
















ORIGINAL ARTICLE

Coxiella burnetii serostatus in dromedary camels (*Camelus dromedarius*) is associated with the presence of *C. burnetii* DNA in attached ticks in Laikipia County, Kenya

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Abstract

Aims: Q fever is a globally distributed, neglected zoonotic disease of conservation and public health importance, caused by the bacterium *Coxiella burnetii*. *Coxiella burnetii* normally causes subclinical infections in livestock, but may also cause reproductive pathology and spontaneous abortions in artiodactyl species. One such artiodactyl, the dromedary camel (*Camelus dromedarius*), is an increasingly important livestock species in semi-arid landscapes. Ticks are naturally infected with *C. burnetii* worldwide and are frequently found on camels in Kenya. In this study, we assessed the relationship between dromedary camels' *C. burnetii* serostatus and whether the camels were carrying *C. burnetii* PCR-positive ticks in Kenya. We hypothesized that there would be a positive association between camel seropositivity and carrying *C. burnetii* PCR-positive ticks.

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Methods and Results: Blood was collected from camels ($N=233$) from three herds, and serum was analysed using commercial ELISA antibody test kits. Ticks were collected ($N=4354$), divided into pools of the same species from the same camel ($N=397$) and tested for *C. burnetii* and *Coxiella*-like endosymbionts. Descriptive statistics were used to summarize seroprevalence by camel demographic and clinical variables. Univariate logistic regression analyses were used to assess relationships between serostatus (outcome) and tick PCR status, camel demographic variables, and camel clinical variables (predictors). Camel *C. burnetii* seroprevalence was 52%. Across tick pools, the prevalence of *C. burnetii* was 15% and *Coxiella*-like endosymbionts was 27%. Camel seropositivity was significantly associated with the presence of a *C. burnetii* PCR-positive tick pool (OR: 2.58; 95% CI: 1.4–5.1; $p=0.0045$), increasing age class, and increasing total solids.

Conclusions: The role of ticks and camels in the epidemiology of Q fever warrants further research to better understand this zoonotic disease that has potential to cause illness and reproductive losses in humans, livestock, and wildlife.

KEYWORDS

arthropod, camelid, livestock, One Health, Q fever, zoonoses

1 | INTRODUCTION

As the human population increases exponentially, expansion into wilderness areas leads to increased contact between livestock species and wildlife. This wildlife–livestock interface facilitates disease transmission to and from wildlife and domestic livestock, increasing the potential for disease spillover into humans. Sixty per cent of emerging infectious diseases (EIDs) in people are zoonotic, with 75% of those EIDs arising from a wildlife host (Jones et al., 2008; Taylor et al., 2001; Deem et al., 2019), emphasizing the need for greater attention to the increasing contact between wild animals and the domestic species that we rely upon.

Q fever (coxiellosis) is a globally distributed, highly infectious, neglected zoonotic pathogen of conservation, public health, and economic importance (Njeru et al., 2016). Q fever is caused by the bacterium *Coxiella burnetii*, a gram-negative, obligate intracellular coccobacillus that is shed by infected humans and animals via faeces, placenta, and mammary and urogenital secretions (Knobel et al., 2013; Maurin & Raoult, 1999; Pirouz et al., 2015; Tejedor-Junco et al., 2016). In addition to contact with reproductive fluids from livestock, humans are at risk of infection by consuming unpasteurized dairy products (Gale et al., 2015; Loftis et al., 2010; Rabaza et al., 2021). *Coxiella burnetii* has historically been associated with small ruminants but a number of artiodactyl species are susceptible to infection. Q fever usually causes subclinical infections in livestock, but in some instances can cause reproductive pathology and spontaneous abortions.

Farmers, veterinarians, slaughterhouse workers, and others who work in proximity to domestic livestock are at increased risk of infection (Koka et al., 2018). Direct transmission to humans via tick bite has been described as of little epidemiological significance, but several

Impacts

- Over half the camels in this study had antibodies against *Coxiella burnetii*.
- Camels were more likely to be seropositive if tick pools collected from the camels were PCR-positive for *C. burnetii*.
- While directionality cannot be determined based on these findings, ticks and camels are suspected to play a role in the epidemiology of Q fever.
- The transmission pathway and associated infection rates between ticks and camels warrant further exploration, and tick prevention efforts in livestock should be a priority for Q fever mitigation.

cases have been reported (Graves et al., 2020; Huang et al., 2021; Maurin & Raoult, 1999; Rolain et al., 2005). In humans, clinical presentations of Q fever range from acute febrile illness to chronic disease in immunosuppressed individuals, as well as spontaneous abortions and premature birth (Maurin & Raoult, 1999; Pirouz et al., 2015). Due to its ability to cause severe disease, capacity for windborne dissemination, and spore-like resistance to heat and desiccation, *C. burnetii* is classified as a Class B biological warfare agent (Centers for Disease Control and Prevention, 2018, 2019; Kagawa et al., 2003).

