Evaluation of *Campylobacter* at the human-wildlife interface: urbanization and *C. jejuni* infection dynamics in wildlife

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Evaluation of *Campylobacter* at the human-wildlife interface: urbanization, life-history traits and infection dynamics in wildlife

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ABSTRACT

Campylobacter spp. infections are an increasing global concern responsible for a significant burden of disease every year. Wildlife and domestic animals are considered important reservoirs, but little is known about host-factors driving pathogen infection dynamics in wild mammal populations. In countries like Botswana, there is significant spatial overlap between humans and wildlife with a large proportion of the population vulnerable to *Campylobacter* infection, making Botswana an ideal location to study these interactions. This thesis reviews mammalian wildlife species that have been identified as carriers of *Campylobacter* spp., identifies life-history traits (urban association, trophic level, and sociality) that may be driving *Campylobacter* infection, and utilizes banded mongoose (*Mungos mungo*) (n=201) as a study species to illuminate potential *Campylobacter* spp. transmission at the human-wildlife interface in northern Botswana. Results of the latter study suggest that human-landscapes are critical to *C. jejuni* infection in banded mongooses, as mongooses utilizing man-made structures as dens had significantly higher levels of *C. jejuni* than mongooses using natural dens (p=0.019). A similar association was found across all wild mammals with significantly greater number of urban dwelling species positive for *C. jejuni* than urban avoiders (p = 0.04). Omnivorous and social mammals were significantly associated with *C. coli* presence (p=0.04 and p<0.00 respectively), but not with *C. jejuni* indicating there may be important differences in transmission dynamics between *Campylobacter* species. These results suggest that landscape features and life-history traits can have important influences on *Campylobacter* species exposure and transmission dynamics in wildlife.

Evaluation of *Campylobacter* at the human-wildlife interface: urbanization, life-history traits and infection dynamics in wildlife

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ABSTRACT (PUBLIC)

Campylobacter infections are increasing worldwide but we still know little about the true burden of disease in the developing world, and even less about the role of wildlife and environmental reservoirs in human exposure and disease. I reviewed life-history traits (urban association, animal rank on the food chain, and sociality) that might be driving *Campylobacter* spp. infection in wildlife and investigated interactions between an urbanizing wildlife species, banded mongoose (*Mungos mungo*), humans, and the environment. Banded mongooses live in close association with humans and infections with *C. jejuni* were greater among mongooses utilizing man-made structures compared to those using natural dens. Across all wild mammal species tested for *Campylobacter* spp., mammals associated with urban living were significantly more likely to be positive for *C. jejuni* than mammals that avoid urban areas. Lowerranking mammals on the food chain and social mammals were associated with presence of *C. coli*, suggesting life-history rates are playing a role in wild mammal exposures to the pathogen and that these exposures are different for *C. coli* than *C. jejuni*. These data suggest that wildlife life-history traits and utilization of human landscapes are important for pathogen presence. In turn, pathogen circulation and transmission in urbanizing wildlife reservoirs may increase human vulnerability to disease, particularly in impoverished populations, where greater environmental exposures are expected. Improvement of waste management and hygiene practices may help reduce transmission between wildlife and humans.

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Attribution

Anthropogenic landscapes associated with *Campylobacter jejuni* infections in urbanizing banded mongoose (*Mungos mungo*): A One Health approach

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Review and metadata analysis: *Campylobacter* in aquatic and terrestrial mammalian wildlife

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Introduction

Epidemiology of Campylobacter spp.

Campylobacter is a diverse genus of zoonotic gastrointestinal pathogens that are among the leading causes of diarrhea-associated death in children [1]. Transmission dynamics are variable and complex with disease patterns varying between rural and urban communities [2] and between developed and developing countries [3]. Where *Campylobacter* spp. are endemic, humans may be able to acquire immunity making it difficult to determine the true pathogen exposure and evaluate the risks of infection [4]. Risk factors for contracting campylobacterosis are associated with environmental exposures, including animal contact, contaminated food and drinking water and access to sanitation [5, 6]. Officials in developing countries often lack knowledge of *Campylobacter* prevalence in livestock, domestic animals and wildlife and may not be able to accurately predict and manage the potential for zoonotic transmission [7]. Considering an increasing trend in global *Campylobacter* incidence and prevalence [8], identifying important reservoirs and patterns of disease is critical to understanding how to reduce transmission.

Host-factors affecting disease transmission in wildlife

Wildlife are generally considered reservoirs or amplifying hosts of *Campylobacter* spp. because wildlife can contaminate the environment or food chain resulting in an increased risk of human infection [9]. This is more complex than detection of the pathogen alone as there are host-specific and generalist *Campylobacter* strains. Generalist *Campylobacter* spp. strains are highly transmittable strains that are capable of infecting a wide variety of hosts where as host-specific strains are primarily found in one group of host species [10]. This is most pronounced in *C.*

jejuni which has distinct generalist lineages that have increased recombination with diverse sources, including host-specific lineages and other *Campylobacter* species, and are capable of colonizing multiple hosts [11]. This evolutionary change in *Campylobacter* spp. to adopt a more "generalist" lifestyle may be a result of increasing *Campylobacter* spp. niche convergence as a result of human disturbances on the landscape [12]. As stable ecological communities are disrupted through urbanization, clear-cut forestry, intensive farming, or surface mining, novel adaptive landscapes are formed that provide opportunities for environmental niches to collide and hybrid species to evolve [13, 14]. The large effective population size of *Campylobacter* and its ability to routinely exchange genes across species allows this pathogen to adapt rapidly to changes in selection pressure that may be occurring from human disturbance [15]. Human disturbance can also change microbial communities in wildlife species. Wildlife at the human-wildlife interface may be more vulnerable to carrying human gastrointestinal pathogens than their counterparts living in their natural habitat [16], putting wildlife at the urban-interface not only at risk of contracting *Campylobacter* spp. but other pathogens as well.

Host-factors likely influence whether *Campylobacter* spp. is transmitted to wildlife species through the food chain or environmental sources. Behaviors driving space use, habitat choice, contact rates and host aggregation are important factors influencing direct and environmental pathogen transmission [17]. Wildlife that utilize urban landscapes may be more at risk of contracting disease due to changes in diet, nutrition, host-pathogen dynamics, and stress-mediated immunosuppression [18]. Multi-host pathogens, such as *Campylobacter* spp., are particularly subject to changes in transmission dynamics that can increase prevalence in urban landscapes [19]. Urban landscapes can increase interspecific contact rates, a key component determining multi-host pathogen transmission [20]. Trophic level and food sources are also

important to pathogen transmission because they can affect exposure risks during foraging [21]. For example, ground-foraging, aquatic feeding, and opportunistic bird species had a higher prevalence of *Campylobacter* spp. than arboreal and herbaceous plant-foraging bird species [22]. These host-factors not only drive *Campylobacter* spp. transmission to wildlife, but also can influence transmission to the human-food chain or domestic animals.

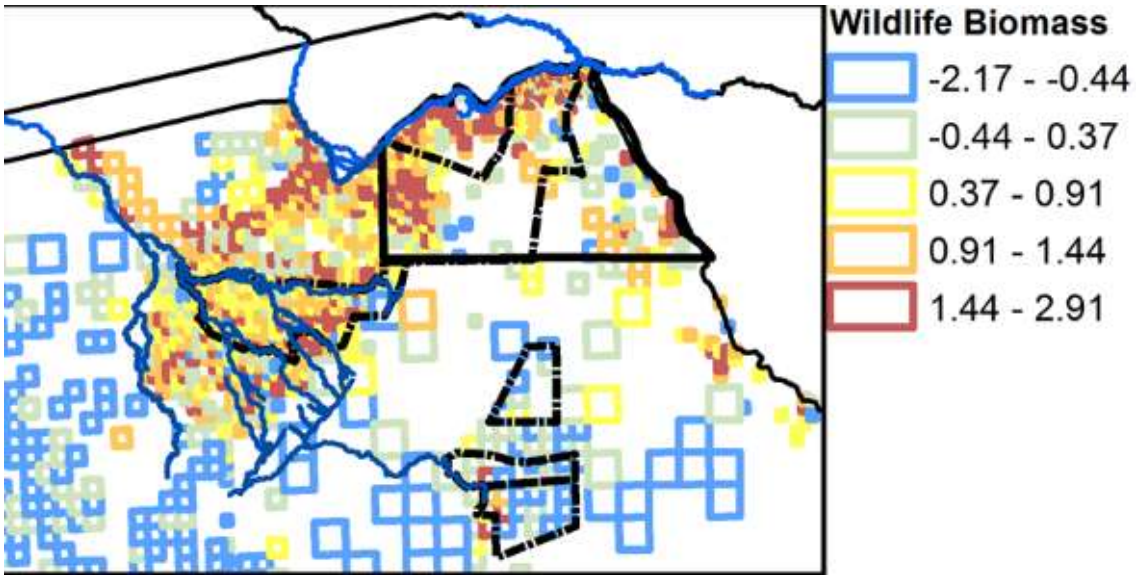

Figure 1. Dry season aerial survey data for northern Botswana from 2012 showing log wildlife biomass (kg/km^2). This shows high wildlife densities in Chobe District (outlined in black) along permanent water sources (solid blue lines) (Figure published in [23]).

Northern Botswana as a model system for wildlife human-health interactions

Botswana provides an ideal model system to evaluate *Campylobacter* spp. transmission at the human-wildlife interface. Diverse *C. jejuni* strains characterized in poultry and clinical cases of campylobacterosis in Botswana suggest that foodborne transmission is not the only factor influencing *Campylobacter* transmission dynamics [24]. Wildlife populations may play an important role in human disease exposures, as wildlife densities near human communities can be

high, especially around limited water resources where wildlife aggregate during the dry season (Figure 1) [23]. Wildlife often compete with humans and livestock for access to these water resources.

In northern Botswana, the Chobe District has one of three permanent water sources in this semi-arid country, and the Chobe River is a shared resource where there is considerable human-wildlife interaction. Spatial overlap between humans and wildlife can increase the transmission of microbes and pathogens [16]. Banded mongoose (*Mungos mungo*) is one species of wildlife that live across anthropogenic and natural land use areas and can provide an important surveillance system for disease transmission dynamics in human-modified landscapes [25]. *E. coli* and multi-drug resistant (MDR) *E. coli* previously have been used to evaluate the transmission of microbes at the human-wildlife interface in this system and suggest that environment-mediated microbial exchange is occurring between wildlife and humans [25, 26]. This transmission can have critical implications for public health when zoonotic diseases are transferred across the human-wildlife interface.

Despite access to improved drinking water sources, seasonal diarrheal disease is a persistent problem in the Chobe District [27]. Outbreaks are influenced by the high prevalence of HIV/AIDS in the region, poor sanitation, nutritional deficiencies, and environmental drivers [28, 29]. Viruses, pathogenic bacteria and parasites are all likely causes of diarrheal disease cases, although rotavirus vaccine (RV1) was introduced in Botswana in 2012 and has led to a 54% reduction of rotavirus-associated hospitalizations [30]. *Cryptosporidium* spp., a common cause of diarrheal disease in developing countries, were identified only once in stool samples analyzed at the hospital serving the Chobe District from August 2007 to October 2011 [27]. Diarrheal disease outbreaks occur primarily during the rainy season (January-March) and during the dry

season (July-October), with several cases leading to mortality every year [27]. Chronic diarrheal disease coupled with complex environmental interactions between humans and wildlife provides an opportunity to explore *Campylobacter* spp. prevalence in humans, wildlife and the environment in northern Botswana in this thesis

In Chapter 1, a One Health approach is used to illuminate potential *Campylobacter* spp. transmission at the human-wildlife interface. Banded mongoose were used as an urbanizing wildlife study species and were analyzed in conjunction with human and environmental (water and sediment) samples. In Chapter 2, I review broad-scale host-factors that can potentially influence *Campylobacter* spp. infection in mammalian wildlife and identify the most critical wildlife species relevant human disease transmission. These two chapters will collectively add to our knowledge of *Campylobacter* spp. in wildlife and in human communities in northern Botswana, a region lacking in information on *Campylobacter* spp. prevalence and transmission dynamics.

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Anthropogenic landscapes associated with *Campylobacter jejuni* infections in urbanizing banded mongoose (*Mungos mungo*): A One Health approach

Abstract

Campylobacter is a common, but neglected foodborne-zoonotic pathogen, identified as a growing cause of disease worldwide. Wildlife and domestic animals are considered important reservoirs, but little is known about pathogen infection dynamics in wildlife populations in sub-Saharan Africa. In countries like Botswana, there is significant overlap between humans and wildlife, with the human population having one of the highest HIV infection rates in the world, increasing vulnerability to infection. We investigated *Campylobacter* occurrence in archived human fecal samples (children and adults, n=122) from 2011, and free-ranging banded mongoose feces (*Mungos mungo*, n= 201), surface water samples (n=70), and river sediments (n=81) collected in 2017 from the Chobe District, northern Botswana. *Campylobacter* spp. was widespread in humans (23.0%, 95% CI 13.9-35.4%), with infections dominantly associated with *C. jejuni* (82.1%, n=28, 95% CI 55.1-94.5%). A small number of patients presented with asymptomatic infections (n=6). While C*ampylobacter* spp. was rare or absent in environmental samples, over half of sampled mongooses tested positive (56%, 95% CI 45.6-65.4%). Across the urban-wilderness continuum, we found significant differences in *Campylobacter* spp. detection associated with the type of den used by study mongooses. Mongooses utilizing man-made structures as den sites had significantly higher levels of *C. jejuni* infection (p=0.019) than mongooses using natural dens. Conversely, mongooses using natural dens had overall higher levels of detection of *Campylobacter* at the genus level (p=0.001). These results suggest that landscape features may have important influences on *Campylobacter* species exposure and transmission dynamics in wildlife. In particular, data suggest that human-modified landscapes may increase C. *jejuni* infection, a primarily human pathogen, in banded mongooses. Pathogen

circulation and transmission in urbanizing wildlife reservoirs may increase human vulnerability to infection, findings that may have critical implications for both public and animal health in regions where people live in close proximity to wildlife.

