvicanthis	Field (Hoogstraal et al., 1979; Diop et al., 2000; Zeller et al., 1997) and experimental (Weinbren and Mason, 1957; Hoogstraal et al., 1979; Diop et al., 2000) studies	Senegal to Sudan and Ethiopia, south to Uganda and Kenya, as well as the Arabian Peninsula
Rodentia	Muridae	<i>Dasymys incomtus</i>	Common dasymys	Field study (Diop et al., 2000)	Eastern to southern Africa
Rodentia	Muridae	<i>Gerbilliscus guineae</i>	Guinean gerbil	Field study (Diop et al., 2000)	Western Africa
Rodentia	Muridae	<i>Gerbillus henleyi</i>	Pygmy gerbil	Field studies (Diop et al., 2000)	Northern Africa east to the Middle East and Arabian Peninsula and south to western Africa
Rodentia	Muridae	<i>Gerbilliscus kempi</i>	Northern savanna gerbil	Field study (Diop et al., 2000)	Western to eastern Africa and south to Democratic Republic of the Congo
Rodentia	Muridae	<i>Gerbilliscus leucogaster</i>	Bushveld gerbil	Field studies (Taylor and Swanepoel, 1980)	Southern Democratic Republic of the Congo to southern Africa
Rodentia	Muridae	<i>Gerbillus</i> sp.	Gerbil	Field studies (Kark et al., 1982)	/
Rodentia	Muridae	<i>Mastomys erythroleucus</i>	Reddish-white mastomys	Field studies (Saluzzo et al., 1987; Diop et al., 2000)	Morocco, and sub-Saharan areas from Senegal to Ethiopia and Uganda

TABLE 3. Continued.

Order	Family	Species	Common name	Studies	Current distribution (Wilson and Reeder, 2005)
Rodentia	Muridae	<i>Mastomys huberti</i>	Hubert's mastomys	Field studies (Diop et al., 2000)	Senegal to southern Mali, northern Burkina Faso, and Nigeria
Rodentia	Muridae	<i>Mastomys natalensis</i>	Natal mastomys	Field (Swanepoel et al., 1978; Taylor and Swanepoel, 1980; Pretorius et al., 1997) and experimental (McIntosh, 1961) studies	Widespread in sub-Saharan Africa except for the southwest
Rodentia	Muridae	<i>Meriones crassus</i>	Sundevall's jird	Field studies (Kark et al., 1982)	Across northern Africa, Niger, and Sudan to the Middle East and Afghanistan
Rodentia	Muridae	<i>Micaelamys namaquensis</i> (syn. <i>Aethomys namaquensis</i>)	Namaqua micaelamys	Field and experimental studies (Pretorius et al., 1997)	Eastern Angola to Mozambique, and South Africa
Rodentia	Muridae	<i>Mus musculus</i>	House mouse	Field study (Diop et al., 2000)	Cosmopolitan
Rodentia	Muridae	<i>Praomys daltoni</i>	Dalton's praomys	Field study (Diop et al., 2000)	Western Africa east to the Sahel and south to the Central African Republic
Rodentia	Muridae	<i>Rattus rattus</i>	Roof rat or black rat	Field (Hoogstraal et al., 1979; Taylor and Swanepoel, 1980; Diop et al., 2000; Bahgat and Hadia, 2000; Bahgat and Hadia, 2001) and experimental studies (Hoogstraal et al., 1979)	Introduced nearly world wide
Rodentia	Muridae	<i>Rhabdomys pumilio</i>	Xeric four-striped grass rat	Field studies (Taylor and Swanepoel, 1980)	Southern Africa
Rodentia	Nesomyidae	<i>Cricetomys gambianus</i>	Northern giant pouched rat	Field study (Diop et al., 2000)	Western to eastern Africa south of the Sahara
Rodentia	Nesomyidae	<i>Mystromys albicaudatus</i>	White-tailed rat	Experimental studies (McIntosh, 1961)	South Africa, Lesotho, and southern Swazi-land

TABLE 3. Continued.

