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Coxiella burnetii in ticks, livestock, pets and wildlife: A mini-review

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Coxiella burnetii is a zoonotic bacterium with an obligatory intracellular lifestyle and has a worldwide distribution. *Coxiella burnetii* is the causative agent of Q fever in humans and coxiellosis in animals. Since its discovery in 1935, it has been shown to infect a wide range of animal species including mammals, birds, reptiles, and arthropods. *Coxiella burnetii* infection is of public and veterinary health and economic concern due to its potential for rapid spread and highly infectious nature. Livestock are the primary source of *C. burnetii* infection in most Q fever outbreaks which occurs mainly through inhalation of contaminated particles. Aside from livestock, many cases of Q fever linked to exposure to wildlife. Changes in the dynamics of human-wildlife interactions may lead to an increased potential risk of interspecies transmission and contribute to the emergence/re-emergence of Q fever. Although *C. burnetii* transmission is mainly airborne, ticks may act as vectors and play an important role in the natural cycle of transmission of coxiellosis among wild vertebrates and livestock. In this review, we aim to compile available information on vectors, domestic, and wild hosts of *C. burnetii*, and to highlight their potential role as bacterial reservoirs in the transmission of *C. burnetii*.

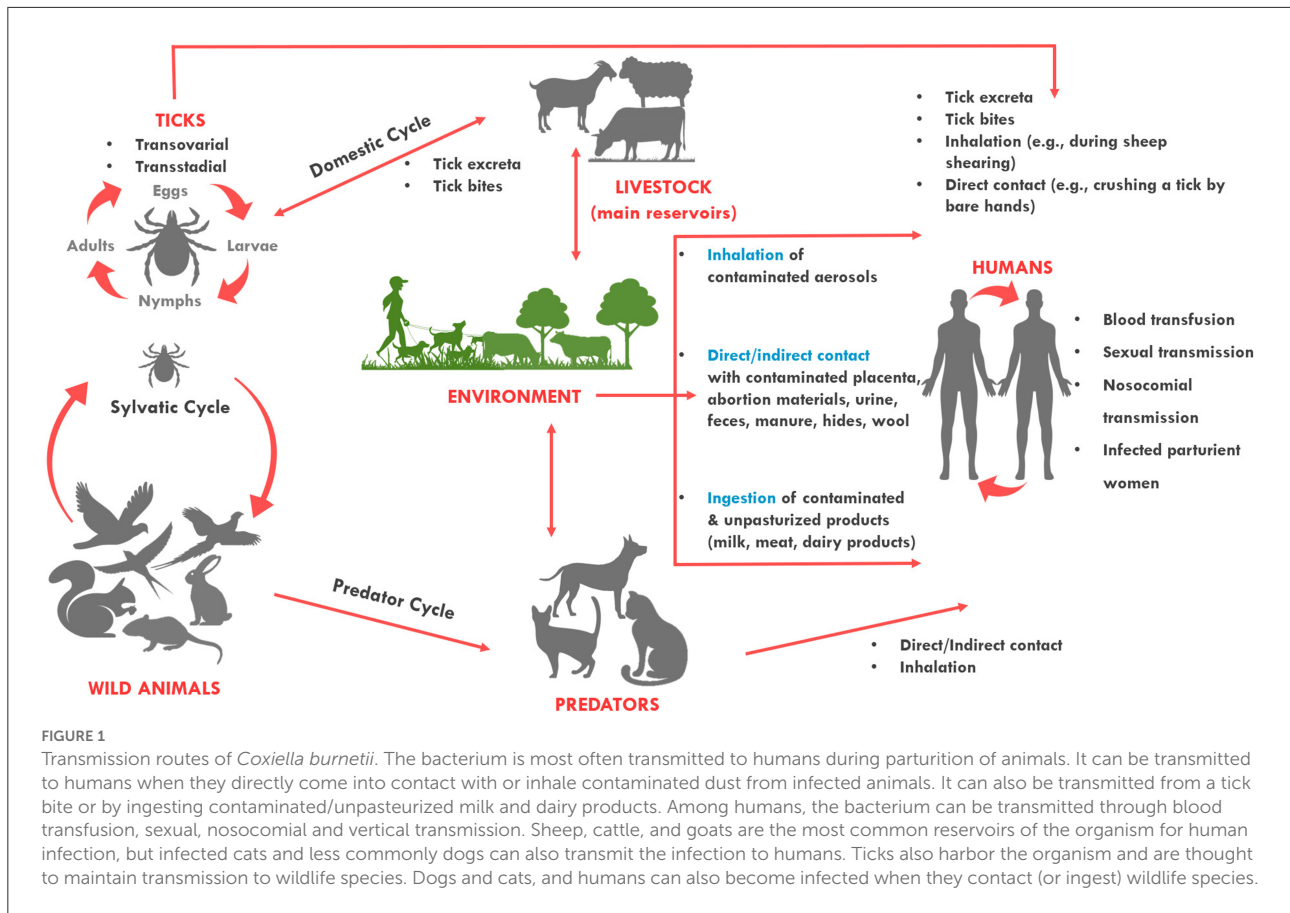
KEYWORDS

Coxiella burnetii, Q fever, coxiellosis, ticks, livestock, wildlife

Introduction

Coxiella burnetii, a member of the *Coxiellaceae* family and the aetiologic agent of Q fever disease in humans and the epizootic disease coxiellosis in animals, is an obligate intracellular gram-negative bacterium. *Coxiella burnetii* infection occurs in a wide variety of animals such as mammals, birds, reptiles, and arthropods (1). Due to its widespread availability, environmental stability, and low infective dose, *C. burnetii* is reported as an emerging pathogen and classified as a potential bioterror agent (2).

Coxiella burnetii has a wide and diverse host range. The pathogen primarily affects sheep, goats, and cattle which are considered the primary reservoirs of the pathogen and the primary source of human outbreaks (3, 4). *Coxiella burnetii* has a worldwide geographical distribution, apart from Antarctica and New Zealand (5, 6). People get infected through inhalation of bacteria contaminated aerosols expelled by infected animal feces, urine, milk, and birth products, while alternative routes of the infection such as sexual, oral, or congenital are uncommon (Figure 1) (7, 8). As the infective



dose through inhalation is <10 bacterial cells, exposure to infected animals and their products poses a significant risk for acquiring the pathogen, particularly for farmers and veterinarians (9–11).

Apart from domestic ruminants, a diverse range of other domestic animals (e.g., dog, cat, rabbit, pig, horse, camel, buffalo, rodent, birds) have been reported to be infected with *C. burnetii*. Additionally, these animals have been also documented to spread the pathogen to humans without manifesting clinical signs of coxiellosis (1). Furthermore, more than a 100 different wild mammal species, which can act as reservoirs for both humans and domestic livestock, have been shown to harbor *C. burnetii* (12).