Introduction

Campylobacter spp. are considered the most common cause of foodborne infections globally, causing an estimated 96 million (95% CI 52–177 million) cases of diarrheal illness annually [1]. The true burden of infection remains uncertain in many developing countries [2, 3], as is the role of wildlife and environmental reservoirs in transmission [4]. Human illnesses are predominantly associated with *C. jejuni*; however, other species of *Campylobacter* of clinical significance are emerging [5]. Differences identified in clinical presentation and serotype distribution indicate that reservoirs and patterns of illness differ at both the local and regional scales [6]. Risk factors for contracting campylobacterosis in developing countries are associated with environmental exposures, including animal contact, contaminated food, contaminated drinking water, and poor sanitation [7, 8]. Zoonotic transmission of *Campylobacter* is thought to occur predominantly from contact with infected livestock and poultry [9]. Wildlife also can act as reservoirs or amplifying hosts, increasing the number of exposure pathways for *Campylobacter* [10]. The incidence and prevalence of *Campylobacter* infections in humans appears to be growing in both developing and developed countries [4]. Across many countries in sub-Saharan Africa, *Campylobacter* is considered to be endemic with both symptomatic and asymptomatic infections a common occurrence [11, 12].

Genetic evidence suggests that the dominant *Campylobacter* strains circulating are generalists, capable of colonizing both animals and humans, but rarer strains may exist that are adapted to

only a single host species [13]. At the human-wildlife interface, where wildlife diversity and density is high, wildlife reservoirs may play a crucial role in pathogen transmission to domestic animals and humans, but our understanding of this linkage is limited [14, 15]. The few studies that have been conducted in sub-Saharan African focused on bushmeat [16], mammals on game farms [17], and avian species [18]. Detailed studies of *Campylobacter* in free-ranging wildlife are lacking.

Persistence of *Campylobacter spp*. in the environment in soils and water, also may play a key role in pathogen exposure and transmission to humans. *Campylobacter* can persist through incorporation into biofilms as well as entry into a physiological state referred to as viable but nonculturable (VBNC) in which metabolic activity and infectivity are maintained [9, 19]. Strains vary in their ability to survive in the environment with certain strains exhibiting aerotolerance, acid tolerance, and starvation survival adaptations [20]. Viable *Campylobacter* also can extend their survival by infecting amoebas and protozoan species, which then may act as both a reservoir and vector for infection [21]. Our limited understanding of pathogen exposure and transmission dynamics at the human-animal-environmental interface has challenged development of appropriate public and animal health intervention strategies. Hence, there is an urgent need to improve our understanding of environmental and animal reservoir dynamics and exposure and transmission pathways, particularly in regions where HIV/AIDS may increase population vulnerability to infection [22].

In northern Botswana, diarrheal disease is a persistent health challenge affecting adults and children alike with the causative agent in most cases remaining unidentified [23]. At the same time HIV/AIDS infection levels are among the highest in the world [24]. Studies previously conducted in Botswana found that *C. jejuni* isolates collected from free-ranging chickens and

commercial broiler chickens were closely related to isolates obtained from humans [25]. However, *C. jejuni* diversity, especially the presence of strains seen in other African countries and Europe indicates that food alone is not the only factor involved in transmission. Here, we take a One Health approach to evaluate the potential role of wildlife and land use in exposure and transmission and assess pathogen presence in humans, free ranging banded mongoose (*Mungos mungo*), surface water and river sediments. Banded mongooses are group living, territorial species that occur across a gradient of anthropogenic land transformation. Here, we report widespread occurrence of *Campylobacter* spp. in humans and wildlife and identify the importance of anthropogenic influences on *Campylobacter* species distribution.

Methods

Study Site

This study was conducted in our long-term study site in northern Botswana along the Chobe River (Fig 1). Chobe National Park is the predominant land area in the district where most of the human population lives in the urban center of Kasane (population 9,008) and the town of Kazungula (population 4,133) [26]. Economic growth is primarily driven by tourism linked to the rich diversity of wildlife resources found in the region. Many tourist lodges surrounding the park concentrate garbage at central non-animal-proof waste storage sites before periodic disposal at the Kasane landfill. There are no commercial chicken or livestock production systems, although many people keep free-range chickens. The Chobe River supplies domestic water needs with two conventional water treatment plants treating and distributing the water supply to indoor and outdoor household and public taps [27]. Medical services are subsidized by the government, charging citizens only a small fee for health services. There is one laboratory located at the

primary hospital in Kasane that analyzes samples collected from health facilities across the District.

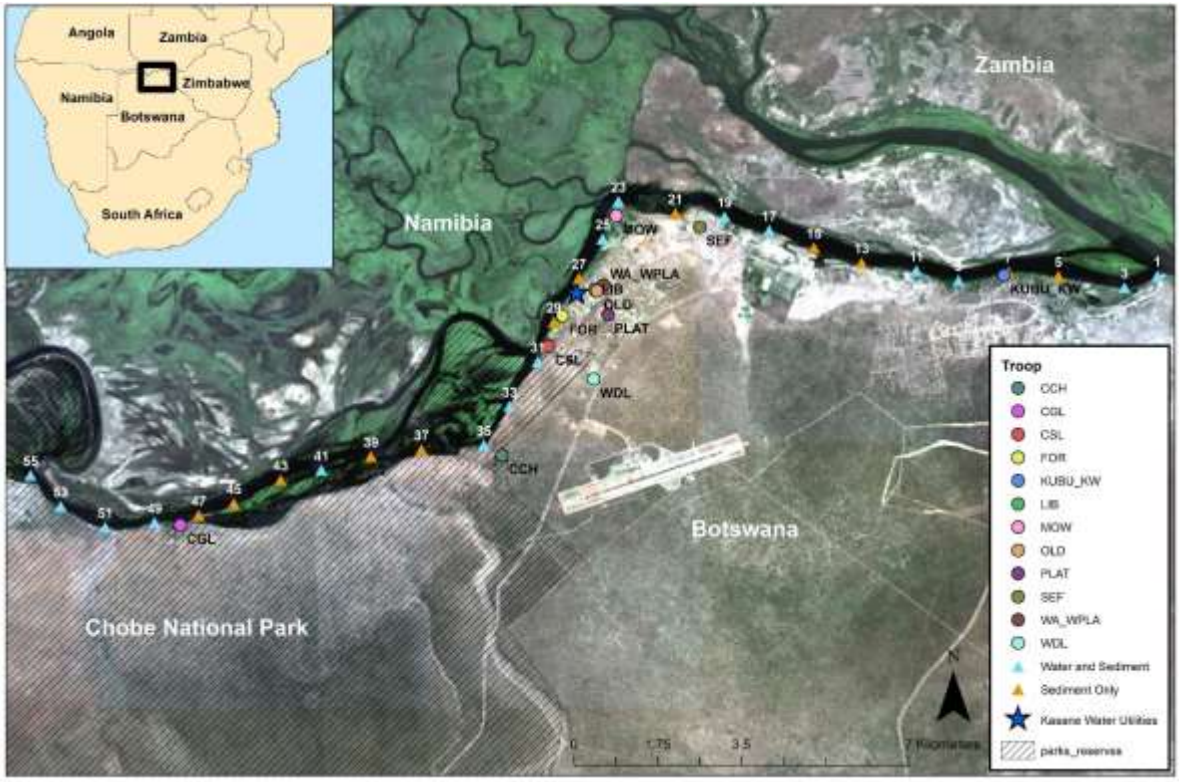

Figure 1. Water and sediment sample locations along the Chobe River and mongoose troop fecal sample locations in Chobe District, northern Botswana

Satellite imagery from 2013 Landsat 8 Operational Land Imager, data available from the U.S. Geological Survey (https://earthexplorer.usgs.gov/)

Sample collection and screening

Human

Archived human stool samples originating from both healthy (from mandatory employment health certifications) and clinically ill patients were collected from District health facilities from August 2011-January 2012. Samples were classified as wet season if they were collected from

November-March and dry season if they were collected from April-October Where available, patient demographic data were collected including date, age, sex, reason for testing, and any positive bacterial culture or virus testing results. Samples were collected and stored at -20 °C until transfer to -80 °C for long-term storage until required for DNA extraction and analysis.

Banded mongoose

Banded mongooses are small diurnal, fossorial carnivores that eat primarily invertebrates and small vertebrates, but are opportunistic and are known to forage on human garbage [28]. They are highly social and live in troops of 5 to 65 individuals. We regularly monitor 12 troops using radio collars [29]. Banded mongooses use communal latrines or defecation sites, providing an opportunity to sample individuals of the troop without duplication. Fecal samples were collected from the 12 study troops from July to August 2017 and January 2019. Briefly, troops were tracked to their denning site the evening prior to fecal collection using radio collars [29]. Fecal samples were collected after the mongooses had used the latrine and vacated the area. A sterile surgical blade was used to sample from the center of the fecal bolus which was transferred into a sterilized 1.5 mL Eppendorf tube and placed on ice for transport back to the laboratory and immediate DNA extraction.

Mongoose troop home ranges occurred across multiple land use types (lodge, national park, residential, undeveloped and urban). Troop land type was identified as the land type predominantly used by the troop over a long-term observation period (2012-2018). These data also were used to calculate the proportion of nights that troops were observed in natural (Fig 2A) or anthropogenic (Fig 2B) dens. Den data were classified into 4 categories, 1 being lowest proportion of nights in anthropogenic dens and 4 being highest proportion based on quantiles.

Figure 2. Banded mongooses at natural and anthropogenic dens

(A) Banded mongoose emerging from scrap pile (anthropogenic den) Photo credit: Dr. Peter Laver. (B) Banded mongooses at termite mound (natural den) Photo credit: Dr. Claire Sanderson.

Water and sediment samples

Water samples were collected and processed using hollow-fiber ultrafiltration as previously published [30]. Hollow-fiber ultrafiltration allows for the simultaneous concentration of bacteria, viruses and parasites from large volumes of water down to approximately 250 mL. From July 2017-August 2017, water (30 L, *n*=70) and sediment samples (*n*=81) were collected per day from 16 locations along the Chobe River. For each sampling event, three to five samples were collected a day over a 4-day period with a total of four sampling events. Samples were collected in 5-gallon (18.93 L) collapsible carboys rinsed with 10% bleach and then distilled water at least 12 hours before sample collection. Once collected, water samples were stored on ice or cold

packs and processed within 24 hours. Sediment samples were collected in a 50-mL tube at each of the 16 locations during the same week. Environmental samples were kept on cold packs until stored at -20°C until further processed. The final volume of retentate was aliquoted into 50-mL tubes and stored at -20˚C until DNA extraction. A negative filtration control with distilled water was filtered and treated the same as samples.

DNA Extraction

Fecal and sediment samples were extracted using the PowerSoil DNA Isolation Kit (Qiagen Inc., Germantown, MD) following a bead beating step and normal manufacturer-recommended protocols. Retentate obtained from water samples was thawed in cool water for 2-3 hours after which 10-mL aliquots were centrifuged and the pellet resuspended in 800 uL of lysis buffer. DNA was then extracted using the PureLinkTM Microbiome DNA Extraction Kit (#A29790, Life Technologies, Carlsbad, CA) following the manufacturer's soil protocol.

Detection of *Campylobacter* spp.

The DNA extracts were screened for *Campylobacter* spp. using polymerase chain reaction (PCR) and genus level primers that targeted the 16s rRNA gene (Table 1 [31]). Briefly, the PCR contained 0.5 µM each primer, 1 x HotstarTaq Master Mix (Qiagen, Germantown, MD), 1 µL template, and molecular grade water to reach a 20 µL reaction. All PCR reactions were conducted on a MyCycler™ thermocycler (Bio-Rad, Hercules, CA). Cycling conditions were set at 95 °C for 5 minutes for initial denaturation, 95 °C for 30 seconds, primer annealing at 56 °C for 30 seconds, and extension at 72 °C for 30 seconds for 35 cycles, with a final extension for 4 minutes [32]. Laboratory-synthesized fragments (gBlocks®, Integrated DNA Technologies Inc., Coralville, IA) containing the same fragment amplified by the primer pairs as a positive control

and water as a negative control were run with each round of PCR. PCR products were visualized on a 1 % (w/v) agarose gel stained with ethidium bromide.