Order	Family	Species	Common name	Studies	Current distribution (Wilson and Reeder, 2005)
Rodentia	Nesomyidae	<i>Saccostomus campestris</i>	Southern African pouched mouse	Experimental studies (McIntosh, 1961; Taylor and Swanepoel, 1980)	Angola to Mozambique and South Africa
Rodentia	Pedetidae	<i>Pedetes capensis</i>	Spring-hare	Field studies (Gear, 1951)	South Africa, Namibia, Angola, Botswana, Mozambique, Zimbabwe, Zambia, south of Democratic Republic of the Congo
Rodentia	Sciuridae	<i>Xerus erythropus</i>	Striped ground squirrel	Field study (Diop et al., 2000)	Northern Africa south to Democratic Republic of the Congo and east to eastern Africa
Lagomorpha	/	Not specified	“Rabbit”	Experimental study (Findlay, 1931; Findlay and Daubney, 1931; Easterday, 1965)	/
Lagomorpha	Leporidae	<i>Lepus capensis</i>	Cape hare	Field studies (Gear, 1951)	From portions of the Middle East, across northern Africa and the Sahel to southern and eastern Africa
Erinaceomorpha	/	Not specified	“Hedgehog”	Experimental study (Findlay, 1931)	/
Soricomorpha	Not investigated				Numerous species occurring on continental Africa
Chiroptera	Hipposideridae	<i>Hipposideros abae</i>	Aba leaf-nosed bat	Field studies (Boiro et al., 1987)	Guinea-Bissau to southwestern Sudan and border Uganda
Chiroptera	Hipposideridae	<i>Hipposideros caffar</i>	Sundevall's leaf-nosed bat	Field studies (Boiro et al., 1987)	Disjunct distribution in Morocco, much of sub-Saharan Africa with the exception of forested central region
Chiroptera	Miniopteridae	<i>Miniopterus schreibersii</i>	Schreiber's long-fingered bat	Experimental studies (Oelofsen and van der Ryst, 1999)	Southern Europe to Azerbaijan and through the Caucasus. Widespread on continental Africa and eastwards to the Indo-Malayan region to Australia
Chiroptera	Molossidae	<i>Tadarida aegyptiaca</i>	Egyptian free-tailed bat	Field studies (Oelofsen and van der Ryst, 1999)	Middle East, India, Sri Lanka, and southern Africa

TABLE 3. Continued.

Order	Family	Species	Common name	Studies	Current distribution (Wilson and Reeder, 2005)
Chiroptera	Pteropodidae	<i>Micropteropus pusillus</i>	Peters' lesser epauletted fruit bat	Field studies (Boiro et al., 1987)	Sub-Saharan Africa from Senegal to western Ethiopia and Uganda until northern Angola, excluding forested central region
Chiroptera	Rhinolophidae	<i>Rhinolophus clivosus</i>	Geoffroy's horseshoe bat	Field studies (Oelofsen and van der Ryst, 1999)	Disjunct distribution in Middle East, Maghreb, eastern and southern Africa
Chiroptera	Vespertilionidae	<i>Laeophotis wintoni</i>	De Winton's long-eared bat	Field studies (Oelofsen and van der Ryst, 1999)	East Africa to South Africa
Chiroptera	Vespertilionidae	<i>Myotis tricolor</i>	Temminck's myotis	Field studies (Oelofsen and van der Ryst, 1999)	Liberia to Ethiopia and South Africa
Chiroptera	Vespertilionidae	<i>Neoromicia capensis</i> (syn. <i>Eptesicus capensis</i>)	Cape serotine	Experimental studies (Oelofsen and van der Ryst, 1999)	Guinea-Bissau, east to Ethiopia and south to South Africa
Pholidota Carnivora	Not investigated Canidae	<i>Canis</i> sp.	"Jackals"	Field studies (House et al., 1996)	Present in portions of sub-Saharan Africa
Carnivora	Canidae	<i>Lycyaon pictus</i>	African wild dog	Field studies (House et al., 1996)	Disjunct distribution from Algeria and western Africa to Sudan and south to South Africa
Carnivora	Felidae	<i>Acinonyx jubatus</i>	Cheetah	Field studies (House et al., 1996)	Disjunct distribution from Algeria and Egypt and south to South Africa
Carnivora	Felidae	<i>Panthera leo</i>	Lion	Field studies (House et al., 1996; Evans et al., 2008)	Disjunct distribution from Ivory Coast, Guinea-Bissau and Angola, Benin to east Africa and south to South Africa and Namibia
Carnivora	Felidae	[<i>Panthera pardus</i>]	Leopard	Field studies (Evans et al., 2008)	/
Carnivora	Herpestidae	Not specified	"Mongoose"	Experimental study (Findlay, 1931)	/
Carnivora	Hyaenidae	<i>Crocuta crocuta</i>	Spotted hyena	Field studies (House et al., 1996)	Sub-Saharan Africa from Senegal to Somalia through central Africa until South Africa