In this review, we provide compiled available information on vectors, domestic, and wild hosts of *C. burnetii*, and highlight their potential role as bacterial reservoirs in the transmission of *C. burnetii*. This review provides a short synopsis of much broader topics that have been covered in depth by recent publications (5, 12–17) for those who are interested in more details on *C. burnetii* in animals.

Coxiella burnetii in animals

Coxiella burnetii in ticks

Q fever was first recognized in 1935 among abattoir workers in Australia by pathologist Derrick (18). Two years later, the pathogenic agent was first isolated from *Dermacentor andersonii* (Nine Mile isolate) (19) and *Haemaphysalis humerosa* (20) in the US. Since then, ticks have been discussed as possible vectors for transmission of the bacterium (21).

The role of ticks in Q fever epidemiology is being disputed due to the rare detection of *C. burnetii* in ticks. Also, difficulties in distinguishing *C. burnetii* from *Coxiella*-like endosymbionts (CLEs) of ticks, which are non-infectious for the vertebrate hosts but necessary for tick fitness, is problematic (13, 22). CLEs have a strong genetic similarity to *C. burnetii* therefore, routine PCR detection usually cross-react and its results may lead to misinterpretation of real prevalence of *C. burnetii* in ticks (23, 24). Moreover, in contrast to majority of vector-borne diseases, ticks are not essential as vector in transmission of *C. burnetii* (25). However, several studies have identified ticks as a potential risk for coxiellosis in livestock and other domestic

animals (26–30). On the other hand, ticks may play a significant role as reservoirs of *C. burnetii* in wild animals (31).

Coxiella burnetii was isolated from over 40 species of hard ticks and 14 soft tick species collected from vegetation, and domestic and wild animals (25, 32). Ticks can get infected with *C. burnetii* either through a blood meal from an infected animal at all stages of their development or transovarially. However, under experimental conditions, not all tick species were capable of being infected or being able to transmit the pathogen to experimental animals or to their offspring (25). Seven species of hard and soft ticks, including *D. andersoni*, *Ha. humerosa*, *Hyalomma aegyptium*, *Hy. asiaticum*, *Ixodes holocyclus*, *Ornithodoros hermsi*, and *Or. moubata* have yet to be demonstrated in experiments to be competent vectors of *C. burnetii* (13). In ticks, *C. burnetii* has been detected in several tick tissues, including midgut, hemolymph, Malpighian tubules, salivary glands, and ovaries (33). Ticks have also been shown to excrete considerable amount of infectious feces (up to 10^{10} organisms per gram of feces) (34). This finding emphasizes the potential risk of tick-borne infection posed by tick excreta, through inhalation (e.g., among shearers), direct contact (e.g., using bare hands to crush a tick), or tick bites (13, 31, 35).