Table 1. Target genes for PCR amplification

Species	Target gene	Size (bp)	Primer	Sequence	Primer annealing temp (˚C)	Reference
Campylobacter Genus	16S rRNA	816	C412F	GGATGACACTTTTCGGAGC	56	[31]
			C1228R	CATTGTAGCACGTGTGTC		
C. jejuni	cj0414	161	C-1	CAAATAAAGTTAGAGGTAGAATGT	58	[33]
			C-3	CCATAAGCACTAGCTAGCTGAT		
C. coli	ask	502	CC18F	GGTATGATTTCTACAAGCGAG	56	[34]*
			CC519R	ATAAAAGACTATCGTCGCGTG		
C. lari	glyA	251	CLF	TAGAGAGATAGCAAAAGAGA	53	[35]
			CLR	TACACATAATAATCCCACCC		
C. fetus	cstA	764	MG3F	GGTAGCCGCAGCTGCTAAGAT	60	[36]
			MG4R	TAGCTACAATAACGACAACT		
C. hyointestinalis	23S rRNA	611	HY01F	ATAATCTAGGTGAGAATCCTAG	53	[37]
			HYOFET23SR	GCTTCGCATAGCTAACAT		

C. upsaliensis	glyA	204	CUF	AATTGAAACTC TTGCTATCC	51	[35]
			CUR	TCATACATTTTA CCCGAGCT		
C. ureolyticus	hsp60	429	CU-HSP60F	GAAGTAAAAAG AGGAATGGATA AAGAAGC	61	[38]
			CU-HSP60R	CTTCACCTTCAA TATCCTCAGCA ATAATTAAAAG A		

*CC18F was modified to correct for an error in the sequence [39].

DNA samples that were positive for the *Campylobacter* genus then were screened for *C. jejuni, C. coli, C. lari, C. fetus, C hyointestinalis, C. upsaliensis,* and *C. ureolyticus* using uniplex species-specific PCR assays adapted from Bullman et al. [40] with primer pairs and annealing temperatures listed in Table 1. Each reaction consisted of 1 x HotstarTaq Master Mix (Qiagen, Germantown, MD), 2-3 µL template DNA and 1 µM of each primer. The final volume was adjusted to 25 µL with molecular grade water. Positive gBlocks® controls and a negative (water) control were run with each round of PCR. All PCR reactions were conducted on a MyCycler™ thermocycler (Bio-Rad, Hercules, CA) with one cycle of 95 ˚C for 5 min, followed by 35 cycles of 95 ˚C for 30 seconds, annealing temp for 1 min, and 72 ˚C for 1 min and ending with a final extension at 72 ˚C for 7 min. PCR products were visualized on a 1.5 % (w/v) agarose gel stained with ethidium bromide.

Statistical analysis

The Pearson chi-square test was used to evaluate differences in *Campylobacter* and *C. jejuni* prevalence by land use and den type. The Pearson chi-square test also was used to evaluate the difference in *Campylobacter* prevalence in human samples based on age group and season. The Wilson score method was used to estimate 95% confidence intervals with Bonferroni adjustments made for multiple comparisons. Figures were made in R version 3.4.4 and chi-square tests were performed in JMP Pro 14.

Study permissions

Human samples were collected from Chobe District health facilities under permit from Government of Botswana Ministry of Health (HPSME:13/18/1 Vol. X (878)) and all patient data was anonymized before analysis. Mongoose and environmental samples were collected under permit from the Government of Botswana Ministry of Environment, Natural Resources Conservation and Tourism (EWT8/36/4). Approval also was obtained from the Virginia Tech Institutional Review Board (#11-573) and Institutional Animal Care and Use Committee (IACUC, protocol 13-164-FIW) for human and animal work conducted in this study.

Results

Almost a quarter of samples collected from patients at local health facilities were positive for *Campylobacter* spp. (23.0%, *n*=122, 95% CI 13.9-35.4%). The mean age of *Campylobacter* infection was 26 (range, 6 months-62 years). Children under five (26.5%, *n*=34, 95% CI 13.4-45.6%) had similar frequencies of *Campylobacter* presence (*P*=0.645) as those found in older children and adults (22.0%, *n*=82, 95% CI 12.4-32.3%) (Table 2). At least six samples positive for *Campylobacter* spp. were from adult patients with no gastrointestinal symptoms; four of those samples were positive for *C. jejuni* and two samples were not identified at the species

level. *C. jejuni*, was the most commonly identified species, representing 82.1% (*n*=28, 95% CI 55.1-94.5%) of *Campylobacter*-positive samples. Two samples were positive for *C. coli*, one sample for *C. fetus*, and two samples were not identified at the species level. No samples were positive for *C. lari*, *C. upsaliensis*, *C. hyointestinalis*, and *C. ureolyticus.* There was no variation in infection by season (*P*=0.153), with 24.3% of dry season samples (*n*=74, 95% CI 15.0-36.9%) and 29.4% of wet season samples (*n*=34, 95% CI 15.5-48.6%) positive for *Campylobacter* spp (Table 2).

Table 2. Pearson Chi-square results used to evaluate differences in *Campylobacter* spp. prevalence in humans between seasons and age groups

Variables	***n*[a]**	***Campylobacter spp.***		***p*[c]**
		Prevalence (%)	**95% CI[b]**	
Season				0.153
Wet	34	24.3	15.5-48.6	
Dry	74	29.4	15.0-36.9	
Age				0.645
Children under 5	34	26.5	13.4-45.6	
Older children and adults	82	22.0	12.4-32.3	

[a] *n* = the number of samples screened for each characteristic

[b] Wilson score 95% Confidence Interval with Bonferroni adjustment

[c] Pearson Chi-square *p* values

We evaluated 201 fecal samples collected from 12 mongoose troops. Of these, 56% (*n*=201; 95% CI 45.6-65.4%) were found positive for *Campylobacter* genus DNA. Of the genus-positive

samples, only 52.7% of mongoose fecal samples were positive for the one of the seven species tested (*n*=112, 95% CI 43.5-61.7%) with most positive for only one species. One mongoose fecal sample (MOW troop) tested positive for three species (*C. jejuni*, *C. lari*, and *C. coli*). Across sampled mongooses, *C. jejuni* was the dominant species identified, accounting for 49.1% (*n*=112, 95% CI 36.1-62.3%) of *Campylobacter*-positive samples infecting nearly a third of all the mongooses sampled across the study system (27.4%, *n*=201, 95% CI 21.7-34.0%) (Table 3). Other species were infrequently identified, including *C. fetus, C. coli* and *C. lari*. As with the human samples, we could not detect *C. upsaliensis*, *C. hyointestinalis,* and *C. ureolyticus* in sampled mongooses (Fig 3).

Table 3. Prevalence of *Campylobacter* genus and percent of *Campylobacter* spp. that are *C. jejuni* by sample group

Sample Group	Land use[a]	*Campylobacter spp*			Percent of *Campylobacter* that are *C. jejuni*		
		***n*[b]**	**Prevalence (%)**	**95% CI[c]**	***N***	**Prevalence (%)**	**95% CI**
CGL	Lodge	15	93.3	56.5-99.3	14	35.7	11.3-70.7
CCH	Lodge	23	34.8	14.0-63.7	8	37.5	8.8-79.0
WLD	Residential	12	50.0	18.5-82.0	6	33.3	5.8-80.1
CSL	Lodge	24	79.2	49.8-93.6	19	73.7	41.2-91.8
FOR	Urban	11	72.7	32.2-93.7	8	62.5	21.0-91.3
PLAT	Residential	19	31.6	11.0-63.4	6	66.7	19.8-94.2
LIB	Urban	6	66.7	19.8-94.1	4	50.0	8.9-91.1
OLD	Urban	33	36.4	17.4-60.8	12	83.3	42.3-97.2
WAWP	Urban	5	60.0	14.6-92.9	3	66.7	12.2-96.6
MOW	Lodge	11	63.6	25.7-89.9	7	14.3	1.4-65.9
SEF	Undeveloped	21	76.2	45.0-92.6	16	37.5	13.1-70.4
KUBU	Lodge	21	42.9	18.5-71.3	9	11.1	1.1-58.4
Human	−	122	23.0	13.9-35.4	28	82.1	55.1-94.5
Mongoose	−	201	55.7	45.6-65.4	112	49.1	36.1-62.3

[a]Land use for each troop was classified the same as comparisons made in Table 2

[b]*n*= the number of samples collected and screened for each troop

[c]95% CI with Bonferroni adjustment visualized below

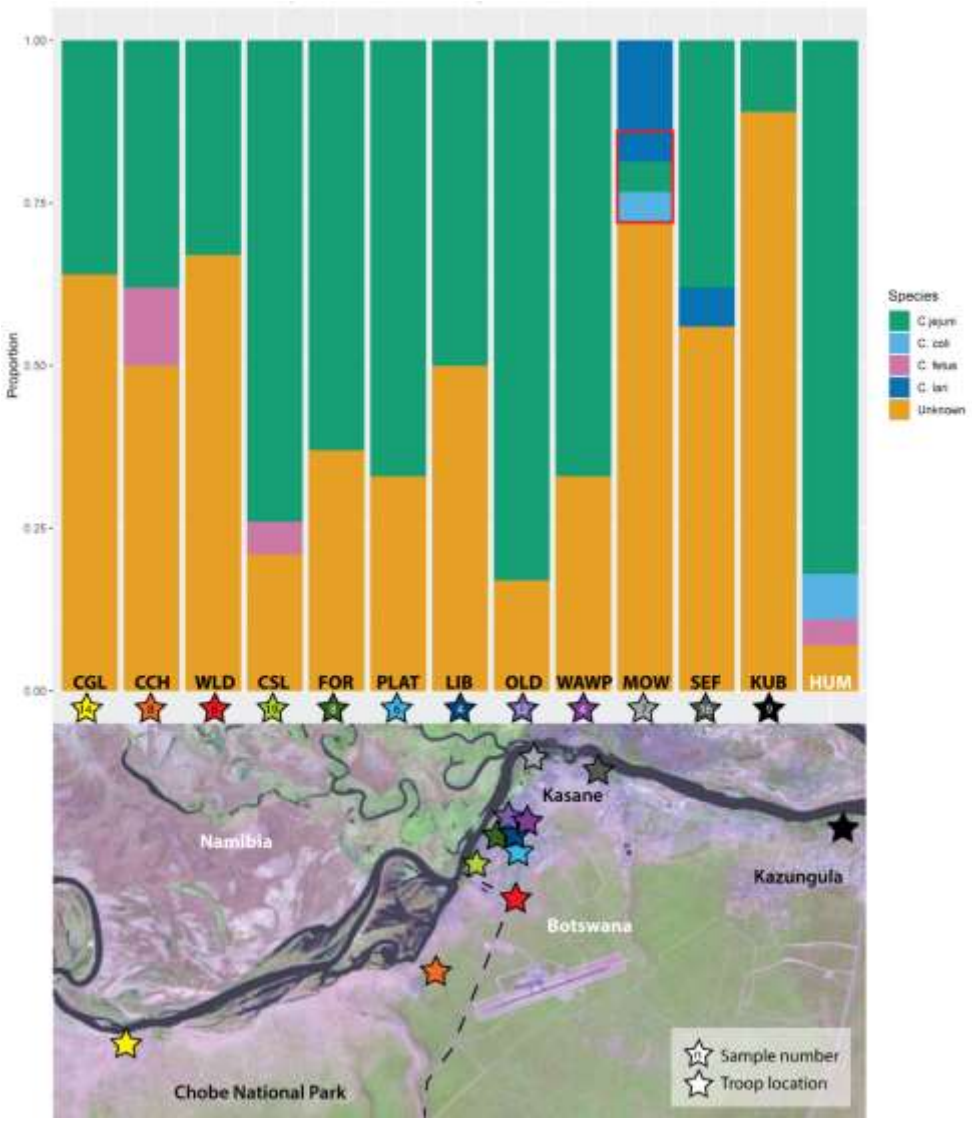

Fig 3. Proportion of samples positive for *C. jejuni, C. coli, C. fetus, C. lari,* and unknown species relative to the number of total *Campylobacter*-positive samples in each mongoose troop and in humans. Numbers located below each bar represent the number of samples for tested for each troop. Highlighted red box represents sample from MOW that was positive for

three species. Satellite imagery from 2017 Sentinel 2 Multispectral Instrument, data available from the U.S. Geological Survey (https://landsatlook.usgs.gov/).

There was no significant variation in occurrence of *Campylobacter* spp in mongoose fecal samples by land use. However, occurrence of *Campylobacter* spp. infections differed significantly by den type (natural or anthropogenic, $P = 0.001$, Table 4). Across troops, mongoose were observed using anthropogenic dens 89% of the time (range 67%-100%, n=412). Troops that den more frequently in natural den sites had an elevated prevalence of *Campylobacter* spp overall (80.8%, n=26, 95% CI 43.4-95.8%). However, troops that used anthropogenic sites had higher prevalence of *C. jejuni* ($P = 0.019$, Table 3).