TABLE 3. Continued.

Order	Family	Species	Common name	Studies	Current distribution (Wilson and Reeder, 2005)
Carnivora	Mustelidae	Not specified	“Ferret”	Experimental studies (Francis and Magill, 1935)	/
Perissodactyla	Equidae	<i>Equus burchellii</i>	Burchell’s zebra	Field studies (Evans et al., 2008)	Angola to South Africa
Perissodactyla	Rhinocerotidae	<i>Diceros bicornis</i>	Black rhinoceros	Field studies (Anderson and Rowe, 1998; Fischer-Tenhagen et al., 2000; Evans et al., 2008)	Kenya to Namibia and South Africa
Perissodactyla	Rhinocerotidae	<i>Ceratotherium simum</i>	White rhinoceros	Field studies (Anderson and Rowe, 1998; Fischer-Tenhagen et al., 2000)	Uganda and Kenya south to South Africa
Artiodactyla	Bovidae	<i>Aepyceros melampus</i>	Impala	Field studies (Anderson and Rowe, 1998; Evans et al., 2008)	Southern Angola and eastern Africa to Zambia and from Kenya to South Africa
Artiodactyla	Bovidae	<i>Alcelaphus buselaphus coxi</i> (syn. <i>Alcelaphus kongoni</i>)	Coke’s hartebeest	Field studies (Maurice, 1967)	From Senegal to Ethiopia, Sudan, and Eritrea through central Africa to South Africa
Artiodactyla	Bovidae	<i>Alcelaphus caama</i> (syn. <i>Alcelaphus leluel</i>)	Hartebeest	Field studies (Maurice, 1967)	Angola to Zimbabwe and South Africa
Artiodactyla	Bovidae	<i>Connochaetes taurinus</i>	Blue wildebeest	Field studies (Anderson and Rowe, 1998)	Angola to Zimbabwe and South Africa
Artiodactyla	Bovidae	<i>Damaliscus korrigum</i>	Topi	Field studies (Maurice, 1967)	Disjunct distribution in west, equatorial to central and eastern Africa (Tanzania and Uganda), and South Africa
Artiodactyla	Bovidae	<i>Damaliscus lunatus</i>	Common tsessebe	Field studies (Maurice, 1967; Anderson and Rowe, 1998)	Disjunct distribution from Angola to Zimbabwe and South Africa
Artiodactyla	Bovidae	<i>Eudorcas rufifrons</i>	Red-fronted gazelle	Field studies (Maurice, 1967)	Coastal northern Senegal, southern Mauritania and portions of the Sahel to Eritrea

TABLE 3. Continued.