Nevertheless, from the perspective of public health, the epidemiological importance of *C. burnetii* tick-borne transmission is lower compared to airborne transmission (13). However, inhaling tick excreta can be a significant source of infection. Additionally, ticks may play a meaningful role in the natural cycle of transmission of coxiellosis among wild-living animals and livestock (31). By crossing these species barriers, *C. burnetii* may increase its diversity of virulence and resistance factors (13).

Furthermore, several studies showed variable *C. burnetii* prevalence in ticks collected from vegetation. Although the prevalence of *C. burnetii* in ticks sampled from animals (6.6%) is higher than in ticks collected from vegetation (2.8%) (36), the *C. burnetii* prevalence in ticks collected from vegetation varies geographically. For instance, *C. burnetii* could not be detected in 1891 *I. ricinus* collected in the Netherlands (37), or 887 *I. ricinus* collected in Sweden (38). However, *C. burnetii* was detected in *I. ricinus*, *D. reticulatus*, *D. marginatus*, *Ha. concinna*, and *Ha. inermis* in Slovakia (39), in *I. ricinus*, *D. marginatus*, and *Ha. concinna* in Hungary (40), in *I. ricinus* in Germany (41), in *Ha. punctata* in Spain (42), and in *I. ricinus* in Austria (43). These results suggest that ticks may play an important role at least in the forest cycle of *C. burnetii* (31).

Coxiella burnetii in livestock and domestic animals

As already mentioned, livestock is the most frequent reservoir of *C. burnetii* and frequent contacts with domestic ruminants are one of the most important risk factors for *C.*

burnetii infection in humans. Therefore, the detection and control of infected herds is a critical issue in control of Q fever from the public health perspective (25). Massive excretion of *C. burnetii* into the environment occurs during parturition in infected females, with shedding a very large number of bacteria in birth products and in urine, feces, and milk. Shedding of *C. burnetii* may persist over several months in various body tissues and fluids such as vaginal mucus, feces, urine, and milk (44). According to experimental studies, *C. burnetii* shedding through vaginal discharge is more frequently observed in sheep, while milk is the most common route of pathogen shedding in cattle and goats (45–47).

In most Q fever outbreaks, infected ruminants are typically the primary source of infection (3, 4) and the number of cases is correlated to the local livestock population (48). Transmission of *C. burnetii* between ruminant hosts mainly occurs *via* the airborne route. However, other factors such as transboundary animal trade and transportation of animal source foods enhance movement of the pathogen across large distances (16, 49). Aside from livestock, pet animals, especially dogs and cats kept in a close contact with their owners, are known to be important reservoirs of *C. burnetii* during urban Q fever outbreaks. Many cases of human Q fever have been reported from infected dogs and cats (15, 50–57). Most of these reported cases of Q fever in humans were associated with exposure to parturient pets. Although the main origins of infection in pets remain poorly understood, it has been speculated that dogs and cats may be infected by tick bite, consumption of placenta or milk from infected livestock, consumption of raw meat, inhalation of aerosolized bacteria in the environment, and preying of contaminated animal species (16, 17).

Coxiella burnetii infection has been reported in other domestic mammals—though less frequently than livestock—, including horses, rabbits, pigs, camels, water buffalo, rats, and mice (11, 30, 35, 58–72). So far, serological evidence of *C. burnetii* infection in many horses have been reported (66, 73–75). However, the epidemiological importance of horses as *C. burnetii* reservoirs has not been adequately studied.

The role of European rabbits as a reservoir for *C. burnetii* was evaluated and rabbits were identified as a major source of coxiellosis in livestock and Q fever in humans in Europe, and it is possible that they have a similar role in Australia (68, 76).

The role of pigs in epidemiology of *C. burnetii* is relatively obscure. Their susceptibility to *C. burnetii* infection has been confirmed based on previous serological study (77), but there is a lack of evidence that pigs serve as reservoirs of *C. burnetii*. Until today, no *C. burnetii* transmission from pigs to humans has been documented. The study on evaluation of the prevalence and genotypes of *C. burnetii* in pigs from South Korea revealed low seropositivity among pigs (59).

Domestic water buffalo (*Bubalus bubalis*) is a globally important livestock species due to its high-quality milk, meat and leather. Many studies revealed that buffalo may have a significant impact on the epidemiology of Q fever and

emphasizes the necessity for *C. burnetii* surveillance and control measures in buffalo (60, 65–67).