Dromedary camels (*Camelus dromedarius*) can be infected with *C. burnetii* and have been increasing in popularity as a hardy livestock species worldwide over the past several decades (Browne et al., 2017). As obligate browsers, camels compete with sympatric

wildlife for resources, creating ample opportunity for sharing ectoparasites and pathogens (Deem, 2019; Maurin & Raoult, 1999; O'Connor et al., 2015).

Coxiella burnetii infects more than 40 species of ticks worldwide (Maurin & Raoult, 1999). Ticks have been proposed as an important reservoir and vector in *C. burnetii* transmission among mammals, maintaining the organism in the environment and transmitting it through blood meals or aerosolized faecal matter (Agerholm, 2013; Angelakis & Raoult, 2010; Kumsa et al., 2015; Sprong et al., 2012). Some authors have proposed that ticks may augment the virulence of *C. burnetii* (Kumsa et al., 2015).

While there is an established association between camel herding or drinking unpasteurized camel milk and *C. burnetii* exposure in humans, the potential role of ticks in maintaining the organism between camel hosts remains relatively unexplored, though it has begun to receive attention in recent years (Abdullah et al., 2018). This study contributes to our understanding of the regional epidemiology of this pathogen by investigating associations between *C. burnetii* exposure in camels (seropositivity) and the presence of *C. burnetii* DNA in camel-associated ticks, as well as camel demographic and clinical variables. We hypothesized that there would be a positive association between camel seropositivity and carrying a tick that tested PCR-positive for *C. burnetii*.

2 | MATERIALS AND METHODS

2.1 | Study area

Laikipia County is a semi-arid region located in central Kenya that has experienced dramatic camel population growth and has abundant wildlife (Deem, 2019) (Figure 1). The human population is approximately 400,000 people, with 76% of people living in rural areas. Livestock farming is the primary means of income: >80% of the population rely on livestock farming for their livelihoods, and 32% are pastoralists. Despite this dependence on farming, 90% of the land has been deemed too dry for cultivation, with less than 2% of the land considered of high value for agriculture. Sixty-five per cent of the land is defined as 'wildlife habitat', including eight forest reserves, one national park, and one national reserve. Laikipia has the second highest density of large free-ranging mammals in Kenya, second to Maasai Mara National Reserve (Butynski & de Jong Lolldaiga, 2015).

2.2 | Study design, population, and sampling

We collected biomaterials from three herds of camels in Laikipia County: Herd 1 (herd size=136), Herd 2 (herd size=124) and Herd 3 (herd size=82). These three commercial livestock ranches used the camels primarily for milk production. Adult male camels at Herd 1 were also used as safari camels in the tourism industry. Camels from all three herds were housed overnight in bomas (livestock corrals) and were sampled before being released to forage for the day. Camels were selected via convenience sampling, and camels of both sexes and

all age groups were selected for the study. All sampling took place in June 2017: two consecutive days were spent at herds 1 and 2, and 3 consecutive days were spent at Herd 3. The animals at these ranches were primarily being used for milk production and thus were mostly adult, lactating female camels. The predominance of female camels in this study is representative of a typical herd in Kenya, where over 70% of households with camels have herds comprised of 60%–90% lactating females (Elhadi et al., 2015). The camels in the present study had skin-branded, unique identification numbers assigned by the ranch. Age classes were assigned as neonate/juvenile (<6 months), subadult (6 months to 1 year), and adult (>1 year) based on herder knowledge of the individuals' ages. Camel herders were asked for a clinical history on each individual. Camels were physically examined and any apparent health conditions noted. Body condition scores (BCSs) were assigned by local veterinarians using a subjective score, categorized as thin, normal, over-conditioned, or obese (Faye et al., 2001).

Camels were manually restrained, and approximately 8 mL of blood was collected via jugular venipuncture using an 18-gauge needle and 10-mL syringe. Blood was transferred into both EDTA and serum separator tubes and labelled with camel identification number, date, and herd. The blood tubes were stored in a cooler with ice packs for transportation back to the laboratory. A sample of the camel's attached tick burden was collected from each camel's body; time spent collecting ticks was limited to the duration of blood collection. The ticks were predominantly collected from the perineal area because of their high concentration at that location, but also from the axilla, groin, and ears. Camels were marked with paint at the end of sample collection to avoid recapture.

2.3 | Semi-structured interview: Camel management practices

The interview was conducted with the senior herder from each herd. The interview consisted of 40 questions that covered topics including awareness of tick-borne disease and preventive measures and land use practices, including camels' interactions with wildlife. A local researcher translated the interview questions into Kiswahili, and the herder's verbal responses were recorded. The interview instrument is available in the [Supplementary Materials](#). Interview response data were reported descriptively.