Order	Family	Species	Common name	Studies	Current distribution (Wilson and Reeder, 2005)
Artiodactyla	Bovidae	<i>Eudorcas thomsonii</i> (syn. <i>Gazella thomsonii</i>)	Thomson's gazelle	Field studies (Evans et al., 2008)	Northern and central Kenya to Tanzania
Artiodactyla	Bovidae	<i>Gazella dorcas</i>	Dorcas gazelle	Field studies (Maurice, 1967)	Morocco to Tunisia and portions of the Sahel
Artiodactyla	Bovidae	<i>Hippotragus niger</i>	Sable antelope	Field studies (Anderson and Rowe, 1998)	Central and eastern Angola, Tanzania to South Africa
Artiodactyla	Bovidae	<i>Kobus ellipsiprymnus</i>	Waterbuck	Field studies (Anderson and Rowe, 1998; Evans et al., 2008)	Sub-Saharan Africa from Senegal to Ethiopia through central Africa to northern South Africa
Artiodactyla	Bovidae	<i>Kobus kob</i> (syn. <i>Adnota kob</i>)	Kob	Field studies (Maurice, 1967)	Sub-Saharan Africa from Senegal to Ethiopia through central Africa to Uganda
Artiodactyla	Bovidae	<i>Litocranius walleri</i>	Gerenuk	Field studies (Evans et al., 2008)	Eastern Ethiopia, Somalia, Kenya, and northeastern Tanzania
Artiodactyla	Bovidae	<i>Nanger dama</i>	Dama gazelle	Field studies (Maurice, 1967)	Disjunct distribution in Algeria, Morocco, Mali, Niger, and Chad
Artiodactyla	Bovidae	<i>Oryx dammah</i> (syn. <i>Oryx algazel</i>)	Scimitar-horned oryx	Field studies (Maurice, 1967)	Survives as captive populations
Artiodactyla	Bovidae	<i>Redunca redunca</i>	Common reedbuck	Field studies (Maurice, 1967)	Sub-Saharan and central Africa from Senegal to Ethiopia and south to Tanzania
Artiodactyla	Bovidae	<i>Syncerus caffer</i>	African buffalo	Suspicion confirmed (ProMED-mail, 1999; Bird et al., 2008), field studies (Maurice, 1967; Anderson and Rowe, 1998; Evans et al., 2008; Klerk, 2009; LaBeaud et al., 2011), and experimental studies (Daubney and Hudson, 1932; Davies and Karstad, 1981)	West Africa from southern Senegal to Benin and eastern Ethiopia to south Africa
Artiodactyla	Bovidae	<i>Taurotragus oryx</i>	Common eland	Field studies (Anderson and Rowe, 1998; Evans et al., 2008)	Border region of Sudan, Ethiopia, Kenya, and Uganda, and areas further south including Angola, Democratic Republic of the Congo, and south to South Africa

TABLE 3. Continued.

Order	Family	Species	Common name	Studies	Current distribution (Wilson and Reeder, 2005)
Artiodactyla	Bovidae	<i>Tragelaphus angasii</i>	Nyala	Field studies (Anderson and Rowe, 1998)	Malawi, Mozambique, South Africa, Swaziland, Zimbabwe, Botswana, and Namibia
Artiodactyla	Bovidae	<i>Tragelaphus scriptus</i>	Bushbuck	Field studies (Anderson and Rowe, 1998)	From sub-Saharan to southern Africa
Artiodactyla	Bovidae	<i>Tragelaphus strepsiceros</i>	Greater kudu	Field studies (Anderson and Rowe, 1998; Evans et al., 2008)	Southeastern Chad, Sudan, Eritrea, and Ethiopia and south to Namibia, Zambia, and South Africa
Artiodactyla	Giraffidae	<i>Giraffa camelopardalis</i>	Giraffe	Field studies (Anderson and Rowe, 1998; Bird et al., 2008; Evans et al., 2008)	Disjunct distribution in Niger, Cameroon, Namibia, Botswana, and South Africa
Artiodactyla	Suidae	<i>Phacochoerus aethiopicus</i>	Desert warthog	Field studies (Anderson and Rowe, 1998; Evans et al., 2008)	Northern Somalia to southern Kenya