Table 4. Pearson Chi-square results used to evaluate differences in *Campylobacter* spp. and *C. jejuni* prevalence in mongoose between different anthropogenic den use and land use

Variables	***N*[a]**	***Campylobacter spp.***		***P*[c]**	***C. jejuni***		***P*[c]**
		Prevalence (%)	**95% CI[b]**		**Prevalence (%)**	**95% CI[b]**	
Anthropogenic Den Use[d]				**0.001**			**0.019**
1	26	80.8	43.4-95.8		23.1	5.7-59.9	
2	71	52.1	31.1-72.5		16.9	6.1- 39.1	
3	41	68.3	39.1-87.9		43.9	20.0-71.1	
4	63	44.4	21.4-64.4		30.2	13.6-54.2	
Land Use[e]				0.025			0.456
Lodge	94	60.6	41.2-77.2		25.5	12.5-45.2	
Residential	31	38.7	14.5-70.2		19.4	4.7-53.7	
Undeveloped	21	76.2	36.0-94.8		28.6	7.1-67.7	
Urban	55	49.1	26.3-72.3		34.6	15.7-59.9	

[a] *N* = the number of samples screened for each characteristic

[b] Wilson score 95% Confidence Interval with Bonferroni adjustment

[c] Pearson Chi-square *P* values, critical *P* value was corrected for multiple comparisons using Bonferroni adjustment

[d] The proportion of nights spent in anthropogenic dens was calculated for each troop based on the total number of den observations from 2012-2018, and classified into 4 categories based on quantiles, with 1 being the lowest and 4 being the highest.

[e] Land use areas used by mongoose troops were classified into land use types (i.e., lodge, national park, residential, undeveloped and urban) and the majority land use used by each troop was calculated based on the total number of observations of the troop from 2012-2018

All the screened water samples were negative for *Camyplobacter* spp (*n*=70, 95% CI 0.0-5.2%). One sediment sample was positive for *Camplyobacter* spp. (*n*=81, 0.2-6.7%) during a sampling event on August 1, 2017, but was not identified for any of the seven species tested.

Discussion

Across the globe, environmental change is occurring at unprecedented rate with uncertain impacts to infectious disease transmission and human and animal health. In this study, we found widespread occurrence of *Campylobacter* spp in both humans and banded mongoose, but environmental detection was rare or absent. Of critical significance was the identification of heightened frequency of the zoonotic pathogen *C. jejuni* in mongoose troops that used anthropogenic den sites in close association with human populations (p=0.019). In contrast, troops that spend a higher proportion of nights in a natural den sites, had an elevated occurrence of *Campylobacter* spp. overall (p=0.001). Mongoose troops have varying levels of access to human garbage, human sewage, and human and domestic animal waste [41], with some troops relying more heavily on these anthropogenic resources. Our data suggest that these urbanizing

behaviors in banded mongoose may be associated with increased exposures to human sources of *C. jejuni* in the environment, leading to heightened frequencies in banded mongoose.

Human infections with *Campylobacter*

In hospitalized humans, *Campylobacter* was detected in 23% of patients sampled with no difference in *Campylobacter* spp. occurrence by age group. Surprisingly our data showed that adults and older children were infected as frequently as children under five, findings that diverge from other studies where infection was predominantly in young children (reviewed in [42]). This outcome could be due to the high frequency of immunocompromised individuals in the local population and their heightened susceptibility to infection due to the high burden of HIV/AIDs [43] or because of the inclusion of healthy adults in this study who may have protective immunity to *Campylobacter* and would not normally be screened for infection (reviewed in [44]). Detection of asymptomatic *Campylobacter* spp. infections in the human population indicates that *Campylobacter* is endemic in this population, convergent with findings observed in other sub-Saharan African countries [45]. The presence of asymptomatic infections has important implications for epidemiology, surveillance and risk assessment for *Campylobacter spp*, complicating the development and implementation of public health prevention and control strategies [44].

The majority of *Campylobacter*-positive human samples (82.1%) were *C. jejuni* which is about the same frequency as previously reported for southern Botswana (94.7%, 95% CI 75.4-99.1%) [25]. The nature of environmental reservoirs may influence exposure to and transmission of *Campylobacter* species with *C. jejuni* appearing to have a greater survival in the environment than other species (reviewed in [9]). Although seasonality has been a prominent feature of *Campylobacter* infections in western countries [46], there was no difference in *Campylobacter*

occurrence by season in this study. A lack of seasonality in *Campylobacter* spp. has also been observed in other developing countries [47], and may be related to warmer ambient temperatures in tropical regions [48]. Human samples were not collected over the same sampling time as mongoose and environmental samples which limits direct comparison, however these results show that *Campylobacter spp* infections occur in this population and at least in 2011, were widespread in patients presenting to local health facilities.

Banded mongoose and *Campylobacter* spp.

Over half of the mongooses sampled in this study tested positive for *Campylobacter* spp which is higher than any other surveyed mammalian species [49-51], and some avian hosts [14, 18]. One mongoose fecal sample (from the MOW troop) tested positive for three *Campylobacter* species (*C. jejuni*, *C. lari*, and *C. coli*). *C. jejuni* was the dominant species identified, infecting nearly a third of all the mongoose sampled in the study (27.4%, n=201, 95% CI 21.7-34.0%, Table 3). Species found in mongooses were similar to those found in humans sampled in the region with an absence of infection with *C. upsaliensis*, *C. hyointestinalis*, and *C. ureolyticus*.

This is the first report of *Campylobacter* infection in banded mongooses and the only report of this pathogen in wildlife in Botswana, findings that have clear implications for both human and animal health given the propensity for banded mongooses to adapt to urbanizing environments. A number of mongoose behaviors may contribute to observed elevations in prevalence. Banded mongooses, for example, are known to scavenge in human waste, a risk factor for *Campylobacter* prevalence in wild birds [52]. This species will forage for insects in the feces of other species, in particular large ruminants [53], and is a fossorial species, denning in the ground and foraging in soil [54], potentially increasing exposure to soil-associated *Campylobacter*. Banded mongooses are also highly social and behaviors such as allogrooming, anogenital

inspection, and scent marking with feces in association with olfactory communication behaviors also may increase microbial exposure and transmission within mongoose social networks [55]. Den sharing by multiple troops occurs frequently in urban and lodge environments [56]. Differences in infection status among species as a function of behavior and ecological niche have been observed in bird species, with bird species that foraged at ground level having higher *Campylobacter* prevalence than aerial or arboreal species [57].

Environmental samples

In this study, no water samples and only one sediment sample were positive for *Campylobacter* spp. False-negatives are common and can occur even when *Campylobacter* is implicated in large waterborne outbreaks [58]. *Campylobacter* spp. are difficult to detect through direct detection of PCR from environmental samples, because they are most likely present in low numbers compared to abundant environmental microbes and there is potential for high concentration of PCR inhibitors [59]. Despite limitations to detection, *Campylobacter* spp have been found in a wide variety of environmental samples, including biofilms on rock, wood, water, and sediment in riverine systems [60], and have been connected to multiple waterborne outbreaks from community water supplies contaminated after chlorination failure, heavy rainfall, or sewage intrusion (reviewed in [61]). The one positive sediment sample in this study was located downstream of where wastewater treatment effluent enters the Chobe River and at a popular recreation spot for accessing the river. The overall low incidence in water and sediment samples in this study suggests that waterborne transmission between humans and wildlife is less likely than transmission through direct contact with anthropogenic wastes, but does not rule out the possibility of sporadic cases.

Conclusion

Zoonotic pathogens such as *Campylobacter* are on the rise across the globe in vulnerable populations [62]. There is a pressing need to improve our understanding of *Campylobacter* transmission dynamics at the human-domestic animal-wildlife-environment interface and of the manner in which landscape transformation may influences human and animal exposures and infection dynamics. Variation in *Campylobacter* spp. infection patterns across banded mongoose troops suggests that human-transformed landscapes may have critical influence on pathogen exposure and transmission dynamics. Here, the territorial banded mongoose provides unique insight into the influence of landscape features on disease transmission, information essential for planning and implementing prevention and infection control strategies. Development of effective public health policy will require that we refine our understanding of human-animal-environmental couplings in campylobacteriosis or we are unlikely to achieve significant progress in management of this growing public health threat.

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Campylobacter in aquatic and terrestrial mammalian wildlife: review and metadanalysis

Abstract

Campylobacter spp. infections are an increasing global concern responsible for a significant burden of disease every year. While a diversity of wild avian species has been well studied as reservoirs of *Campylobacter*, our understanding of the role of wild mammalian species in disease transmission and persistence is limited. Host-factors driving infection in wild mammals have been particularly neglected, making it difficult to understand the role that wildlife reservoirs may play in *Campylobacter* transmission. Here, we review our current understanding of *Campylobacter* in wildlife and the potential impacts of these species in human *Campylobacter* transmission dynamics. We conducted a meta-analysis of published data to review *Campylobacter* infection in mammals and potential associations with life-history traits (urban association, trophic level, and sociality). Notably, half of urban-dwelling species (50%, 95% CI 32.1-67.9%) were positive for *C. jejuni* which was significantly more than urban avoiders (χ^2 = 6.74, p = 0.009). When evaluating the influence of trophic level and sociality on infection, omnivores and social species were significantly associated with *C. coli* presence (p=0.04 and p=0.009 respectively), but not with *C. jejuni* indicating that there may be critical differences in transmission dynamics between different *Campylobacter* spp in wildlife. Over half (55.7%, 95% CI 43.3-67.5%) of wildlife species consumed by humans were positive for *Campylobacter* spp., emphasizing the need for better understanding of the foodborne threat of *Campylobacter* from consumed wildlife products. As *Campylobacter* spp, and *C. jejuni* in particular are rapidly evolving species, this study identifies the most important and potentially influential wildlife

species that should be considered in disease transmission and public health and animal management.

Introduction

Campylobacter spp. are a diverse group of gastrointestinal zoonotic pathogens that infect a wide range of animal hosts [1], and are responsible for an estimated 96 million cases of foodborne illness in humans annually [2]. Indeed, *Campylobacter* is identified as one of the top four diarrheal disease-causing agents, important in both the developing and developed world [2]. *C. jejuni* and *C. coli* have been the primary species associated with clinical disease in humans, but a growing number of *Campylobacter* spp. have been recognized as emerging human pathogens [1]. Contact with animals is considered a common risk factor for campylobacterosis in both developing and developed countries, especially in young children [3-6]. However, transmission pathways often vary between rural and urban areas, with human *Campylobacter* infections in large urban areas more commonly attributed to the consumption of tainted poultry, while in rural communities a higher proportion of human infections are attributed to wildlife and environmental sources [7]. Wildlife are known to be important reservoirs of *Campylobacter* spp., including important human pathogens such as *C. jejuni* and *C. coli*. Transmission of *Campylobacter* to humans occurs through direct contact with animals and their feces, consumption of contaminated meat, or indirectly through a contaminated environment [8].

It is becoming increasingly clear that complex factors may influence Campylobacter transmission at the human-wildlife interface. Mammalian and avian wildlife can carry both species-specific strains that show evidence of host adaptations and generalist strains of *Campylobacter* spp that have little host association and are evolving rapidly [9-11]. The

specificity of the *Campylobacter* strain can affect its ability to transmit and infect hosts which has important consequences for epidemiology of this disease [12]. Genetic characterization of *C. jejuni* and *C. coli* isolates suggests that there is increasing exchange of *Campylobacter* strains among different ecological niches which is most likely a result of human activity and could have consequences for its ability to infect diverse hosts [11, 13]. Movement of *Campylobacter* spp across ecological niches could be especially important for wildlife species likely to exchange *Campylobacter* at the human-wildlife interface and acquire strains commonly responsible for human disease.

Disease transmission in wildlife species and life history traits

Life-history traits, such as diet and sociality, are known to influence disease transmission dynamics within and between species [14-16], with behavioral patterns of the host influencing both direct and indirect (i.e., environmental) pathogen transmission pathways. Pathogen transmission and persistence can be strongly influenced by host space use and species behaviors that influence host aggregations and contact rates [17]. Sociality (social group size) for example can increase contact rates and immunocompetence as a result of chronic social stress [18] Land use may also significantly influence host space use and pathogen transmission potential in certain host pathogen systems. For example, urban landscapes can alter host-pathogen dynamics through landscape change processes and can impair immune system response due to increases in wildlife host stress and nutritional deficiencies (reviewed in [19]). Additionally, multi-host pathogens, such as *Campylobacter*, can have altered transmission dynamics in urban landscapes that can increase pathogen prevalence [20] This is because urban landscapes can increase interspecific contact rates, a key component determining multi-host pathogen transmission [21]. Trophic level may also be important in transmission dynamics influencing exposure risks, and

has been associated with evidence of higher disease transmission in carnivores than browsers in some mammalian host-pathogen systems [22].

Among *Campylobacter*-wildlife hosts, wild birds have been the most well studied, and prevalence of *Campylobacter* spp. in some species has been associated with foraging at human refuse sites and in sewage sludge [23]. Differences between *Campylobacter* spp. presence in wild bird species also has been attributed to their ecological guild [24], with diet being a significant risk factor [23-25]. Specifically, shore-line invertebrate feeders, opportunistic feeders, and ground-foraging invertebrate feeders have the highest prevalence of *Campylobacter* across avian studies [24, 26]. A study from Italy also found a high prevalence in arboreal and herbaceous insectivore bird species [26], indicating that local and regional drivers may also influence infection variation in species groups. Other behaviors may also affect *Campylobacter* infection of wild birds. For example, a study of several wild bird species found the Eurasian coot (*Fulica atra*) had the highest prevalence of *Campylobacter* spp. (78.05%) which they hypothesized might be related to its behavior of consuming feces [27]. Patterns of infection may also be dependent on social behavior of birds, with a higher prevalence of *Campylobacter* found in crows (*Corvus brachyrhynchos*) during seasons with high social aggregation and an increased risk of *Campylobacter* among nestlings sharing the same nest [28].