2.4 | Laboratory testing

2.4.1 | Packed cell volume, total solids, and serum antibody detection

Whole blood was drawn into microhematocrit tubes, centrifuged and used to determine packed cell volume (PCV). Plasma total solids (TS), an estimate of plasma total protein, were determined using a refractometer. Blood in the serum separator tubes was centrifuged within 8 h of sample collection, and serum was aliquoted into cryovials for

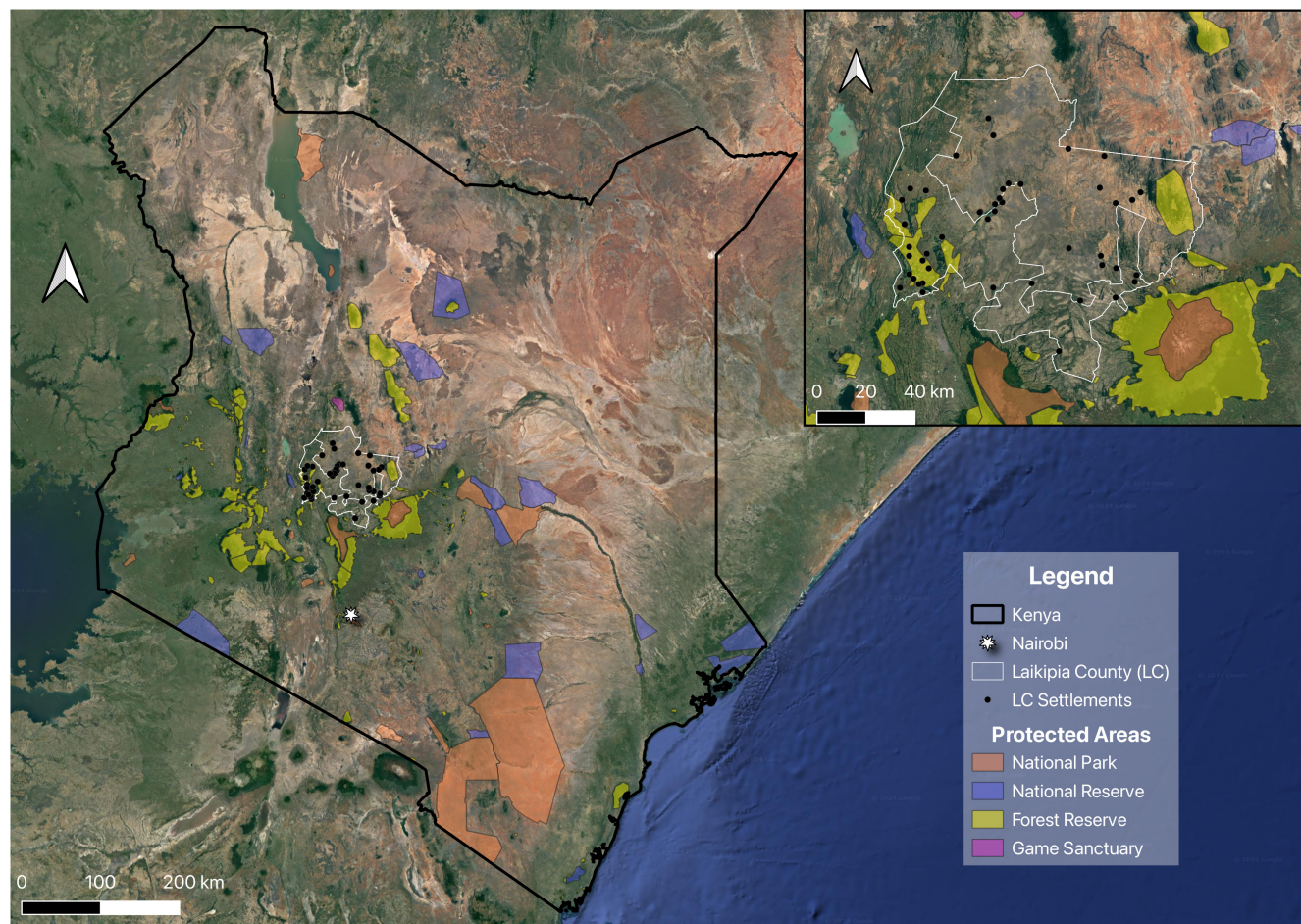


FIGURE 1 Map of Kenya showing the study area, Laikipia County.

storage in liquid nitrogen until transport on dry ice to a -80°F freezer at the Institute for Primate Research in Nairobi. To determine seroconversion, Q fever (*C. burnetii*) antibodies were detected in diluted serum samples (1:400) using the IDEXX Q Fever (*C. burnetii*) Ab Test (IDEXX Europe B.V., Scorpius 60 Building F, Hoofddorp 2132 LR, The Netherlands) at the International Livestock Research Institute according to the manufacturer's instructions.

2.4.2 | Ticks

Ticks were identified based on their morphological characteristics using Multikey 2.1, a digital dichotomous key and other reference texts (Walker et al., 2000; Walker, 2003). All collected ticks from an individual camel were separated by species and stored in 70% ethanol at room temperature. Ticks of the same species from the same camel were pooled prior to analysis.