In camels, *C. burnetii* is among the most widespread zoonotic pathogens (61). Camel populations worldwide are estimated to be ~30 million, with dromedary camels constituting 95% of the population (78). Dromedary camels (*Camelus dromedarius*) play an important role as a high-quality protein source for people in semi-dry and arid zones of Africa (5). The most recent *C. burnetii* serological studies conducted in herds and farms in Africa, Arabian Peninsula, and Asia reported a very high prevalence of Q fever antibodies in the sera of camels (5, 79, 80).

The pathogenesis of Q fever in domestic animals is not fully understood. *Coxiella burnetii* infections in animals are frequently asymptomatic. In the acute phase, *C. burnetii* can be detected in the blood, lungs, spleen, and liver (17). When persistent shedding of bacterium occurs in feces and urine, the infection often becomes chronic. However, unlike humans, animals do not usually develop chronic endocarditis (17). Nonetheless, recent studies reported *C. burnetii* detection in inflamed cardiac valves in slaughtered cattle (81) as well as chronic endometritis in dairy cattle, resulting chronic subfertility (82). Chronic *C. burnetii* infection mostly affects female uterus and mammary glands. Therefore, the most significant clinical cases of *C. burnetii* infection is limited to pregnant animals and are commonly associated with abortions, stillbirths, the birth of small or weak offspring, and mastitis (17, 25).

In laboratory animals, *C. burnetii* inoculation of guinea pigs and mice leads to pneumonia, hepatitis and splenomegaly (83, 84). In addition, the importance of *C. burnetii* strain in determining the severity of pathological changes was reported (17). Splenomegaly in guinea pigs and mice is considered to be an indication of *C. burnetii* strain pathogenicity. Furthermore, the method of inoculation appears to impact pathogenesis. In mice, intranasal inoculation causes pneumonia, whereas intraperitoneal inoculation causes hepatosplenomegaly (84).

Little is known about the pathogenesis of *C. burnetii* infections in companion animals. In pet animals, especially dogs and cats, reproductive anomalies, including dystocia, stillbirths and perinatal mortality have been recorded. However, many studies reported short-lived bacterial shedding and indicated that bacterial shedding by companion animals is rare given the lack of *C. burnetii* DNA in samples from companion animals (85).

Coxiella burnetii in wildlife

Coxiella burnetii occurs in many free-living and captive wildlife species worldwide that have been suspected to play a role in the epidemiology of Q fever (12, 86–92). González-Barrio and Ruiz-Fons discussed in details about how it is

exceedingly difficult to identify *C. burnetii* infection in wildlife, particularly farmed wild species and free-roaming wildlife (12, 93, 94), and highlighted the importance of daily survey to easily detect reproductive disorders associated to *C. burnetii* in captive animals of zoological gardens (12).

Natural infections of *C. burnetii* have been reported in a large variety of wild species (Table 1). Starting with birds, *C. burnetii* infection has been documented in avian wildlife in addition to farm and pet birds (14, 98)—e.g., barn swallow (*Hirundo rustica*), eclectus parrot (*Eclectus roratus*), hen (*Gallus gallus domesticus*), turkey (*Meleagris* spp.), magpie (*Pica* spp.), pheasant (*Phasianus colchicus*), wood-pigeon (*Columba palumbus*), turtle dove (*Streptopelia turtur*), pigeon (*Columba livia*), house sparrow (*Passer domesticus*), Italian sparrow (*Passer italiae*), rook (*Corvus frugileus*), hooded crow (*Corvus cornix*), carrion crow (*Corvus corone*), raven (*Corvus corax*), Eurasian griffon vulture (*Gyps fulvus*), black kite (*Milvus migrans*), redstart (*Phoenicurus phoenicurus*), white wagtail (*Motacilla alba*), western yellow wagtail (*Motacilla flava*), common quail (*Coturnix coturnix*), Japanese quail (*Coturnix japonica*), black-headed gull (*Chroicocephalus ridibundus*), common gull (*Larus canus*), white-winged tern (*Chlidonias leucopterus*), common tern (*Sterna hirundo*), common starling (*Sturnus vulgaris*), wild ducks (*Anas* spp.), common blackbird (*Turdus merula*), fieldfare (*Turdus pilaris*), thrush nightingale (*Luscinia luscinia*), willow warbler (*Phylloscopus trochilus*), great white pelican (*Pelecanus onocrotalus*), Eurasian reed warbler (*Acrocephalus scirpaceus*), and wood sandpiper (*Tringa graleola*). Ebani and Mancianti reviewed *C. burnetii* infections in birds from 1952, when they were first documented, to the present, and supports the potential role of avian populations in the epidemiology of *C. burnetii* (14). However, it is yet unclear how *C. burnetii* spreads among avian wildlife and what factors affect the transmission of the pathogen, as information about prevalence rates in different geographic locations is scarce (14).