that these animals may not support RVFV replication (Evans et al., 2008). Sera from black and white rhinoceros (*Diceros bicornis* and *Ceratotherium simum*, respectively) from Kenya, South Africa, Namibia, and Zimbabwe have been tested for RVFV antibodies using hemagglutination inhibition (Anderson and Rowe, 1998), indirect ELISA (Anderson and Rowe, 1998; Fischer-Tenhagen et al., 2000), indirect immunofluorescence (Fischer-Tenhagen et al., 2000), and the RVFV-neutralizing antibodies technique (Evans et al., 2008). Although RVFV antibodies were detected in some sera (Anderson and Rowe, 1998; Evans et al., 2008), it is unlikely that rhinoceros, with their low population densities in nature, could play a significant role in RVFV maintenance during IEP (Evans et al., 2008).

Domestic cats and dogs (Carnivora), especially subadults, have been experimentally susceptible to RVFV by subcutaneous, intraperitoneal, and respiratory infection routes (Findlay, 1931; Walker, Remmele et al., 1970; Walker, Stephen et al., 1970; Keefer et al., 1972). Other Carnivora, such as ferrets, demonstrated an increase in body temperature following intranasal inoculation (inoculum from human cases, dose not specified), and sera samples from infected ferrets inoculated into mice caused death (Francis and Magill, 1935). Serologic surveys of wild and domestic species of Carnivora in Kenya, South Africa, Tanzania, Zimbabwe, and Botswana revealed RVFV antibodies in the sera of lions (*Panthera leo*; $n=113$) sampled in 1991 using hemagglutination inhibition and plaque-reduction neutralization tests (House et al., 1996). To our knowledge, no more-recent information on RVFV in Carnivora has been published.

The single identified study on RVFV in the order Proboscidea detected neutralizing antibodies in five of 83 sera from African elephants (*Loxodonta africana*) tested with the RVFV-neutralizing antibodies technique (Evans et al., 2008). For the order Erinaceomorpha, hedgehogs have not been found

susceptible to RVFV (Easterday, 1965). Similarly, for the order Lagomorpha, experimental inoculation through several routes failed to induce RVFV or associated isolates in domestic rabbits (*Oryctolagus cuniculus*), and these animals have been defined as not susceptible to RVFV (Findlay and Daubney, 1931). During the 1951 outbreak in South Africa, a serum sample from one Cape hare (*Lepus capensis*) was negative by complement fixation (Gear et al., 1951). In contrast, others have hypothesized that lagomorphs may be RVFV-susceptible mammals, but without apparent infection (Findlay, 1931; Easterday, 1965; Gerdes, 2004).

In conclusion, few studies have been undertaken to examine at least 10 orders of wild mammals containing species that are candidates in the maintenance of RVFV, based on their geographic sympatry with known RVF outbreaks. One general assumption, however, is that some species of Carnivora and Perissodactyla may not support RVFV replication (House et al., 1996; Anderson and Rowe, 1998; Fischer-Tenhagen et al., 2000; Evans et al., 2008).

GENERAL CONCLUSION

Wild ruminants, especially African buffaloes, and some domestic ruminants may be involved in the maintenance of RVFV. During IEP, however, circulation of RVFV among these animals probably leads to dead-end infection, as suggested by their low levels of seroconversion. Wild ruminants are absent on Madagascar, so other mammals may be involved in maintenance of RVFV there; yet other mechanisms could be responsible for recurrence, such as reintroduction of the virus through movement of infected cattle from other zones of Africa (Carroll et al., 2011). Given the available data and the biology of the reviewed mammalian orders, we propose that further research should be concentrated on species of Rodentia and Chiroptera that are sympatric with RVFV in order to find the wild

mammalian host (reservoir) involved in the maintenance of RVFV.