While wildlife are considered important reservoirs of *Campylobacter* spp., our understanding of infection and transmission dynamics is largely limited to avian species. Our knowledge of *Campylobacter* among mammalian wildlife hosts is inadequate to fully engage a One Health approach in disease control strategies. Here, we review and summarize the literature, identifying our current understanding of *Campylobacter* in mammalian wildlife species, both

aquatic and terrestrial. We explore the potential role of key life-history traits including trophic level, urban association, and sociality in species infection. We explore these results and identify key knowledge gaps and important areas of future research.

Methods

Collection of literature

Published studies of *Campylobacter* in wildlife were extracted from online scientific search engines (Web of Science and Google Scholar) through the use of key words: 'wildlife + Campylobacter,' 'wild mammals + Campylobacter', and 'Campylobacter + name of taxon (at family level).' Reference lists of pertinent publications were searched for additional related articles. Information was collected on the location of sample collection, order, genus, and species of the wildlife species studied, animal status (captive, wild feces or wild carcass), prevalence of *Campylobacter* spp. and particular *Campylobacter* species identified, and method of molecular genetic testing (16S rRNA sequencing, multi-locus sequence typing (MLST), amplified fragment length polymorphism (AFLP), pulse-field gel electrophoresis (PFGE), random amplification of polymorphic DNA polymerase chain reaction (RAPD-PCR), or whole-genome sequencing (WGS)), when available.

Classification of life-history traits

Mammals that had *Campylobacter* prevalence data were also categorized by trophic group (herbivore, omnivore, and carnivore) and sociality using the PanTHERIA database [29] and the Animal Diversity Web (ADW) [30]. In cases where species are occasionally omnivores but are dominantly herbivores or carnivores, the predominant trophic level was chosen for analysis. Sociality of the species was defined as either social or solitary, depending on whether

species lived alone or within a social group [30]. Mammals were also classified based on their association with urban areas. The classification system from Santini et al. [31] was used to classify species into urban 'dwellers' and urban 'visitors', with species meeting more than one criterion labeled as both (i.e., 'dwellers\visitors'). Urban association for species that were not included in the Santini et al [31] review were searched for using 'taxon name (genus and species) + urban, urbanization or humans' (Table S1). An additional category was added for purposes of this study to classify species that had no urban interaction, which were labeled as urban 'avoiders' based on an absence of urban interaction in the literature. The Antarctic fur seal (*Arctocephalus gazella*) was assumed an avoider due to habitat needs that did not overlap with urban areas. Information on consumption of species by humans was collected from the IUCN Red List [32] and Mildenstein et al [33] for some bat species.

Statistical analyses

Once data had been compiled, duplicate species were removed from the database. If the same species was studied in two different regions of the world, and no subspecies are apparent, only one entry for this species was kept in our database. Due to the significant differences in sample sizes from different manuscripts (sample sizes varied from one to 1168; *Sus scrofa*), we used a dummy variable for *Campylobacter* presence in wildlife species, with 1 indicating that *Campylobacter* spp. have been isolated from that species, and 0, indicating that no *Campylobacter* spp. have been isolated from that species. This dummy variable was used in creating graphs and carrying out statistical analyses of the data. All statistical analyses were conducted in R 3.3.2, an open source integrated programming environment [34]. Pearson's chi square tests were used to determine possible associations between life-history variables and *Campylobacter* presence. Chi-square tests with more than three explanatory variables were

followed up by multiple post-hoc tests for each possible paired comparison with Bonferroni adjustments. We used the R package, *ggplot2* [35] to create graphs.

Results

Forty-six unique studies had data recorded on prevalence of *Campylobacter* spp. in specific mammalian wildlife and were included in the statistical analyses. These studies investigated 105 different free-ranging mammal species representing 36 families and 8 orders. Most studies were conducted on European wildlife (n=18), but most world regions, including North and South America, the Caribbean, the Middle East, Africa, Asia, and Antarctica were represented, having at least one published study on *Campylobacter* spp. in mammalian wildlife. Four papers were included that investigated *Campylobacter* spp. in wildlife carcasses destined for human consumption. A full list of species and studies included in our statistical analyses are listed in Table S2. An additional 12 studies analyzed *Campylobacter* spp. presence in captive wild mammals. These studies were excluded from statistical analyses but included in our discussion due to the added value they provide in understanding *Campylobacter* spp. infection in wildlife species. Over the last ten years, five new wildlife-specific *Campylobacter* spp. have been discovered, and five species of *Campylobacter* found in domestic animals have emerged in wildlife (both captive and free-ranging; Table 1).

Table 1. Emerging *Campylobacter* species identified in mammalian wildlife

Emerging Campylobacter species	Host species	Location	Year of discovery	References
Novel spp. first identified in mammalian wildlife				
C. insulaenigrae	Northern elephant seals Harbor porpoises South American sea lions Antarctic fur seals	California, Scotland, Chile, and Antarctica	2004	[36-39]
C. blaseri	Harbor seals	Netherlands	2018	[40]
C. pinnipediorum	California sea lions Harbor seals	California and Scotland	2017	[41]

	Grey seals			
C. troglodytis	Chimpanzees	Tanzania	2011	[42]
C. corcagiensis	Lion-tailed macaques	Ireland (captive)	2014	[43]
C. cuniculorum	Rabbits	Italy (captive)	2009	[44]
Emerging species in wildlife previously novel to domestic animals				
C. lanienae	Chinchilla	Massachusetts (captive)	2014	[45]
C. sputorum	Feral pig	California	2012	[46]
C. hyointestinalis	Wild boar/feral pig House mouse African elephant Orangutan Chimpanzee Lowland gorilla Japanese macaque	California, Netherlands, and Japan (captive and wild)	2000-2012	[46-49]
C. upasalinesis	Emperor tamarin	Minnesota (Captive)	2018	[50]
C. fetus	Feral pig Banded mongoose	California and Botswana	2012, 2019	[46]

Wildlife species included in the analysis were predominately classified as visitors (n=40), followed by dwellers (n=30), visitor/dwellers (n=21) and avoiders (n=15). Urban association was significantly associated with *C. jejuni* presence in a Chi-square analysis (χ^2 = 8.19, p = 0.04) (Table 2). Detection of *C. jejuni* was significantly more associated with urban dwellers (50%, 95% CI 32.1-67.9%) than urban avoiders (χ^2 = 6.74, p = 0.009). Fewer fecal samples from urban avoiders were reported to contain *C. coli* (7.1%, 95% CI 1.3-31.5%) and total *Campylobacter* spp. (26.7%, 95% CI 10.9-52%), but this was not significantly less than in visitors or dwellers. Across trophic levels, wildlife species were evenly distributed, (36 carnivores, 34 herbivores, and 37 omnivores). More omnivores were detected with *C. jejuni* (47.1%, 95% CI 15.1-44.2%), *C. coli* (27.3%, 95% CI 15.1-44.2%), and total *Campylobacter* spp. (59.5%, 95% CI 43.5-73.7%) than were carnivores and herbivores. This was only significant for *C. coli* infections (χ^2 = 6.68, p=0.04), with fewer carnivores detected with *C. coli* than omnivores (χ^2 = 7.943, p=0.0048) (Table 2 and Figure 2). When considering sociality, 65% of wildlife species included in the analyses were categorized as social, with the remaining 35% being solitary. A greater number of solitary species were detected with *C. jejuni* (44.1%, 95% CI 28.9-60.5%) and total *Campylobacter* spp. (51.4%, 95% CI 35.9-66.6%) than social species.

However, the opposite was true with *C. coli* presence, where significantly fewer solitary species were detected with *C. coli* than social species in a Chi-square analysis ($\chi^2 = 6.85$, p =0.009). Approximately half of the wildlife species included in the analyses are used as a human food resource (57%) with over half of these wildlife species (55.7%, 95% CI 43.3-67.5%) positive for *Campylobacter* spp. Less than half (38.1%, 95% CI 26.5-51.4%) were positive for *C. jejuni* and only 25.5% (95% CI 15.6-38.9%) were positive for *C. coli*.

Table 2. Statistical associations between the categories of each variable based on presence or absence of Campylobacter species in mammalian wildlife.

	C. jejuni n=97 species				***C. coli*** n=90 species				***Campy spp.*** n=107 species			
Variable	%	95% CI	χ^2	p	%	95% CI	χ^2	p	%	95% CI	χ^2	p
Urban association												
Avoider	6.7	1.2-29.8			7.1	1.3-31.5			26.7	10.9-52		
Dweller	50	32.1-67.9	8.16	0.04	16.7	6.7-35.9	6.68	0.08	48.4	32-65.2	3.6	0.31
Visitor	34.3	20.8-50.9			30.3	17.4-47.3			53.9	38.6-68.4		
Visitor/Dweller	30	14.5-51.9			5.3	0.9-24.6			40.0	21.9-61.3		
Trophic level												
Carnivore	27.3	15.1-44.2	5.3	0.07	3.3	0.6-16.7	6.68	0.04	36.1	22.5-52.4	5.3	0.07
Omnivore	48.5	32.5-64.8			27.3	15.1-44.2			61.1	44.9-75.2		
Herbivore	23.3	11.8-40.9			22.2	10.6-40.8			39.4	24.7-56.3		
Sociality												
Social	27.4	17.9-39.6	2.76	0.10	25.4	16.1-37.8	6.85	0.009	42.7	31.6-54.5	0.73	0.39
Solitary	44.1	28.9-60.5			3.2	0.6-16.2			51.4	35.9-66.6		

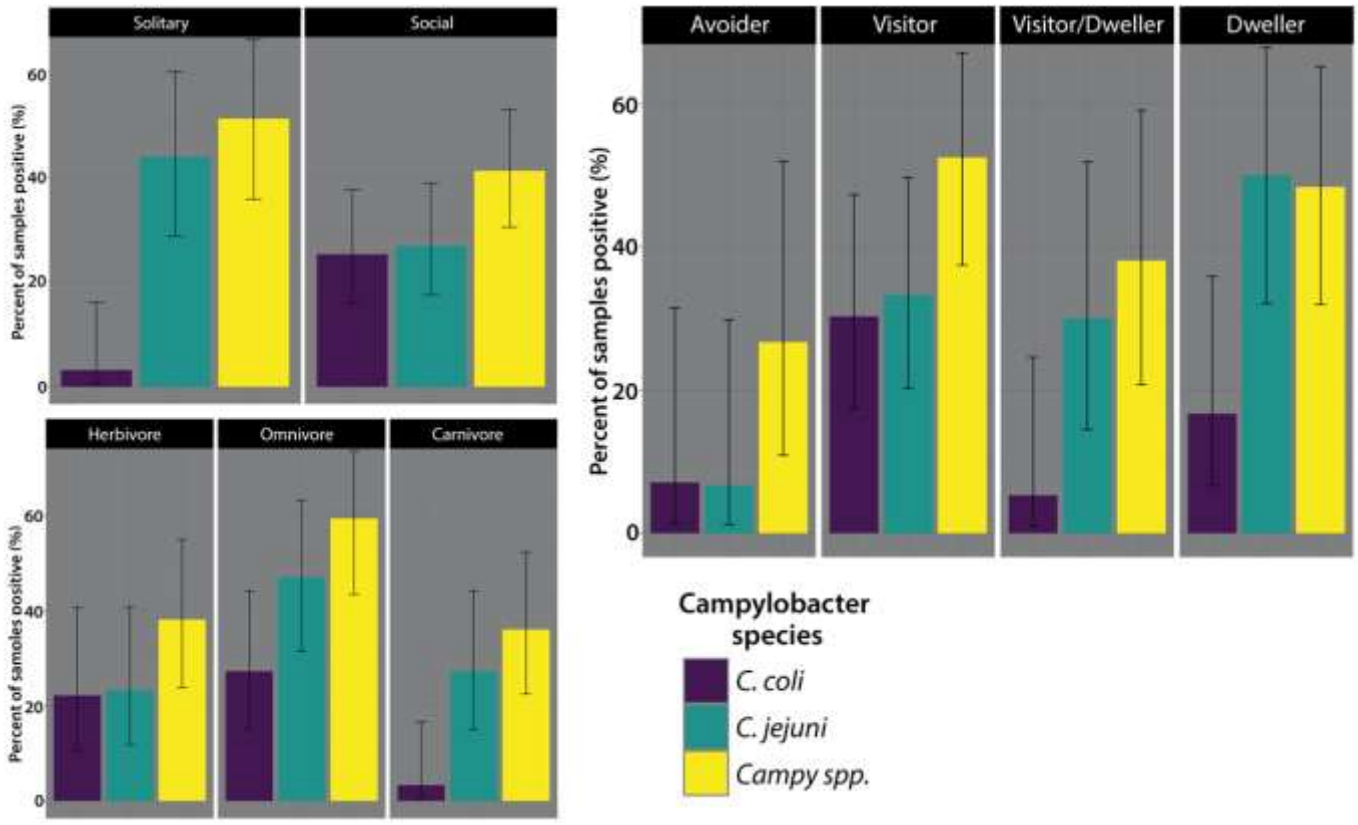

Figure 1. Difference in *C. jejuni*, *C. coli*, and total *Campylobacter* spp. detection in wildlife species for urban behavior, trophic level and sociality with 95% confidence intervals.