The pathogenesis of *C. burnetii* infection in birds is not well-defined. Previous studies observed *Coxiella* persistence in birds with (polyorganous lesions resulting in mortality) and without clinical signs (101, 106, 154).

In reptiles, two earlier studies have identified *C. burnetii* in India, where two tortoises, snakes and skinks were seropositive for *C. burnetii* (108, 155). A recent study examined turtles in Illinois and Wisconsin, USA, for *C. burnetii* using qPCR, and 5 out of 605 turtles yielded positive results for *C. burnetii* (107). Furthermore, *C. burnetii* has been detected in various reptilian ticks, including tortoise tick *H. aegyptium* from Romania (156), *Amblyomma exornatum* from Guinea Bissau, *A. nuttalli* from Ghana, and *A. variegatum* in Africa (157).

In mammals, *C. burnetii* infection has been detected in a broad range of species. In cervids, *C. burnetii* has been reported in black-tailed deer (*Odocoileus hemionus colombianus*), California mule deer (*O. h. californicus*), Rocky Mountain mule deer (*O. h. hemionus*), and white-tailed deer

TABLE 1 List of animal species infected by *Coxiella burnetii*.

Family	Common name	Scientific name	Country	Reference
<i>Coxiella burnetii</i> infection in birds				
Accipitridae	Black kite	<i>Milvus migrans</i>	Spain	(95)
	Eurasian griffon vulture	<i>Gyps fulvus</i>	Spain	(95)
Acrocephalidae	Eurasian reed warbler	<i>Acrocephalus scirpaceus</i>	Bulgaria	(96)
Anatidae	Eurasian teal	<i>Anas crecca</i>	Italy	(97)
	Eurasian wigeon	<i>Anas penelope</i>	Italy	(97)
	Mallard	<i>Anas platyrhynchos</i>	Russia	(96)
Columbidae	Pigeon	<i>Columba livia</i>	Japan	(98)
			Bulgaria	(99)
			Czechoslovakia	(100)
			Italy	(101)
			Slovakia	(102)
	France	(102)		
	Italy	(103)		
	Japan	(98)		
	Turtle dove	<i>Streptopelia turtur</i>	Bulgaria	(99)
	Wood-pigeon	<i>Columba palumbus</i>	Bulgaria	(99)
Corvidae	Crow	<i>Corvus spp.</i>	Bulgaria	(99)
			Japan	(98)
	Carrion crow	<i>Corvus corone</i>	Japan	(98)
	Hooded crow	<i>Corvus cornix</i>	Russia	(96)
	Magpie	<i>Pica spp.</i>	Bulgaria	(99)
	Raven	<i>Corvus corax</i>	Bulgaria	(99)
	Rook	<i>Corvus frugileus</i>	Russia	(104)
Hirundinidae	Barn swallow	<i>Hirundo rustica</i>	Czechoslovakia	(100)
Laridae	Black-headed gull	<i>Chroicocephalus ridibundus</i>	Russia	(105)
				(96)
	Common gull	<i>Larus canus</i>	Russia	(105)
	Common tern	<i>Sterna hirundo</i>	Russia	(105)
	White-winged tern	<i>Chlidonias leucopterus</i>	Russia	(105)
Motacillidae	Western yellow wagtail	<i>Motacilla flava</i>	Bulgaria	(96)
	White wagtail	<i>Motacilla alba</i>	Czechoslovakia	(100)
			Russia	(96)
Muscicapidae	Redstart	<i>Phoenicurus phoenicurus</i>	Czechoslovakia	(100)
	Thrush nightingale	<i>Luscinia luscinia</i>	Bulgaria	(96)
Passeridae	House sparrow	<i>Passer domesticus</i>	Russia	(96)
	Italian sparrow	<i>Passer italiae</i>	Italy	(103)
Pelecanidae	Great white pelican	<i>Pelecanus onocrotalus</i>	Bulgaria	(96)
Phasianidae	Common quail	<i>Coturnix coturnix</i>	Japan	(98)
			Russia	(96)
	Hens	<i>Gallus gallus domesticus</i>	Czechoslovakia	(100)
			Bulgaria	(99)
	Japanese quail	<i>Coturnix japonica</i>	Japan	(98)
	Pheasant	<i>Phasianus colchicus</i>	Bulgaria	(99)
	Turkey	<i>Meleagris spp.</i>	Czechoslovakia	(100)
Phylloscopidae	Willow warbler	<i>Phylloscopus trochilus</i>	Bulgaria	(96)
Psittaculidae	Eclectus parrot	<i>Eclectus roratus</i>	USA	(106)

(Continued)

TABLE 1 (Continued)