Conflicting results have been published regarding native and nonnative African rodents, but the best candidates for further research, based on current information, are *A. niloticus*, *M. namaquensis*, and *R. rattus*, but the majority of species on the continent have not been tested. In particular, *R. rattus* should be examined more closely because it has been introduced to all regions where RVF is known. Further studies should be carried out to assess the role of these rodents in the maintenance of the virus, such as testing sera during IEP and during outbreaks in diverse areas, and investigating RVFV experimental transmission through excreta to explain the maintenance of the virus when mosquito vectors are absent.

Other select mammalian orders should also be investigated, such as the Afrosoricida and the Soricomorpha, which are common and prolific in areas where RVF is known. Notably, Chiroptera, known to be reservoirs for a variety of virus families, especially the *Bunyaviridae* which includes RVFV (Calisher et al., 2006), should receive greater attention for their possible role in the maintenance of RVFV or as reservoirs. The first step in future research programs should be to conduct serologic and virologic surveys during RVF epizootics to examine possible infection in these candidate mammalian orders. In cases of positive results, surveys should be extended into IEP to explore their potential roles as reservoirs maintaining the virus. Ideally, based on predictive models of meteorologic conditions, particularly rainfall, as indicators of impending RVF outbreaks (Anyamba et al., 2006, 2009, 2010), such conditions should be monitored to direct the timing of serosurveys of candidate reservoir mammals. In many cases, by the time human RVF cases are documented, the first phase of the outbreak, which occurred between reservoirs and primary *Aedes* mosquito vectors, has long passed.

Rift Valley fever virus is known to occur on the African continent and islands of the southwestern Indian Ocean (Comoros and Madagascar) and Arabian Peninsula, and its potential of spread to other continents should not be underestimated. For example, other areas of the Middle East have not sufficiently evaluated for the presence of RVFV among wild animals. Since the beginning of the 21st Century, and in association with: 1) the emergence of other arboviruses in Europe (dengue virus and Chikungunya virus), 2) the introduction and maintenance of West Nile virus in North America, and 3) the potential use of RVFV as a bioterrorist threat (Anderson et al., 1999; Rezza et al., 2007; La Ruche et al., 2010), the potential risk of introduction and persistence of RVFV on these continents has been studied (EFSA, 2005; Britch and Linthicum, 2007; Kasari et al., 2008; Hartley et al., 2011). Thus, in the case of the risk analysis of RVFV, the potential role of wild mammals in the release and exposure pathways should be considered, as has been done in the United States (Britch and Linthicum, 2007; Kasari et al., 2008; Hartley et al., 2011). Further, studies on the potential impact of RVF transmission in ungulates such as the white-tailed deer (*Odocoileus virginianus*) (Kakani et al., 2010), as well as potentially associated vectors (Turell et al., 2010), need to be considered for areas of the New World. Kasari and co-authors (2008) presented a pathway analysis of RVFV infection in wild mammals as a potential source of introduction, particularly in ruminants and nonhuman primates, with the former as potential maintenance mechanisms for the virus. Importation of wild animals from affected areas, whether legal or not, is a possible means of introduction that needs to be considered. If rodents, particularly *R. rattus*, are involved in the maintenance of RVFV, the installation of the virus across the world is a serious potential problem. Finally, if indeed wild ruminants are important in the maintenance of RVFV, and considering the

different phylogenetic lineages found on the African continent as compared to the rest of the world, the critical question of susceptibility of domestic and wild ruminants merits serious consideration.

The definitive existence of a wild mammal reservoir of RVFV has not been demonstrated. In the meantime, the current explanation of how the virus is maintained in nature, at least on continental Africa, is via circulation at low levels among domestic and wild ruminants and via vertical transmission by *Aedes* mosquitoes.

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