2.4.3 | Molecular detection of *Coxiella*

Tick pools were tested for *C. burnetii* and *Coxiella*-like endosymbiont DNA at the International Centre of Insect Physiology and Ecology

(icipe). *Coxiella burnetii* was detected using primers Trans 1 (5'-TAT GTA TCC ACC GTA GCC AGT C-3') and Trans 2 (5'-CCC AAC AAC ACC TCC TTA TTC-3') designed to target a 687-bp fragment of the repetitive, transposon-like IS1111 region (Vaidya et al., 2008). The PCR mixtures included 4 μL of 5 \times HOT FIREPol® Blend Master Mix (Solis BioDyne, Tartu, Estonia), 1 μL of 10 μM of each primer and 20 ng of template DNA. The volume was brought to 20 μL using nuclease-free water. The PCR amplifications were conducted in a ProFlex PCR systems thermocycler (Applied Biosystems, Foster City, CA, USA) using the following conditions: initial denaturation at 95°C for 15 minutes, followed by five cycles at 95°C for 30 s, with the temperature decreasing by 1°C in each consecutive step, ranging from 66 to 61°C , for 1 min, and finally 72°C for 1 min. This was then followed by 35 cycles at 95°C for 30 s, 61°C for 30 s and 72°C for 1 min, with a final extension step at 72°C for 10 min. *Coxiella burnetii* DNA from previous studies (Getange et al., 2021) was used as a positive control, while nuclease-free water served as the negative control. The successful amplification of the target PCR amplicon was determined by separating 5 μL of the PCR products by gel electrophoresis using 2% (w/v) ethidium bromide-stained agarose gels and visualized under ultraviolet light using MYECL Imager (Thermo Fisher Scientific, MA, USA). The size of the products was determined by comparing them to a GeneRuler 100 bp DNA ladder (Thermo Fisher Scientific).

Coxiella-like endosymbionts were detected using PCR-high-resolution melting (HRM) analysis Rick16S F (GAACGCTATCGGTATGCTTAACACA) and Rick16S R (CATCACTCACTCGGTATTGCTGGA) primers (Nijhof et al., 2007) following a previously described protocol (Mwamuye et al., 2017). The analysis was carried out in Quant Studio 3 Real-Time PCR System (Applied Biosystem, Foster City, CA, USA) thermocycler.

Positive *C. burnetii* and *Coxiella*-like endosymbiont PCR products were purified using ExoSAP-IT PCR Product Cleanup kit (Affymetrix, Santa Clara, CA, USA) and submitted to Macrogen (Amsterdam, The Netherlands) for Sanger sequencing. The resulting chromatograms were trimmed, edited and aligned to generate consensus sequences using Geneious Prime software v. 2020.2.2 (Biomatters; Auckland, New Zealand).

Any camel associated with one or more tick pools that tested positive for *C. burnetii* was considered a positive tick camel. If all tick pools associated with a camel tested negative for *C. burnetii*, this was considered a negative tick camel.

2.5 | Statistical analysis

Descriptive statistics were used to determine seroprevalence of *C. burnetii* stratified by age class, sex, herd, PCV, and TS. Univariate logistic regression was performed to evaluate potential associations between camel seropositivity and tick *C. burnetii* PCR positivity, as well as camel demographic and clinical variables. Body condition score was excluded from analysis because only two animals were classified as other than normal. Likewise, health status was excluded because the abnormal health conditions in the study population were varied, infrequent, and not plausibly associated with infection. Additional logistic regression analyses were conducted to determine associations between tick species and pool positivity for *C. burnetii* or endosymbionts. All statistics were performed using RStudio Version 2022.12.0 + 353 (RStudio Team 2022). A *p* value of ≤ 0.05 was considered significant for all analyses.

3 | RESULTS

3.1 | Camels

Complete datasets including biological information and PCV/TS were obtained for 233 camels. Two hundred fifty-one camels were initially included in this study, but 18 camels were excluded due to sample labelling errors. The measured variables from these camels were similar to those with complete datasets. Because of this similarity and because the missing data were considered 'missing completely at random' (MCAR), data from these 18 camels were excluded from analyses. Overall seroprevalence of *C. burnetii* was 52% (95% CI: 46–59). Seropositivity was significantly associated with the presence of *C. burnetii*-positive tick pools (OR: 2.58; 95%

CI: 1.4–5.1; $p=0.0045$). Increasing age class (adult: OR: 14.2; 95% CI: 6.9–31.3; subadult: OR: 3.4; 95% CI: 1.5–8.1; juvenile: reference category), and plasma total solids (OR: 2.0 per 0.5 mg/dL increase; 95% CI: 1.5–2.6) were significantly associated with seropositivity (Table 1).

3.2 | Semi-structured interview

All three herds reported use of topical tick acaricides at least once monthly, including the product Triatix® Stock Spray (CKL Africa Limited, Mashiara Park, Kaptagat Rd., Loresho, Kenya). One herd also reported using Norotraz (Bukoola Vet, 18 Nakivubo Rd, Kampala, Uganda) and Farmtraz® (Murphy Chemicals, Baba dogo Rd, Ruaraka, Kenya) as well. These three acaricides are all amitraz-based products. All herds reported that their camels browsed during the day and generally covered 2–4 km per day. Two of the herds reported that wildlife species, including African painted dogs (*Lycaon pictus*), lions (*Panthera leo*), leopards (*Panthera pardus pardus*), elephants (*Loxodonta africana*), zebras (*Equus* spp.), jackals (*Canis mesomelas*), hyenas (*Crocuta crocuta*), buffalo (*Syncerus caffer*), and birds, were frequently seen within 400 m of their camels.