Family	Common name	Scientific name	Country	Reference	
Scolopacidae	Wood sandpiper	<i>Tringa graleola</i>	Bulgaria	(96)	
Sturnidae	Common starling	<i>Sturnus vulgaris</i>	Russia	(96)	
Turdidae	Common blackbird	<i>Turdus merula</i>	Russia	(96)	
	Fieldfare	<i>Turdus pilaris</i>	Bulgaria	(96)	
			Russia	(96)	
<i>Coxiella burnetii</i> infection in reptiles					
Emydidae	Blanding's turtle	<i>Emydoidea blandingii</i>	USA	(107)	
	Ornate box turtle	<i>Terrapene ornata</i>			
	Painted turtle	<i>Chrysemys picta</i>			
Geoemydidae	Roofed turtles	<i>Batagur and Pangshura</i> spp. (formerly in genus <i>Kachuga</i>)	India	(108)	
Colubridae	Chinese ratsnake	<i>Ptyas korros</i>	India	(108)	
	Grass snake	<i>Natrix natrix</i>			
Pythonidae	Indian python	<i>Python molurus</i>	India	(108)	
<i>Coxiella burnetii</i> infection in terrestrial mammals					
Bovidae	Alpine chamois	<i>Rupicapra rubicapra</i>	France	(109)	
	Alpine ibex	<i>Capra ibex</i>	Switzerland	(110)	
	Bighorn sheep	<i>Ovis canadensis</i>	USA	(111)	
	Cuvier's gazelle	<i>Gazella cuvieri</i>	Europe	(112)	
	Dama gazelle		<i>Nanger dama</i>	UAE	(113)
				Europe	(112)
	Mouflon		<i>Ovis orientalis</i>	Spain	(114)
				Czech Republic	(115)
				Cyprus	(116)
					(117)
		Muskox	<i>Ovibos moschatus</i>	USA	(118)
		Sable antelope	<i>Hippotragus niger</i>	Portugal	(119)
		Saiga antelope	<i>Saiga tatarica</i>	Kazakhstan	(120)
		Spanish ibex	<i>Capra pyrenaica</i>	Spain	(121)
		Waterbuck	<i>Kobus ellipsiprymnus</i>	Portugal	(119)
		Yak	<i>Bos mutus</i>	China	(122)
Cervidae	Black-tailed deer	<i>Odocoileus hemionus</i>	USA	(123)	
		<i>colombianus</i>			
	California mule deer	<i>Odocoileus hemionus</i>	USA	(123)	
		<i>californicus</i>			
	Fallow deer	<i>Dama dama</i>	Czech Republic	(115)	
			Italy	(124)	
			Spain	(121)	
			Czech Republic	(115)	
			Slovakia	(125)	
			Spain	(121)	
		Spain	(94)		
Red deer	<i>Cervus elaphus</i>	Spain	(126)		
			(114)		
		France	(127)		
		Italy	(128)		
		Hungary	(129)		

(Continued)

TABLE 1 (Continued)

Family	Common name	Scientific name	Country	Reference
	Rocky mountain mule deer	<i>Odocoileus hemionus</i> .	USA	(123)
		<i>hemionus</i>		
	Roe deer	<i>Capreolus capreolus</i>	France	(130)
				(131)
				(127)
				(132)
			Netherlands	(133)
			Czech Republic	(115)
			Slovakia	(95)
			Spain	(94)
	Sika deer	<i>Cervus nippon</i>	Japan	(134)
	White-tailed deer	<i>Odocoileus virginianus</i>	Canada	(135)
			USA	(136)
Suidae	Eurasian wild boar	<i>Sus scrofa</i>	Czech Republic	(115)
			Spain	(137)
				(95)
Leporidae	European hare	<i>Lepus europaeus</i>	Cyprus	(116)
			Spain	(95)
	European rabbit	<i>Oryctolagus cuniculus</i>	Spain	(95)
				(76)
				(70)
			Australia	(68)
	Japanese hare	<i>Lepus brachyurus</i>	Japan	(134)
Cricetidae	Bank vole	<i>Myodes glareolus</i>	UK	(88)
	Cursor Grass Mouse	<i>Akodon cursor</i>	Brazil	(138)
	Delta Pygmy Rice Rat	<i>Oligoryzomys nigripes</i>	Brazil	(138)
	Field vole	<i>Microtus agrestis</i>	UK	(88)
	Red vole	<i>Myodes rutilus</i>	Russia/China	(139)
	Reed vole	<i>Microtus fortis</i>	Russia/China	(139)
	The Atlantic hucicudo	<i>Oxymycterus dasytrichus</i>	Brazil	(138)
Muridae	Black rat	<i>Rattus rattus</i>	Netherlands	(140)
	Brown rat	<i>Rattus norvegicus</i>	Russia/China	(139)
			Germany	(141)
			Netherl.	(140)
	House mouse	<i>Mus musculus</i>	Spain	(42)
			Brazil	(138)
	Large Japanese Field Mouse	<i>Apodemus speciosus</i>	Russia/China	(139)
	Long-tailed field mouse	<i>Apodemus sylvaticus</i>	Italy	(142)
			Spain	(42)
			UK	(88)
	Striped Field Mouse	<i>Apodemus agrarius</i>	Russia/China	(139)
Sciuridae	American red squirrel	<i>Tamiasciurus hudsonicus</i>	Canada	(143)
	Carolina flying squirrel	<i>Glaucomys sabrinus</i>	Canada	(143)
	Siberian Chipmunk	<i>Tamias sibiricus</i>	Russia/China	(139)
Canidae	Coyote	<i>Canis latrans</i>	USA	(144)
	Red fox	<i>Vulpes vulpes</i>	Cyprus	(116)