Discussion

Wildlife *Campylobacter* hosts

Campylobacter spp have been discovered in a wide range of mammalian wildlife species from diverse phylogenetic lineages, including small mammals, non-human primates, bats and marine mammals representing diverse guilds. Some of these free-ranging wildlife species had *Campylobacter* species and strains genetically distinct from those found in human, livestock and poultry [47, 51, 52]. Host-specificity was observed even in captive situations where multiple species were housed together and would have had potential for contact or environmental

transmission [48, 50]. Conversely, other *Campylobacter* found in wildlife have been from generalist *C. jejuni* and *C. coli* clades that represent highly diverse and highly transmittable strains that are more likely to be transmitted to humans and domestic animals [9]. For example, several monkey species have been detected with generalist *Campylobacter* spp. strains that are highly similar to human and domestic animal strains [9, 53, 54]. Generalist and host-specific subtypes are being observed in wildlife species at a global scale, indicating that large-scale ecological and evolutionary drivers influence this dichotomy, not just local transmission dynamics [10, 54, 55]. Generalist *C. jejuni* strains found in the northern hemisphere have even been discovered in wildlife species inhabiting Antarctica [55]. It is postulated that the formation of generalist clades is a recent occurrence that has evolved from escalating human disturbance resulting in increasing genetic exchange between *Campylobacter* spp [13]. The weak host association of generalist *Campylobacter* makes it difficult to pinpoint sources of human infections even with more powerful genome sequencing, making it important to complete intensive sampling of any potential transmission reservoirs, including wildlife [56].

Six novel species of *Campylobacter* have recently been isolated for the first time from wildlife species and several other emerging *Campylobacter* spp. from humans and domestic animals have also been identified in wildlife. Of these, three novel *Campylobacter* species were identified in marine wildlife along populous coastal areas [57] and in remote areas of Antarctica [39, 55]. While the role of these novel *Campylobacter* spp. as potential human pathogens are largely unknown, *C. insulaenigrae* has been isolated from a clinical gastroenteritis and septicemia case in an immunocompromised patient in Australia, indicating some pathogenic capability [58]. A novel spp., *C. troglodytes*, was also isolated from chimpanzees (*Pan troglodytes*) living close to human settlements in Tanzania [42]. Other novel spp. have been

identified for the first time from captive species at a zoo and in farmed wildlife [43, 44]. This is most likely a reflection of increased monitoring of captive wildlife, and there likely are many more *Campylobacter* spp. in wildlife species that have yet to be discovered [1]. In other cases, emerging species that previously have been found mostly in human and domestic animals have been newly identified in wildlife, for example, the discovery of high prevalence of *C. lanienae* (44.4%; 12/27) in laboratory chinchillas (*Chinchilla laniger*) [45]. This is the first time this species was isolated outside of livestock or livestock employees, although it has not been associated with human disease cases [59]. Identifying emerging *Campylobacter* spp. can help us to understand *Campylobacter* diversity, pathogenicity and niche preferences [60].

While *Campylobacter* spp. occurs in many wildlife species, clinical signs of gastrointestinal illness or adverse health effects have only been observed in a few species. Two noctule bats (*Nyctalus noctula*) [61], a dozen rhesus monkeys (*Macaca mulatta*) [62], and several vervet monkeys (*Chlorocebus pygerythrus*) [63] infected with *Campylobacter* spp. presented symptoms of acute gastroenteric infections. The infections could prove fatal, with one wild vervet monkey dying from suspected antibiotic resistant *Campylobacter* infection during laboratory quarantine, while several other monkeys in poor condition had to be euthanized [63]. This outcome suggests that some free-ranging wildlife may be just as susceptible to acute *Campylobacter* infections as are humans, potentially affecting the quantity of pathogen shed into the environment and subsequent transmission to other animals and humans [64]. Even in the absence of acute signs of disease, evidence suggests that *Campylobacter* spp. infection in wildlife can affect body mass and their overall health [65].

Both geographic and temporal variation in *Campylobacter* detection was observed in wildlife species. At a global scale, bats have been detected with *Campylobacter* spp. in Asia and

Europe [61, 66], but no *Campylobacter* spp. were isolated from bats in the Caribbean [67]. Geographic variability also has been observed in browsers (i.e, herbivores that feed on shrubs, trees and forbs), with moose and deer positive for *Campylobacter* in Europe [68, 69], but no browsing species positive in North or South America [70, 71]. Variation was also evident at more regional scales with prevalence of *Campylobacter* spp. significantly higher in captive monkeys from Cambodia (41.7%, 15/36) and Indonesia (49.2%, 31/63) than in China (10.1%, 12/119) [72]. These results suggest that local and regional environmental and dietary factors may play a role in *Campylobacter* prevalence. Temporal variation in *Campylobacter* infection has not been well-studied in wildlife, but limited research suggests that wildlife may only be periodically infected with or intermittently shed *Campylobacter* spp [28]. Only one study in wild boar has identified seasonal variation of *Campylobacter* spp. infection, with a higher risk associated in winter months [73]. Additionally, the risks for acquiring disease may change over time in some wildlife populations with a longitudinal study of captive rhesus macaques in Brazil showing having increasing levels of infection over an 8-year period [74].

Life-history traits

Life-history traits have been used to find the most competent hosts for other host-pathogen systems [75], however, results from this meta-analysis are the first time an association has been made for *Campylobacter* spp. across mammalian wildlife species. Our results show that life-history traits play a significant role in the presence and species of *Campylobacter* detected in wildlife. Urban association, tropic level, and sociality all had significant associations with *Campylobacter* detection, which illustrates the complexity of transmission dynamics of this group of pathogens.

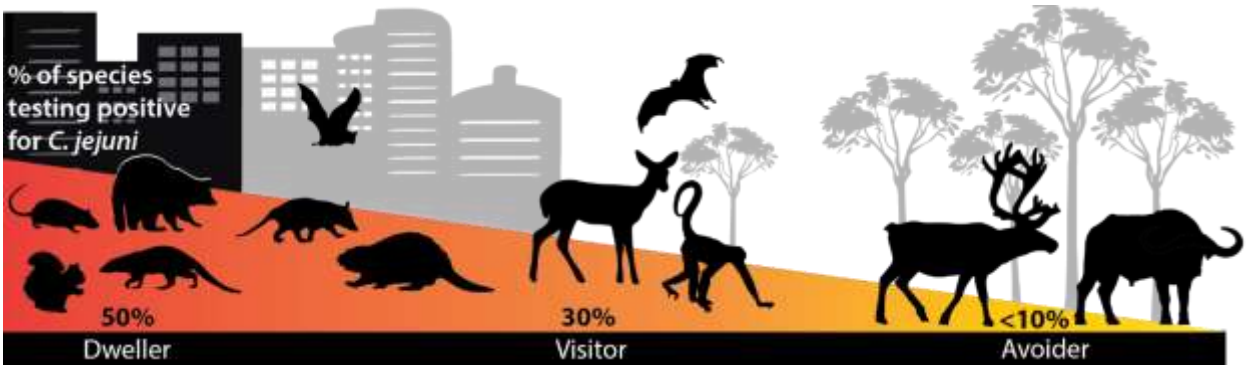

Figure 2. Difference in *C. jejuni* detection among wildlife species based on urban behavior association. Urban dwellers had significantly greater numbers of species infected with *C. jejuni* than urban avoiders, and visitor and visitor/dwellers were intermediate.

Urbanization

The most striking association we discovered was that wildlife species categorized as urban dwellers were significantly more likely to carry *C. jejuni* than urban avoiders (Figure 2). Likewise, more urban-dwelling species were positive for *C. jejuni* than visitors and visitors/dwellers, however, this association was not statistically significant in our analyses. *C. jejuni* has been found in raccoons and civets inhabiting urban centers [76], rodents overwintering in human dwellings [77] and even in wildlife feces on playgrounds [78, 79]. Urban dwellers are more likely to interact with waste from humans and domestic animals infected with *C. jejuni*, which may be reflected in our results. However, the occurrence of *C. jejuni* in wildlife species is not exclusively dependent on human transmission. Wild birds are known carriers of *C. jejuni*, having their own distinct *C. jejuni* subtypes [80], and may act as a pathogen source for other wildlife species in these environments. This reservoir incorporates an extra layer of complexity to transmission dynamics, given that wild-bird associated *C. jejuni* is commonly found in water sources [81] and is responsible for a small fraction of human campylobacterosis cases annually

[82]. Indeed, endangered Persian fallow deer (*Dama mesopotamica*) in a wildlife refuge were found to have a high prevalence of *Campylobacter* spp. (52.3%, 33/63) and *C. jejuni* (27.0%, 17/63), with the suspected route of transmission being water sources used by migratory birds [83]. On the other hand, urban dwellers did not have significantly more *C. coli* or total *Campylobacter* compared to non-urban associated wildlife species. There is a reduced risk of *C. coli* infection in humans who live in urban areas [84], which may explain this observation.

Species-specific, as well as human-associated strains of *Campylobacter* have been discovered in marine species that inhabit the terrestrial-marine interface [55, 85]. Here, *Campylobacter* pathogens are likely transferred from land through urban and agricultural run-off, with variations in prevalence associated with host behavior. Indeed, half of grey seal pups in a breeding colony off the coast of Scotland were positive for *C. jejuni* or *C. coli*, while all returning yearling seals were negative. [85]. Isolates were genetically similar to human clinical isolates, indicating either a common source of infection or transmission of human pathogens to seals through the environment [85]. Behavior also influenced prevalence in northern elephant seals in California, with stranded juvenile seals six times more likely to be infected with *Campylobacter* spp. and approximately four times more likely to be infected with *C. jejuni* than young seals that had not left the colony [57]. Stranded seals are under more stress than colony seals and may have been exposed to higher pathogen levels from terrestrial sources such as freshwater outflows [86]. Seals are unlikely to be a common source of transmission to humans, and these most likely represent reverse zoonotic transmission or zooanthroponosis. The effect on seal health is unclear, but elevated *C. jejuni* has also been correlated with antimicrobial-resistant species of *E. coli*, which indicates that seals may be exposed to elevated levels of multiple biological pollutants that could have a compounding effect [86].

Trophic level and sociality

Diet and social behavior can be critical risk factors in infectious disease transmission, and results from our meta-analysis indicate that they may be influencing *Campylobacter* spp transmission patterns in wildlife. Omnivores had the most species with *C. jejuni*, *C. coli* and total *Campylobacter* spp. which may be related to differences in host foraging behavior or bacterial survival rates in different environments. This was only significant for *C. coli*, with carnivore species having significantly less *C. coli* than omnivores, suggesting that there may be something about *C. coli* survival and transmission that is different. *C. jejuni* and *C. coli* have shown differences in adhesion capabilities, with *C. coli* less capable of adhering to inert surfaces than *C. jejuni* [87]. Adhesion is an important survival mechanism that can increase the probability of environmental contamination and transmission in food industries [87], but could also influence *C. jejuni* and *C. coli* transmission potential in natural and urban environments where wildlife may encounter *Campylobacter*. Another factor is different transmission pathways that may be influencing *C. coli* compared to other *Campylobacter* species. Different risk factors have been associated with *C. coli* and *C. jejuni* in human infections, including age, season and location [84, 88], which implies that different risk factors also could be associated with *C. coli* in wildlife. Similar differences in transmission pathways also may explain why *C. coli* was significantly more common in social than solitary species, while no such distinct relationship was seen for *C. jejuni* or total *Campylobacter*. Results of *Campylobacter* in carnivores should be taken with discretion as the majority of carnivore species that have been sampled are insectivores or piscivores which could influence results. A more robust investigation of *Campylobacter* spp. in different carnivore species based on prey type may yield different results.

Public health implications

Consumption of wild game/bush meat

Overall, we found that over half of wildlife species used as human food resources were positive for *Campylobacter* spp. and 38.8% were positive for *C. jejuni*, highlighting an important public health concern. In contrast, *C. coli* was only detected in a quarter of wildlife consumed by humans, suggesting that the transmission pathway of *C. coli* may be different in these species and subsequently plays a less important role in wildlife infection. Additionally, some wildlife species consumed by humans contained antibiotic resistance strains of *Campylobacter* spp., which may have significant public health implications [49].