3.3 | Ticks

A total of 4354 ticks, representing 3 genera and 9 species (Table 2), were collected from camels in this study. Between 2 and 69 ticks were collected on every camel, with a median of 13 ticks per camel (IQR 9–26). *Rhipicephalus pulchellus* represented 92% (3987/4354) of individual ticks collected. Ticks of the same species and from the same camel were pooled ($N=397$ pools), resulting in 1 to 66 ticks per pool. The overall PCR prevalence among the tick pools was 15% ($N=61/397$) for *C. burnetii* and 27% ($N=108/397$) for *Coxiella*-like endosymbionts and 4% ($N=15/397$) were positive for both *C. burnetii* and *Coxiella*-like endosymbionts (Table 3). Fifty-three per cent ($N=8$) of the tick pools that were positive for both *C. burnetii* and *Coxiella*-like endosymbionts were *Am. gemma* pools, despite this species representing only 12% (49/398) of total tick pools. The remaining pools were *Rh. evertsi* ($N=4$; 27%), *Rh. appendiculatus* ($N=1$; 7%), *Hy. marginatum* ($N=1$; 7%), and *Hy. truncatum* ($N=1$; 7%).

3.4 | Tick species association with *C. burnetii*-positive tick pools

Coxiella burnetii positivity in tick pools was significantly associated with tick species. *Coxiella burnetii* positivity was significantly more likely in *Rh. evertsi* (OR: 14.3; 95% CI: 5.3–43.0; $p<0.001$), *Rh. praetextatus* (OR: 15.8; 95% CI: 0.68–190; $p=0.03$), *Hy. marginatum* (OR: 8.9; 95% CI: 3.48–25.75; $p<0.001$), *Hy. truncatum* (OR: 17.81;

Demographic and clinical variables	Seronegative	Seropositive (%)	Odds ratio (95% CI)	p value
Total, N	111	122 (52)	–	–
Age				
Neonate/juvenile, N	55	12 (18)	Reference	–
Subadult, N	27	20 (43)	3.4 (1.5–8.1)	0.0049
Adult, N	29	90 (76)	14.2 (6.9–31.3)	<0.001
Sex				
Female, N	77	98 (56)	Reference	–
Male, N	34	24 (41)	0.55 (0.30–1.01)	0.055
Herd				
1, N	42	52 (55)	Reference	–
2, N	35	33 (49)	0.76 (0.41–1.4)	0.39
3, N	34	37 (52)	0.88 (0.47–1.6)	0.68
Packed cell volume, mean \pm SD ^a	26.7 \pm 3.5	26.9 \pm 4.2	1.1 ^b (0.76–1.5)	0.70
Total solids, mean \pm SD ^a	6.8 \pm 0.7	7.4 \pm 0.6	2.0 ^c (1.5–2.6)	<0.001

^aPCV and TS data available from 219 and 218 individuals, respectively.

^bOdds ratio per 5% increase in PCV.

^cOdds ratio per 0.5 mg/dL increase in TS.

TABLE 2 Summary of tick species identification (N=4354) collected from dromedary camels in Laikipia County, Kenya.

Genus	Species	N	%
<i>Rhipicephalus</i>		4099	94.2
	<i>pulchellus</i>	3987	91.6
	<i>appendiculatus</i>	5	0.1
	<i>evertsi</i>	102	2.3
	<i>decoratus</i>	1	<0.1
	<i>praetextatus</i>	4	0.1
<i>Hyalomma</i>	<i>dromedarii</i>	1	0.0
		153	3.5
	<i>marginatum</i>	116	2.7
	<i>truncatum</i>	34	0.8
<i>Amblyomma</i>	Unidentified	2	<0.1
		102	2.3
	<i>gemma</i>	101	2.3
	Unidentified	1	<0.1

95% CI: 5.74–59.49; $p=0.001$), and *Am. gemma* (OR: 12.67; 95% CI: 4.75–3.79; $p<0.001$), compared to the most sampled tick species, *Rh. pulchellus* (reference category). *Coxiella burnetii* positivity was not significantly different in the other tick species compared to *Rh. pulchellus*, although this may be attributable in part to low sample size (each with $N \leq 5$).

3.5 | Tick species association with endosymbiont-positive tick pools

Endosymbiont positivity in tick pools was also significantly associated with tick species. Endosymbiont positivity was significantly less

TABLE 1 Univariate logistic regressions assessing relationships between Kenyan dromedary camel (*Camelus dromedarius*) seropositivity for *Coxiella burnetii* antibodies and camel demographic and clinical variables.

likely in *Hy. marginatum* (OR: 0.15; 95% CI: 0.04–0.38; $p<0.001$) and *Hy. truncatum* (OR: 0.22; 95% CI: 0.04–0.79; $p=0.047$), but more likely in *Am. gemma* (OR: 2.1; 95% CI 1.1–3.98; $p=0.025$) compared to the most sampled species, *Rh. pulchellus* (reference category). Endosymbiont positivity was not significantly different in the other tick species compared to *Rh. pulchellus*.