(Continued)

TABLE 1 (Continued)

Family	Common name	Scientific name	Country	Reference
			Spain	(145)
			UK	(88)
Erinaceidae	Amur hedgehog	<i>Erinaceus amurensis</i>	China	(146)
	North African Hedgehog	<i>Atelerix algirus</i>	Tunisia	(147)
Felidae	Jaguar	<i>Panthera onca</i>	Brazil	(148)
	Wild cat	<i>Felis silvestris</i>	Spain	(121)
Macropodidae	Western grey kangaroo	<i>Macropus fuliginosus</i>	Australia	(149)
Viverridae	Common genet	<i>Genetta genetta</i>	Spain	(145)
<i>Coxiella burnetii</i> infection in marine mammals				
Mustelidae	Sea otter	<i>Enhydra lutris</i>	USA	(150)
Otariidae	Northern fur seal	<i>Callorhinus ursinus</i>	USA	(151)
				(152)
	Steller sea lion	<i>Eumetopias jubatus</i>	USA	(151)
				(153)
Phocidae	Harbor seal	<i>Phoca vitulina richardsi</i>	USA	(153)

(*Odocoileus virginianus*) in Canada and US (123, 135, 136). For European cervids, the infection has been documented in fallow deer (*Dama dama*), red deer (*Cervus elaphus*), and roe deer (*Capreolus capreolus*) (94, 95, 114, 115, 121, 124–133). The serological evidence of the infection was also reported in Sika deer (*Cervus arbor*) in Japan (134). Furthermore, the presence of *C. burnetii* has been detected in wild boars, hares, and many rodent species; including Eurasian wild boars (*Sus scrofa*) (95, 115, 137), European hares (*Lepus europaeus*) (95, 116), European rabbit (*Oryctolagus cuniculus*) (68, 70, 76), Japanese hare (*Lepus brachyurus*) (134), cursor grass mouse (*Akodon cursor*) (138, 158), bank vole (*Myodes glareolus*) (88), delta pygmy rice rat (*Oligoryzomys nigripes*) (138), the Atlantic forest holicudo (*Oxymycterus dasytrichus*) (138), field vole (*Microtus agrestis*) (88), reed vole (*Microtus fortis*) (139), red vole (*Myodes rutilus*) (139), black rat (*Rattus rattus*) (140), brown rat (*Rattus norvegicus*) (139–141), house mouse (*Mus musculus*) (42, 138), long-tailed field mouse (*Apodemus sylvaticus*) (42, 88, 142), large Japanese field mouse (*Apodemus speciosus*) (139), striped field mouse (*Apodemus agrarius*) (139), American red squirrel (*Tamiasciurus hudsonicus*) (143), Carolina flying squirrel (*Glaucomys sabrinus*) (143), and Siberian chipmunk (*Tamias sibiricus*) (139). Rodents are considered to be significant reservoirs of infection in the domestic cycle of *C. burnetii* (159), and several rodent species have been found to be a source of livestock coxiellosis (140, 160).

Additionally, *C. burnetii* has been implicated in reproductive losses in captive exotic ungulates, including waterbuck (*Kobus ellipsiprymnus*) (119), sable antelope (*Hippotragus niger*) (119), and many gazelles, such as arbor gazelle (*Gazella arbor neglecta*), dama gazelle (*Nanger dama mhorh*) and Cuvier's gazelle (*Gazella cuvieri*) (112, 113). Reproductive disorders caused by *C. burnetii* in endangered species such as exotic ungulates that are bred in

captivity for conservation programs may be of critical threat and pose a risk for the programs (113). Other bovids reported to be exposed to/infected by *C. burnetii* are Alpine ibex (*Capra ibex*) (110), Bighorn sheep (*Ovis arboris*) (111), Alpine chamois (*Rupicapra rupicapra*) (109), Spanish ibex (*Capra pyrenaica*) (121), mouflon (*Ovis orientalis*) (114–117), muskox (*Ovibos moschatus*) (118), saiga antelope (*Saiga tatarica*) (120), and yak (*Bos mutus*) (122).