Although, there is an association between *Campylobacter* spp presence and wildlife consumed by humans, most wild game killed by hunters or in markets do not present a significant public health threat. *Campylobacter spp.* were only rarely detected in moose (*Alces alces;* 6%) and deer (*Odocoileus virginianus*; 2%) carcasses in Finland [69], and were not detected in any deer carcasses (*Capreolus capreolus* and *Cervus elaphus*) in Germany [89]. *Campylobacter* was also not detected at all in monkey, porcupine, duiker or river hog muscle meat (n=104) in Gabon [90]. Results from wild boar studies have been more varied, with some detecting no or low *Campylobacter* spp prevalence [89, 91, 92], and others detecting high *Campylobacter* spp. prevalence [46, 49, 93]. It also may be that wild boar carry different *Campylobacter* spp. not detected by traditional culture methods. For example, a study in Spain found that 66% (188/287) of wild boar were positive for *Campylobacter* spp, but only one was positive for *C. jejuni* and no isolates were positive for *C. coli* or *C. lari* [93]. In contrast, another study in Spain identified *C. lanienae* as the dominant species in wild boar, making up 67.3% (34/49) of *Campylobacter* isolates [73], and found that it was significantly higher ($p < 0.01$) in wild boar than free-ranging cattle [94]. *C. lanienae* has primarily been isolated from livestock

and slaughterhouse workers, and its pathogenicity and role as a human gastrointestinal pathogen is not well known [95, 96]. Other species commonly isolated from wild boar include *C. hyointestinalis* [49], while *C. coli* and *C. jejuni* have been consistently less common [46, 92].

The greatest public health concern from wild game is associated with cross-contamination during butchering and processing. For example, Stella et al [97] found that although only 16.7% (5/30) of wild boar carcass samples were positive for *Campylobacter*, 51.8% (29/56) of caecal contents were positive, and two carcass samples that were positive did not have positive caecal content. Further, processed wild game meat that was smoked in the Democratic Republic of Congo was contaminated with *Campylobacter* spp. in 11.1-26.6% of buffalo (*Syncerus caffer*), common duiker (*Sylvicapra grimmia*), and desert warthog (*Phacochoerus aethiopicus*) samples [98]. Exotic wildlife species, including turtles and frogs used in cooking have also been suspected as potential sources of foodborne campylobacterosis [99]. Although the risks of infection from consuming contaminated poultry are much greater than from wild game, communities who rely heavily on wild game meat need to be cautious during butchering and processing to reduce contamination.

Wildlife transmission to livestock

As *Campylobacter* is primarily a foodborne pathogen, a prominent concern is wildlife transmission to domestic species commonly consumed by humans. There is conflicting evidence regarding the role of wildlife in *Campylobacter* transmission to livestock and poultry production. In one study from Spain, *Campylobacter* spp. from wild boar were deemed an unlikely reservoir for cattle because they each had their own dominant species: *C. lanienae in* boar and *C. jejuni* in cattle [94]. In other studies, a low prevalence in wildlife coupled with minimal genetic similarity between wildlife and livestock genotypes suggests that transmission between wildlife and

livestock is infrequent [47, 100, 101]. When wildlife-specific strains were compared to generalist strains there were missing regions from wildlife-specific strains that may explain why they are unable to colonize as many species [102]. Although Viswanathan et al [52] found most *C. jejuni* isolates phylogenetically grouped in distinct wildlife and livestock clusters, 31.25% (5/16) of dairy cattle isolates and 17.6% (3/17) beef cattle isolates did cluster with small mammal (raccoons, skunks and mice) isolates collected from farms, suggesting that some transmission is occurring between wildlife and livestock. It may be that some wildlife species are more likely to be infected with livestock and human strains than others, as a study from wildlife and livestock in the UK found little genetic overlap between cattle and wild birds, but rabbit isolates were genetically similar to cattle isolates [103]. Additional studies have identified identical *Campylobacter* spp. clones from rodents, sparrows, flies and livestock [104], and high genetic similarity between *Campylobacter* spp. isolated from wild birds, mice and poultry [105]. This similarity can provide real transmission risk to poultry flocks as an environment contaminated with feces from other animals, including wildlife, rodents and domestic animals is a risk factor of poultry infection with *Campylobacter* spp. [106].

It is unclear whether wildlife are transmitting *Campylobacter* to livestock and poultry or whether wildlife are acquiring *Campylobacter* from the environment. In a study of wild rodents across chicken and pig farms, *Campylobacter* species in rodents varied between the farm type, with *C. jejuni* more common on poultry farms and *C. coli* more common on pig farms [107]. Further analysis of mammalian wildlife and livestock species that incorporates both behavior and phylogenetic analysis of *Campylobacter* spp. is necessary and has proven valuable in wild bird studies [28]. It is also difficult to make broad conclusions on the role of wildlife in transmission of *Campylobacter* in agriculture as the majority of studies have been conducted in the United

States and Europe. As our food production systems are increasingly globalized it is important to understand the role of wildlife in agricultural production at a global level, especially as *Campylobacter* spp. has been found in food products internationally [108-111].

Limitations and knowledge gaps

This study provides a broad overview of *Campylobacter* spp. infection in free-ranging mammalian wildlife. Statistical analyses in this study were based on presence/absence data and did not include *Campylobacter* prevalence data. Prevalence often varied greatly between species and studies, ranging between 1-87.5%. Culture methods also varied greatly between the studies which can have a significant impact on the prevalence, species and genotypes isolated [112]. Detection methods often are biased toward *C. jejuni* and *C. coli* isolation which can skew the representation of *Campylobacter* species present [113]. The age and storage of feces also impacts *Camplyobacter* isolation, with fresh fecal samples significantly more likely to likely to be positive for *Campylobacter* spp than older feces using culture methods [78]. This may be particularly relevant for *Campylobacter* isolation from wildlife samples, especially if samples are taken from remote sites, far from a laboratory, which was not accounted for in this study. Culture methods are also increasingly being found inferior to immunoassay and molecular methods for sensitivity and specificity of *Campylobacter* detection [114].

Pathogen prevalence and transmission have been well studied in European and North American wildlife and bird species, but relatively few studies on *Campylobacter* prevalence and transmission in wildlife are occurring in developing countries where Campylobacter burden is highest [115] and where transmission dynamics may differ [116]. There is also a lack of phylogenetic information on *Campylobacter* spp. in mammalian wildlife. *Campylobacter* spp and *C. jejuni* in particular, are evolving rapidly [117] which could mean that relationships

between wildlife-associated *Camplyobacter* and human-associated *Campylobacter* is also changing. Most papers that do incorporate genetic or phylogenetic information rely on MLST techniques which have been the gold-standard for defining clonal groups but has proven inferior at establishing epidemiological dynamics [118]. Only two recent papers incorporate WGS on free-ranging wildlife and both papers found human-associated *Campylobacter* genotypes in their respective wildlife species [61, 85]. Future research should focus on incorporating WGS methods on targeted wildlife species at the human-wildlife interface that are most likely to contribute to *Campylobacter* transmission and human disease.

Conclusions

Multi-host pathogens, such as *Campylobacter,* have complex transmission dynamics that can be altered by human-landscapes and behavior of hosts. Our understanding of *Camplyobacter* spp. in mammalian wildlife at the human-wildlife interface is limited yet it is important to understand wildlife transmission dynamics in order to target disease control. Considering that large-scale surveillance for *Campylobacter* is often economically unfeasible, this study may assist surveillance efforts by identifying the most important and potentially influential wildlife species in *Campylobacter* transmission. In this study we found that life-history traits influenced the presence and species of *Campylobacter* spp. in free-ranging wildlife and that urban association of wildlife was significantly associated with the presence of *C. jejuni.* As *C. jejuni* is a rapidly evolving species at the human-animal interface, targeted monitoring of urban dwelling species may be important to understanding transmission dynamics in the future.

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Conclusions

I identified interesting relationships between host-factors, landscape features and *Campylobacter* spp. in a wildlife species. I established banded mongoose as a potential reservoir of *Campylobacter* spp. in northern Botswana, where *Campylobacter* spp. appears to be endemic in the human population. Variation in *Campylobacter* spp. infection patterns in banded mongoose suggest that anthropogenic landscapes may promote pathogen exposure and transmission dynamics. Denning in urban landscapes increased the prevalence of *C. jejuni* in banded mongoose troops whereas natural dens had an elevated occurrence of total *Campylobacter* spp. Different transmission patterns are most likely occurring between troops that mostly den in anthropogenic landscapes and those mostly denning in natural areas. In contrast, waterborne transmission likely plays only a small role in *Campylobacter* spp. transmission across this interface.

In a review and meta-analysis of the literature, I showed life-history traits influenced the presence of *Campylobacter* spp. across all free-ranging mammalian wildlife that have been studied for *Campylobacter* spp. Urban association of wildlife species was significantly associated with the presence of *C. jejuni*. This finding highlights the importance of human-disturbed landscapes on *C. jejuni* evolution. Trophic level and sociality on the other hand were significantly associated with *C. coli* presence, suggesting that even though there are similarities between the two species transmission dynamics to wildlife species differ.

As *Campylobacter* spp are rapidly evolving species, it is important to continue to monitor these pathogens in wildlife at the human-wildlife interface. The urban environment appears to substantially increase the risk of wildlife infection by *C. jeuni* and future studies on *Campylobacter* spp. infection in wildlife should focus on targeted monitoring of urban-dwelling wildlife species coupled with behavioral risk assessments of wildlife and humans to understand transmission dynamics there. Additional focus should be placed on applying DNA sequencing methods that can more accurately identify similarities or differences between wildlife and human strains. This approach will allow us to understand to what extent urban-dwelling wildlife are important to *Campylobacter* transmission to humans.

Appendix

Table S1: List of all species and variables included in metadata analysis of *Campylobacter* spp. presence in wildlife with references

Species	Common name	Urban behavior	Sociality	Trophic level	Human Consumption	References
Alces alces	moose	Visitor	Solitary	Herbivore	Yes	[1-3]
Antilocapra americana	pronghorn	Avoider	Social	Herbivore	Yes	[4]
Aotus spp	night monkeys	Visitor	Social	Omnivore	No	[5]
Apodemus flavicollis	yellow-necked mouse	Dweller	Solitary	Omnivore	No	[6-8]
Apodemus speciosusæ	large Japanese field mouse	Dweller	Solitary	Herbivore	No	[9]
Apodemus sylvaticus	wood mouse	Dweller	Solitary	Omnivore	No	[7, 8, 10]
Arctocephalus gazella	Antarctic fur seal	Avoider	Solitary	Carnivore	No	[11, 12]
Ateles paniscus	red-faced spider monkey	Visitor	Social	Omnivore	Yes	[5]
Blarina brevicauda	northern short-tailed shrew	Dweller	Solitary	Carnivore	No	[13]
Blastocerus dichotomus	marsh deer	Visitor	Solitary	Herbivore	Yes	[14]
Callithrix spp	monkeys	Dweller	Social	Omnivore	Yes	[15]
Capra pyrenaica	iberian ibex	Avoider	Social	Herbivore	Yes	[16]
Capreolus capreolus	roe deer	Visitor	Social	Herbivore	Yes	[1, 3, 17]
Carollia perspicillata	Seba's short-tailed bat	Visitor/Dweller	Social	Herbivore	Yes	[18]
Castor canadensis	beaver	Visitor/Dweller	Social	Herbivore	Yes	[19]
Castor fiber	Eurasian beaver	Visitor/Dweller	Social	Herbivore	Yes	[20]
Cebus albifrons	white-fronted capuchin	Visitor	Social	Omnivore	Yes	[5]
Cebus apella	tufted capuchin	Visitor	Social	Omnivore	Yes	[5]
Cervus canadensis	elk	Visitor	Solitary	Herbivore	Yes	[19]
Cervus elaphus	red deer	Visitor	Social	Herbivore	Yes	[1, 3, 17, 21]
Cervus nippon	sika deer	Dweller	Solitary	Herbivore	Yes	[22]

Species	Common name	Urban behavior	Sociality	Trophic level	Human Consumption	References
Chlorocebus aethiops	green monkey	Visitor	Social	Herbivore	Yes	[23]
Clethrionomys glareolus	bank vole	Avoider	Solitary	Omnivore	No	[7, 8, 10]
Crocidura russula	white-toothed shrew	Dweller	Solitary	Carnivore	No	[10]
Cynopterus brachyotis	lesser short-nosed fruit bat	Visitor/Dweller	Solitary	Herbivore	Yes	[24]
Dama dama	fallow deer	Visitor	Social	Herbivore	Yes	[1, 21]
Dama mesopotamica	persian fallow deer	Visitor	Social	Herbivore	Yes	[25]
Desmodus rotundus	common vampire bat	Visitor/Dweller	Social	Carnivore	No	[18]
Diaemus youngi	white-winged vampire bat	Visitor	Social	Carnivore	No	[18]
Didelphis virginiana	opossum	Visitor/Dweller	Solitary	Omnivore	Yes	[13]
Eonycteris spelaea	cave necter bat	Visitor/Dweller	Social	Herbivore	Yes	[24]
Eptesicus serotinus	serotine bat	Dweller	Social	Carnivore	No	[26]
Gorilla gorilla beringei	mountain gorilla	Visitor	Social	Omnivore	Yes	[27]
Halichoerus grypus	grey seal	Visitor	Solitary	Carnivore	Yes	[28]
Herpestes javanicus	small indian mongoose	Dweller	Solitary	Omnivore	Yes	[29, 30]
Hipposideros diadema	diadem leaf-nosed bat	Visitor	Social	Carnivore	Yes	[24]
Lagothrix lagotricha	brown woolly monkey	Visitor	Social	Omnivore	Yes	[5]
Lepus spp.	rabbits	Visitor/Dweller	Social	Herbivore	Yes	[1, 19]
Lepus timidus	mountain hare	Visitor	Social	Herbivore	Yes	[9]
Macroglossus minimus	long-tongued nectar bat	Visitor/Dweller	Solitary	Herbivore	Yes	[24]
Marmota monax	groundhog	Dweller	Solitary	Omnivore	Yes	[13]
Mephitis mephitis	striped skunk	Dweller	Solitary	Omnivore	Yes	[13]
Micromys minutus	harvest mouse	Avoider	Social	Omnivore	No	[10]
Microtus agrestis	short-tailed field vole	Visitor	Social	Herbivore	No	[8, 10]
Microtus arvalis	common vole	Dweller	Social	Herbivore	No	[10]
Microtus montebelli	Japanese grass vole	Dweller	Social	Herbivore	No	[9]
Microtus oeconomus	northern vole	Avoider	Solitary	Herbivore	No	[10]