4 | DISCUSSION

This study revealed a *C. burnetii* seroprevalence of 52% in the sampled dromedary camels across three herds in Laikipia County and found a *C. burnetii* PCR prevalence of 15% across tick pools collected from these camels. This seroprevalence and tick positivity are both markedly higher than previous reports in camels and other livestock in this part of Kenya (Table 4) (Browne et al., 2017; DePuy et al., 2014; Schelling et al., 2003). A previous study in Kenya reported a 5.5% overall PCR prevalence of *C. burnetii* in ticks collected from livestock; however, they reported that none of the tick pools collected from camels were positive (Koka et al., 2018). In our study, the significantly higher number of individual ticks collected from camels may have increased the opportunity to sample positive ticks compared with studies that collected fewer individual ticks from camels.

In this study, seropositivity was positively associated with increasing age class and increasing total solids. The odds of seropositivity in adult animals were 14.2 times higher and subadults were 3.4 times higher than the neonate/juvenile age class, which was the reference category. This finding is consistent in direction but greater in magnitude than the findings of a study in Laikipia County with odds of seropositivity 5.4 times higher in camels >2 years of age and 2.9 times higher in camels 6 months to 2 years old than in camels <6 months of age (Browne et al., 2017). Increasing age may provide

TABLE 3 PCR status of ticks collected from dromedary camels in Laikipia County, Kenya.

Tick genus	Tick pools, N	<i>Coxiella burnetii</i> +, N (%)	Endosymbiont +, N (%)	Both +, N (%)
<i>Rhipicephalus</i>	249	22 (9)	80 (32)	5 (2)
<i>Hyalomma</i>	99	25 (25)	6 (6)	2 (2)
<i>Amblyomma</i>	49	14 (29)	22 (45)	8 (16)
Total	397	61 (15)	108 (27)	15 (4)

TABLE 4 Summary of *Coxiella burnetii* seroprevalence studies in livestock species in Kenya.

	N tested	Seroprevalence (%)	Study
Camel	233	52	Present
	72	70	DePuy et al. (2014)
	334	19	Browne et al. (2017)
	312	20	Larson et al. (2019)
	142	80	Schelling et al. (2003)
Cattle	195	4	Schelling et al. (2003)
	113	2	DePuy et al. (2014)
Goat	134	13	Schelling et al. (2003)
	26	35	DePuy et al. (2014)
Sheep	142	11	Schelling et al. (2003)
	23	17	DePuy et al. (2014)

more opportunities for infection, whether that be through contact with ticks or with other animals. Additionally, camels acquire immunoglobulins from colostrum at birth, which may provide protection from some infections until around 6 months of age (Meyer et al., 2016); thus, camels that were exposed to *C. burnetii* in the first 6 months of life may not have seroconverted nor become infected due to maternal antibodies. Increased immunoglobulins in exposed camels may also explain the increased odds of seropositivity with an increase in total solids, a finding consistent with those of Browne et al. (2017).

Coxiella burnetii DNA was detected in eight of nine species of ticks, and 22% of all tick pools were PCR-positive for *C. burnetii*, which is dramatically higher than the majority of previous reports of tick pools collected from various species in Kenya. In western Kenya, tick pools collected from domestic livestock and dogs had a *C. burnetii* PCR prevalence of 2.5% (Knobel et al., 2013), and a previous study on tick pools collected from various wildlife species in Laikipia County had a *C. burnetii* PCR prevalence of 2.92% (Ndeereh et al., 2017). As in the present study, a study in Kenya found that *Rhipicephalus* was the most common tick genus collected from wildlife hosts; however, these authors also found that *Rhipicephalus* was the only genera to test positive for *C. burnetii* at an individual prevalence of 0.54% (Ndeereh et al., 2017). A *C. burnetii* prevalence of 2.5% in pooled *Amblyomma* spp. ticks collected from cattle in Kenya was previously reported (Knobel et al., 2013). Our study collected ticks only from camels, and the significantly higher *C. burnetii* prevalence that we detected compared with previous studies of wildlife and cattle in Kenya suggests that ticks may be acquiring the bacterium from the camels.

Importantly, camels were 2.5 times more likely to be seropositive if a tick pool collected from them was PCR-positive for *C. burnetii*. Although directionality of infection cannot be stated based on these findings, the results do suggest that ticks in this region play a role in Q fever epidemiology. Extensive farming strategies involving livestock browsing may facilitate ectoparasite transmission between wildlife and livestock and thus transmission of pathogens such as *C. burnetii*. While many studies have tested ticks from livestock for *C. burnetii* (Browne et al., 2017; DePuy et al., 2014; Koka et al., 2018; Larson et al., 2019; Schelling et al., 2003), few have tested ticks from wildlife (Ndeereh et al., 2017). Future studies evaluating the prevalence of *C. burnetii* in ticks from sympatric wildlife are warranted.