Apart from terrestrial mammals, *C. burnetii* has also been detected in marine wildlife—e.g., sea otter (*Enhydra lutris*) (150), northern fur seal (*Callorhinus ursinus*) (151, 152), steller sea lion (*Eumetopias jubatus*) (151, 153, 161), and harbor seal (*Phoca vitulina richardsi*) (153).

Other mammals that have been shown to harbor *C. burnetii* are coyote (*Canis latrans*) (144), red fox (*Vulpes vulpes*) (88, 116, 145), jaguar (*Panthera onca*) (148), wild cat (*Felis silvestris*) (121), common genet (*Genetta genetta*) (145), western grey kangaroo (*Macropus fuliginosus*) (149), North African hedgehog (*Atelerix algirus*) (147), and Amur hedgehog (*Erinaceus amurensis*) (146).

Coxiellosis causes similar clinical outcomes and pathologies in wild animals as it does in domestic animals (12). Placentitis is one of the most common lesions identified in wild animals with coxiellosis which have been observed in dama gazelle (113), Steller sea lion (161), and Pacific harbor seal (162).

Disease control

Preventive veterinary practices are critical in the control of coxiellosis. Two methods are available to control coxiellosis in animals: vaccination and antibiotic treatment.

Vaccination is one of the most effective management strategies to reduce abortion rates and spread of the bacterium. WHO recommends only the administration of vaccines containing or prepared from phase I *C. burnetii* as it has been scientifically shown that the full-length phase I lipopolysaccharide is the protective antigen of *C. burnetii* (163). Vaccines prevent successive transmission to healthy individuals and humans, and reduce but do not eliminate shedding of the bacterium (164–166). Two vaccines against *C. burnetii* are currently commercially available for veterinary use in many regions of the world. The first one is an inactivated bivalent vaccine developed from *Chlamydia abortus* and phase II *C. burnetii* (Chlamyvac[®], Merial, Lyon, France), indicated for use in sheep and goats. The second one is an inactivated non-adjuvanted phase I *C. burnetii* antigen Nine Mile strain vaccine (Coxevac[®], CEVA Santé Animale, Libourne, France) recommended for use in goats and cattle (167).

Antibiotic treatment is another available option to control coxiellosis in animals. Pregnant animals might have a decrease in abortion rates and *C. burnetii* shedding by receiving antibiotic treatment with oxytetracycline (20 mg/kg) during the last trimester of pregnancy (168). However, antibiotic treatment of animals is not recommended since the effect of the treatment is not sufficiently demonstrated and proportionate use of antibiotics is required to avoid microbial resistance (8).

Conclusion

Q fever is a significant zoonotic disease worldwide that affects both public and veterinary health, as well as has a detrimental socioeconomic impact on livestock industry. In view of the threats related to this disease, a thorough understanding of transmission routes and potential sources of infection is crucial. *Coxiella burnetii* has been detected in various hosts, including humans, domestic and wild animals, pets, birds, and arthropods. Ticks are considered as vectors of *C. burnetii* and may pose a risk for infection of animals and humans. However, further field studies should be implemented to assess the role of the ticks as vectors for *C. burnetii* under natural conditions. Understanding their role can help us to develop and/or improve vector control strategies that would lead to decrease of *C. burnetii* risk. It is also noteworthy that our understanding about *C. burnetii* infection patterns in ticks and role of ticks as possible *C. burnetii* vectors are limited since CLEs are likely to have been mistakenly

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identified as *C. burnetii* in many studies. The development of the diagnostic tests to distinguish between *C. burnetii* and CLEs to improve our understanding of Q fever epidemiology should also be a key area of future research.

Another point of contention is the role of wildlife—livestock—human interactions which should be further investigated. It is important to develop effective preventive and control strategies using on evidence-based “One Health” approach. In the context of inadequate biosafety controls implemented in the wildlife—livestock—human interface, the possibility of a high rate of transmission of the zoonotic pathogens, including *C. burnetii*, at these interfaces cannot be precluded.

Further studies are also required to better understand the pathogenicity of *C. burnetii* for its arthropod and wild hosts. Research about possible routes of transmission of *C. burnetii* between different host should not be omitted as well. Finally, we should focus also on research evaluating the pathogenicity of CLEs for humans and other mammals or at least their ability to infect them.

Author contributions

SSC and JČ: conceptualization and writing—review and editing. SSC: writing—original draft preparation and visualization. JČ: supervision. All authors contributed to the article and approved the submitted version.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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