Species	Common name	Urban behavior	Sociality	Trophic level	Human Consumption	References
Microtus pennsylvanicus	vole	Visitor	Solitary	Omnivore	No	[13]
Mirounga angustirostris	northern elephant seal	Visitor	Solitary	Carnivore	No	[31]
Molossus molossus	velvety free-tailed bat	Visitor/Dweller	Social	Carnivore	No	[18]
Molossus rufus	black mastiff bat	Visitor/Dweller	Social	Carnivore	No	[18]
Mormoop spp.	ghost-faced bats	Dweller	Social	Carnivore	No	[18]
Mungos mungo	banded mongoose	Dweller	Social	Omnivore	Yes	[32]
Mus musculus	house mouse	Dweller	Social	Omnivore	No	[6-10, 13, 33]
Mustela siberica	Siberian weasal	Dweller	Solitary	Carnivore	Yes	[9]
Myotis bechsteinii	Bechstein's bat	Visitor	Social	Carnivore	No	[26]
Myotis brandtii	Brandt's bat	Visitor	Social	Carnivore	No	[26]
Myotis dasycneme	pond bat	Visitor/Dweller	Social	Carnivore	No	[26]
Myotis daubentonii	Daubenton's bat	Visitor/Dweller	Social	Carnivore	No	[26]
Myotis emarginatus	Geoffroy's bat	Visitor/Dweller	Social	Carnivore	Yes	[26]
Myotis myotis	greater mouse-eared bat	Visitor/Dweller	Social	Carnivore	No	[26]
Myotis mystacinus	whiskered bat	Visitor/Dweller	Social	Carnivore	Yes	[26]
Myotis natteri	Natterer's bat	Avoider	Social	Carnivore	Yes	[26]
Neomys fodiens	water shrew	Visitor/Dweller	Solitary	Carnivore	No	[8]
Noctilio leporinus	greater bulldog bat	Visitor	Social	Carnivore	No	[18]
Nyctalus noctula	common noctule	Dweller	Solitary	Carnivore	No	[26]
Nyctereutes procyonoides	Raccoon dog	Visitor	Social	Omnivore	Yes	[9]
Odocoileus hemionus	mule deer	Visitor	Social	Herbivore	Yes	[4]
Odocoileus virginianus	white-tailed deer	Visitor	Solitary	Herbivore	Yes	[2]
Ondatra zibethica	muskrat	Visitor/Dweller	Social	Herbivore	Yes	[34]
Otaria flavescens	south American seal lion	Dweller	Social	Carnivore	Yes	[35]
Ovis musimon	mouflon	Avoider	Social	Herbivore	Yes	[21]
Paguma larvata	masked palm civet	Dweller	Solitary	Omnivore	Yes	[36]

Species	Common name	Urban behavior	Sociality	Trophic level	Human Consumption	References
Pan troglodytes schweinfurthii	chimpanzees	Visitor	Social	Omnivore	Yes	[37]
Papio ursinus	chacma baboon	Visitor	Social	Omnivore	Yes	[38]
Peromyscus spp.	deer mouse	Dweller	Solitary	Omnivore	No	[13, 33]
Phacochoerus aethiopicus	desert warthog	Visitor	Social	Herbivore	Yes	[39]
Phoca vitulina	common seal	Visitor	Social	Carnivore	Yes	[40]
Phyllostomus discolor	pale spear-nosed bat	Dweller	Social	Omnivore	No	[37]
Phyllostomus hastatus	greater spear-nosed bat	Avoider	Social	Omnivore	No	[37]
Pipistrellus abramus	Japanese house bat	Dweller	Social	Carnivore	No	[9]
Pipistrellus nathusii	Nathusius' pipistrelle	Dweller	Social	Carnivore	No	[26]
Pipistrellus pipistrellus	common pipistrelle	Visitor	Solitary	Carnivore	No	[26]
Pithecia monachus	monk saki	Visitor	Social	Omnivore	Yes	[5]
Plecotus auritus	brown long-eared bat	Avoider	Social	Carnivore	No	[26]
Plecotus austriacus	grey long-eared bat	Avoider	Solitary	Carnivore	No	[26]
Procyon lotor	raccoon	Dweller	Solitary	Omnivore	Yes	[13, 36]
Pteronotus parnellii	Parnell's mustached bat	Avoider	Social	Carnivore	No	[18]
Rangifer tarandus	wild reindeer	Avoider	Social	Herbivore	Yes	[3]
Rattus norvegicus	brown rat	Dweller	Social	Omnivore	Yes	[6, 10, 13, 33]
Rattus rattus	black rat	Dweller	Social	Omnivore	Yes	[9, 41]
Rhinolophus ferrumequinum nippon	Japanese greater horseshoe bat	Visitor	Social	Carnivore	No	[9]
Rousettus amplexicaudatus	Geoffroy's rousette bat	Visitor/Dweller	Social	Herbivore	Yes	[24]
Saguinus labiatus	white-lipped tamarin	Visitor	Social	Omnivore	Yes	[5]
Saguinus mystax	moustached tamarin	Visitor	Social	Omnivore	No	[5]
Saimiri sciureus	common squirrel monkey	Visitor	Social	Omnivore	No	[5]
Scalopus aquaticus	eastern mole	Avoider	Solitary	Carnivore	No	[33]
Sciurus vulgaris	red squirrel	Dweller	Solitary	Omnivore	Yes	[42]

Species	Common name	Urban behavior	Sociality	Trophic level	Human Consumption	References
Sorex araneus	common shrew	Dweller	Solitary	Carnivore	No	[8, 10]
Sorex minutus	pygmy shrew	Dweller	Solitary	Carnivore	No	[8]
Sus scrofa	wild boar	Visitor	Social	Omnivore	Yes	[1, 9, 15-17, 21, 22, 43-46]
Sylvicapra grimmia	common duiker	Visitor	Solitary	Herbivore	Yes	[39]
Syncerus caffer	African buffalo	Avoider	Social	Herbivore	Yes	[39]
Ursus spp.	bear	Visitor/Dweller	Solitary	Omnivore	Yes	[19]
Vulpes vulpes	red fox	Dweller	Solitary	Omnivore	Yes	[9]

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Table S2: Classification of mammals into urban behavior (dwellers, visitors, avoiders or dwellers\visitors), with relevant references.

Family	Species	Common name	Urban	References
Antilocapridae	*Antilocapra americana*	pronghorn	avoider	[1]
Aotidae	*Aotus* spp	night monkeys	visitor	[2, 3]
Atelidae	*Lagothrix lagotricha*	brown woolly monkey	visitor	[4]
Atelidae	*Ateles paniscus*	red-faced spider monkey	visitor	[4]
Bovidae	*Capra pyrenaica*	iberian ibex	avoider	[5]
Bovidae	*Syncerus caffer*	African buffalo	avoider	[6]
Bovidae	*Sylvicapra grimmia*	common duiker	visitor	[7, 8]
Bovidae	*Ovis musimon*	mouflon	avoider	[9]
Callitrichidae	*Saguinus labiatus*	white-lipped tamarin	visitor	[4]
Callitrichidae	*Saguinus mystax*	moustached tamarin	visitor	[4]
Castoridae	*Castor canadensis*	beaver	visitor/dweller	[10]
Castoridae	*Castor fiber*	Eurasian beaver	visitor/dweller	[11, 12]
Cebidae	*Cebus apella*	tufted capuchin	visitor	[4]
Cebidae	*Cebus albifrons*	white-fronted capuchin	visitor	[4]
Cebidae	*Saimiri sciureus*	common squirrel monkey	visitor	[4]
Cervidae	*Alces alces*	moose	visitor	[13]
Cervidae	*Rangifer tarandus*	wild reindeer	avoider	[14]
Cervidae	*Dama mesopotamica*	persian fallow deer	visitor	[15]
Cervidae	*Alces alces*	moose	visitor	[13]
Cervidae	*Odocoileus hemionus*	mule deer	visitor	[16]
Cervidae	*Cervus canadensis*	elk	visitor	[17]
Cervidae	*Blastocerus dichotomus*	marsh deer	visitor	[18]
Cricetidae	*Microtus pennslyvanicus*	vole	visitor	[19]
Cricetidae	*Microtus agrestis*	field vole	visitor	[20, 21]
Cricetidae	*Clethrionomys glareolus*	bank vole	avoider	[22]
Cricetidae	*Microtus oeconomus*	northern vole	avoider	[23]
Cricetidae	*Microtus montebelli*	Japanese grass vole	dweller	[24]
Cricetidae	*Ondatra zibethica*	muskrat	visitor/dweller	[25, 26]
Cricetidae	*Clethrionomys glareolus*	bank vole	avoider	[22]
Cricetidae	*Microtus agrestis*	short-tailed field vole	visitor	[20, 21]
Hominidae	*Pan troglodytes schweinfurthii*	chimpanzees	visitor	[27]
Hominidae	*Gorilla gorilla beringei*	mountain gorilla	visitor	[28]
Leporidae	*Lepus* spp.	hare	visitor/dweller	[29]
Leporidae	*Lepus timidus*	mountain hare	visitor	[29]
Mormoopidae	*Mormoops*spp.	ghost-faced bats	dweller	[30]
Mormoopidae	*Pteronotus parnellii*	Parnell's mustached bat	avoider	[31, 32]
Muridae	*Micromys minutus*	harvest mouse	avoider	[33, 34]
Muridae	*Apodemus speciosus*	large Japanese field mouse	dweller	[35]

Mustelidae	*Mustela siberica*	Siberian weasal	dweller	[36]
Noctilionidae	*Noctilio leporinus*	greater bulldog bat	visitor	[31]
Otariidae	*Arctocephalus gazella*	Antarctic fur seal	avoider	[37]
Otariidae	*Otaria flavescens*	south American seal lion	dweller	[38]
Phocidae	*Halichoerus grypus*	grey seal	visitor	[39]
Phocidae	*Mirounga angustirostris*	northern elephant seal	visitor	[40]
Phocidae	Multiple spp	harbor and grey seal	visitor	[41]
Phocoenidae	*Phocoena phocoena*	harbor pourpoise seal	visitor	[41]
Phyllostomidae	*Diaemus youngi*	white-winged vampire bat	visitor	[42]
Phyllostomidae	*Phyllostomus discolor*	pale spear-nosed bat	dweller	[43]
Phyllostomidae	*Phyllostomus hastatus*	greater spear-nosed bat	avoider	[31]
Pitheciidae	*Pithecia monachus*	monk saki	visitor	[4]
Pteropodidae	*Cynopterus brachyotis*	lesser short-nosed fruit bat	visitor/dweller	[44, 45]
Pteropodidae	*Eonycteris spelaea*	cave necter bat	visitor/dweller	[46, 47]
Pteropodidae	*Macroglossus minimus*	long-tongued nectar bat	visitor/dweller	[46, 48]
Pteropodidae	*Rousettus amplexicaudatus*	Geoffroy's rousette bat	visitor/dweller	[49]
Rhinolophidae	*Hipposideros diadema*	diadem leaf-nosed bat	visitor	[46]
Soricidae	*Neomys fodiens*	water shrew	visitor/dweller	[50]
Suidae	*Phacochoerus aethiopicus*	desert warthog	visitor	[51]
Talpidae	*Scalopus aquaticus*	eastern mole	avoider	[52]
Talpidae	*Talpa micrura*	Japanese mole	visitor	[53]
Vespertilionidae	*Myotis bechsteinii*	Bechstein's bat	visitor	[54]
Vespertilionidae	*Pipistrellus nathusii*	Nathusius' pipistrelle bat	dweller	[54]
Vespertilionidae	*Myotis brandtii*	Brandt's bat	visitor	[55]
Vespertilionidae	*Myotis dasycneme*	pond bat	visitor/dweller	[56, 57]
Vespertilionidae	*Myotis daubentonii*	Daubenton's bat	visitor/dweller	[54, 58]
Vespertilionidae	*Myotis emarginatus*	Geoffroy's bat	visitor/dweller	[59, 60]
Vespertilionidae	*Myotis myotis*	greater mouse-eared bat	visitor/dweller	[54, 56]
Vespertilionidae	*Myotis mystacinus*	whiskered bat	visitor/dweller	[54, 61]
Vespertilionidae	*Myotis nattereri*	Natterer's bat	avoider	[54, 62]

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