Endosymbiotic *Coxiella* bacteria are genetically related yet ecologically distinct organisms from *C. burnetii* (Duron, 2015; Duron et al., 2015). Endosymbionts are transmitted vertically between ticks and may have a symbiotic relationship with tick hosts (Duron, 2015; Duron, Noël, et al., 2015). Commonly employed diagnostics for *C. burnetii* may not be specific to *C. burnetii* and thus risk misidentifying endosymbionts as *C. burnetii* and over-reporting *C. burnetii* prevalence (Duron, Sidi-Boumedine, et al., 2015; Pearson et al., 2016). Previous studies in Kenya have documented *C. burnetii* and endosymbionts in ticks collected from camels (Getange et al., 2021) and other livestock (Oundo et al., 2020). Though a recent metagenomic study reported that 46% of ticks collected from Kenyan wildlife had *C. burnetii* DNA (Ergunay et al., 2022), it is unclear whether some of the sequences scored were of the highly similar *Coxiella*-like endosymbionts. In the present study, endosymbionts were detected in all tick species besides *Hy. dromedarii*, of which there was a very low sample size (a single pool). The significance of these endosymbionts is unclear and warrants further investigation (Getange et al., 2021).

The results from our interview indicate that herders are aware of tickborne disease and attempt to mitigate disease transmission through use of topical acaricides on livestock. Without a control group, it is impossible to comment upon the efficacy of these acaricides. However, there is an abundance of literature pertaining to acaricide ineffectiveness and ectoparasite resistance in Africa (Klafke et al., 2018; Mutavi et al., 2021), which may be due to sub-therapeutic dosing (leading to acquired resistance) and/or inherent ectoparasite resistance. A previous study evaluated the types of acaricides and herders' application practices in Laikipia County (Mutavi et al., 2021). The authors concluded that a lack of technical understanding of the acaricides' mechanisms led to product misuse; they documented improper dilutions of acaricide and proposed that dilute formulations may not be lethal to the parasites,

thus producing resistance (Mutavi et al., 2021). In our study, the different herds' dilution practices and application schedules were not evaluated, but it is possible that lack of adherence to the manufacturer's usage protocols (i.e., underdosing) and/or acquired resistance to amitraz-based products due to historic, widespread misuse of these products, is reducing the efficacy of these products. As mentioned, resistance to even correctly dosed amitraz has been documented in multiple species of *Rhipicephalus* ticks (including *Rh. pulchellus*, which accounted for over 90% of the individual ticks in the present study) (Klafke et al., 2018). Four molecular mechanisms have been proposed to explain inherent ectoparasite resistance (Klafke et al., 2018) so it is possible that even if acaricide protocols were followed perfectly, a degree of inherent parasite resistance may exist, rendering the use of amitraz-based products futile.

Camel populations continue to grow globally; according to the Food and Agriculture Organization of the United Nations, the world's dromedary camel population grew by nearly 150% over the past two decades from approximately 23.6 million animals in 2003 to 35.5 million animals in 2018 (FAO, 2020). In Kenya specifically, the population grew from 895,000 animals in 2003 to 3.3 million animals in 2018, making Kenya home to the third largest population of dromedaries in Africa behind Somalia and Sudan (FAO, 2020). Given climatological changes across the Horn of Africa, it is likely that camels will become an increasingly attractive species for livestock herders (Deem, 2019; Lawrence et al., 2023).

Similar to findings in Middle East respiratory syndrome-related coronavirus (MERS-CoV), previous studies in Africa have documented that camel breeders are more likely to be exposed to *C. burnetii* than cattle breeders or non-camel breeders (Browne et al., 2017; Gossner et al., 2016; Schelling et al., 2003; Sikkema et al., 2017; Vanderburg et al., 2014; Wardrop et al., 2016). Those in close contact with camels are not the only people at risk of contracting Q fever, however, as an estimated 10% of Kenyans consume unpasteurized camel milk daily (Browne et al., 2017; Kaindi et al., 2011), which is a known route of human *C. burnetii* infection (Centers for Disease Control and Prevention, 2019; Pexara et al., 2018; Raoult et al., 2000; Signs et al., 2012; Tisson-Dupont & Raoult, 2008). *C. burnetii* is the most heat-resistant organism found in raw milk and thus sets the standard for milk pasteurization time and temperature (Cerf & Condron, 2006; Holsinger et al., 1997); it follows that those consuming unpasteurized milk are at increased risk of Q fever.

Q fever has been proposed as an underreported infection that may be a significant source of febrile illness in Kenya (Koka et al., 2018). Since 2000, the Rift Valley region has experienced two reported outbreaks of Q fever in humans, affecting a total of 81 individuals and resulting in six deaths (Kaindi et al., 2011). Malaria is often presumptively over-diagnosed as the cause of febrile illness in Africa, and recent efforts to accurately characterize acute febrile illness have prompted increasing interest in Q fever as an important differential diagnosis (Vanderburg et al., 2014). Multiple systematic reviews on Q fever prevalence in humans in Africa

demonstrated overall seroprevalences ranging from 2.5% to 26% (Knobel et al., 2013; Koka et al., 2018; Njeru et al., 2016). While Q fever is poorly understood and likely underdiagnosed, especially in rural locations in Africa, it poses a significant risk to human health, underscoring the importance of ongoing surveillance and epidemiologic research relating to *C. burnetii* and other camel-borne pathogens (Frean & Blumberg, 2007).

As the global camel population is growing, regions with high density of camels as a livestock species are considered hot spots for potential zoonotic disease emergence (Watson et al., 2016; Zhu et al., 2019). Besides *C. burnetii*, camels are known to serve as reservoirs of several diseases to humans: MERS (Middle Eastern respiratory syndrome virus), brucellosis, echinococcosis, Rift Valley fever, plague (*Yersinia pestis*) and Crimean-Congo haemorrhagic fever, to name a few (Zhu et al., 2019; Deem et al., 2015). Infectious disease accounts for roughly one-third of the most common causes of human morbidity and mortality, and zoonotic organisms are twice as likely to be associated with EIDs than non-zoonoses (Taylor et al., 2001). The pervasiveness of zoonotic EIDs of wildlife origin underscores the need to elucidate risk factors that facilitate disease spillover from wildlife to humans (Jones et al., 2008); livestock that share habitat with wildlife, such as semi-free-ranging camels, are one such avenue for disease spread that warrants further attention. Given that camels are a potential source and amplifier of zoonotic and vector-borne disease, and the significant increase in their importance as food animals due to climate change, they represent a livestock species that should be monitored closely with careful attention to the handling process relating to milk and meat (Deem, 2019; Zhu et al., 2019).

Coxiella burnetii also has potential conservation impacts in the wildlife setting and for wildlife under human care. Q fever has been reported in numerous animals in zoological collections, leading to abortions, stillbirths, and poor-doer young. Pathology has been attributed to Q fever in captive white rhinoceros (*Ceratotherium simum*), South American fur seals (*Arctocephalus australis*), South American sea lions (*Otaria byronia*), Cuvier's gazelle (*Gazella cuvieri*), greater kudu (*Tragelaphus strepsiceros*), and psittacines, and in one retrospective study, *C. burnetii* DNA was detected in placentas from 32 zoo-housed ungulate species (Bercier et al., 2018; Garner et al., 2007; Jurczynski & Flügger, 2005; Stalis & Rideout, 1996; Winkel et al., 2008). It has been proposed that Q fever may go undiagnosed as a cause for reproductive disease and failure in wildlife (Stalis & Rideout, 1996). The suggested underdiagnosis of this disease in both humans and endangered species demands attention.

Several limitations are to be noted in this study. Host exposure to *C. burnetii* was evaluated based on seroconversion, but it may take 7–15 days for camels to mount an antibody response to an acute infection (Ndeereh et al., 2017). As previously mentioned, young animals may have been exposed to *C. burnetii* when maternal antibodies were still conferring a protective effect and thus may not have seroconverted despite exposure; conversely, maternal antibodies could be detected in neonates, rendering false positives for seropositivity in this age class. Thus, assessing seroconversion as a measure of

exposure may inherently lead to underreporting if camels had either been recently infected or exposed to *C. burnetii* at a young age, respectively. Further, camels in this study were assessed for antibody response but not antigen presence, so active infection could not be confirmed. Tick burden was not quantified in this study, so it is not possible to comment on a potential association between severity of tick burden and seroconversion in these camels. A previous study did document an association between tick burden and seroconversion in camels, so tick burden is considered worthy of inclusion as a variable in future studies (Hussain et al., 2022). Finally, ticks were collected only for the duration of blood sampling. This non-standardized approach to tick collection may have led to error; for camels with a particularly high tick burden, the proportion of collected ticks may have been lower, making this group at high risk of misclassification. In other words, some camels that had uncollected *C. burnetii* positive ticks may have been classified as not having any positive tick pools. Because camel serostatus would not affect whether positive ticks went undetected, the estimated association between serostatus and tick positivity should be unaffected, although with less precision than ideal.

This study highlights several areas where continued research is indicated, including transmission studies to determine the directionality of *C. burnetii* infection, possibly using in vivo experimental settings (i.e., camel to tick, vice versa or both) and antigen testing in camels that have seroconverted for *C. burnetii*. A better understanding of the pathogenicity of endosymbionts and their relationship or lack thereof to *C. burnetii* is needed. Clinical trials to assess the effectiveness of different tick preventive measures (i.e., acaricides) for livestock and personal protective equipment for those in close contact with potentially infected camels would also be of benefit.

5 | CONCLUSIONS

The data presented in this study suggest that ticks and camels may play an important role in the epidemiology of Q fever in Laikipia County, Kenya. The transmission pathway and associated infection rates between ticks and camels warrant further exploration, and tick prevention efforts in livestock should be a priority for Q fever mitigation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in 'Datacat' at [10.17638/datacat.liverpool.ac.uk/2F2269](https://datacat.liverpool.ac.uk/2F2269), reference number 2629.

ETHICS STATEMENT


Approval for animal sampling was obtained through the International Livestock Research Institute's Institutional Animal Care and Use Committee (IACUC reference number 2015.01). Approval for the interview was obtained through Tufts' Social, Behavioral & Educational Research Institutional Review Board and was granted 'Exempt' status (IRB Study #1706001). Two separate informed consent documents, written in English and translated verbally into Kiswahili, were signed prior to camel sampling and interviews.

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