Campylobacter in aquatic and terrestrial mammals is driven by life traits: A systematic review and meta-analysis

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Introduction: Campylobacter spp. infections are responsible for significant diarrheal disease burden across the globe, with prevalence thought to be increasing. Although wild avian species have been studied as reservoirs of Campylobacter spp., our understanding of the role of wild mammalian species in disease transmission and persistence is limited. Host factors influencing infection dynamics in wild mammals have been neglected, particularly life traits, and the role of these factors in zoonotic spillover risk is largely unknown.

Methods: Here, we conducted a systematic literature review, identifying mammalian species that had been tested for Campylobacter spp. infections (molecular and culture based). We used logistic regression to evaluate the relationship between the detection of Campylobacter spp. in feces and host life traits (urban association, trophic level, and sociality).

Results: Our analysis suggest that C. jejuni transmission is associated with urban living and trophic level. The probability of carriage was highest in urban-associated species (p =0.02793) and the most informative model included trophic level. In contrast, C. coli carriage appears to be strongly influenced by sociality (p =0.0113) with trophic level still being important. Detection of Campylobacter organisms at the genus level, however, was only associated with trophic level (p =0.0156), highlighting the importance of this trait in exposure dynamics across host and Campylobacter pathogen systems.

Discussion: While many challenges remain in the detection and characterization of Camploybacter spp., these results suggest that host life traits may have important influence on pathogen exposure and transmission dynamics, providing a useful starting point for more directed surveillance approaches.

KEYWORDS

zoonotic, Campylobacter, life histories, spillover, wildlife, foodbome pathogen

Introduction

Campylobacter spp. are a diverse group of gastrointestinal zoonotic pathogens that are responsible for an estimated 96 million cases of foodborne illness in humans annually (Kirk et al., 2015) an important cause of human illness in both economically developed and developing nations (Devleesschauwer et al., 2017). This pathogen group infects a wide range of animal hosts, although domestic species such as cattle and chickens are thought to be the largest known reservoirs of infection (Man, 2011; Wagenaar et al., 2013). Campylobacter jejuni and C. coli are the primary species associated with clinical disease in humans, but a growing number of Campylobacter spp. have been recognized as emerging human pathogens (Man, 2011). Risk factors for Campylobacter

infection include consumption of poultry, household water from wells, and exposure to animals (Levesque et al., 2013; MacDonald et al., 2015). This exposure has typically focused on occupational contact with livestock, owning a dog, or allowing animals access to sleeping and food preparation areas (Levesque et al., 2013; Mughini Gras et al., 2013; Kirk et al., 2015; MacDonald et al., 2015; Osbjer et al., 2016). Although consumption of poultry is the most common risk factor in urban environments, increased odds ratios of campylobacteriosis in rural populations are associated with poultry husbandry (Potter et al., 2003), high ruminant density (Arsenault et al., 2012), and contact with wild bird feces (Kapperud et al., 2003). Attribution studies have been performed to examine genetic similarities between clinical cases and animal isolates, with some evidence of contribution from wildlife (French et al., 2009; Strachan et al., 2009). In some studies, wildlife has also been demonstrated to be a competent reservoir of *Campylobacter*, including important human pathogens such as *C. jejuni* and *C. coli* (Weis et al., 2016; Newell et al., 2017). Wildlife may be an important source of *Campylobacter* spillover to humans, but it is unclear which species present the greatest public health risk. Challenges in both detection and characterization continue to complicate progress in this area of research (Couturier et al., 2013; Frasao et al., 2017).

Life traits and species interactions with conspecifics and socio-ecological systems

Host life traits can have important influence on the way a particular host species interfaces with conspecifics, animal communities, humans, and the environment, creating or eliminating opportunities for pathogen transmission. For example, a study carried out in Northern Botswana found that antibiotic resistance is higher in carnivores and water-associated species, demonstrating that the way an organism interacts with its environment can alter pathogen transmission and carriage (Alexander et al., 2010; Jobbins and Alexander, 2015).

Multi-host pathogens, such as *Campylobacter*, can have altered transmission dynamics in urban landscapes increasing pathogen prevalence (Woolhouse et al., 2001; Bradley and Altizer, 2007) in relation to changes in interspecific contact rates, a key determinant of multi-host pathogen transmission (Woolhouse et al., 2001; Renteria-Solis et al., 2014). Indeed, urbanization is increasingly identified as a potential driver of infectious disease emergence as it can change host spatial dynamics and pathogen transmission patterns in ways that are unpredictable (Neiderud, 2015; Hassell et al., 2017). For example, urban landscapes may alter host-pathogen dynamics directly by changing the way pathogens move through a system, or indirectly through changes to host immunocompetence or behavior (Brearley et al., 2013; Brunton et al., 2020). Urbanization has been shown to increase individual dispersal between troops in the banded mongoose (*Mungos mungo*), which may heighten the transmission risk of pathogens that spread through close contact (Verble et al., 2021). Evidence of increased stress (typically measured by fecal cortisol) and immunosuppression in urban-associated wildlife, however, is mixed. Some species associated with urban landscapes have in fact demonstrated lower stress levels and more robust immune responses, likely associated with consistent resource availability (Audet et al., 2015; Lyons et al., 2017; Iglesias-Carrasco et al., 2020). This was demonstrated in a population of banded mongoose in northern Botswana, where access to anthropogenic food sources was associated with lower levels of circulating glucocorticoids (Laver et al., 2012).

While *Campylobacter* occurs in many wildlife species, clinical signs of gastrointestinal illness or adverse health effects have rarely been observed. Two noctule bats (*Nyctalus noctula*; Hazeleger et al., 2018), a dozen rhesus monkeys (*Macaca mulatta*; Kalashnikova et al., 2002), and several vervet monkeys (*Chlorocebus pygerythrus*; Ngotho et al., 2006) infected with *Campylobacter* spp. presented with signs of acute gastrointestinal disease. These infections have the potential to cause mortality, with one wild vervet monkey dying from suspected antibiotic-resistant *Campylobacter* infection during laboratory quarantine, while several other monkeys in poor condition were euthanized (Ngotho et al., 2006). This outcome suggests that some free-ranging wildlife may be susceptible to acute *Campylobacter* infections, potentially affecting the quantity of pathogen shed into the environment and subsequent transmission to other animals and humans (Chaban et al., 2010). Even in the absence of acute signs of disease, however, evidence suggests that *Campylobacter* spp. infection in wildlife can affect body mass and overall health (Taff and Townsend, 2017).

Campylobacter transmission at the human-wildlife interface is also likely influenced by the intrinsic properties of the pathogen itself, including its persistence within infected animals across time (Inglis et al., 2004). In a study of clinical *Campylobacter* isolates, it was found that there is extensive evolutionary potential due to frequent recombination events, and that genetic exchange occurs regularly between *C. coli* and *C. jejuni*, important human pathogens (Wilson et al., 2009). This exchange may be accelerated by human activity and could increase the host range of these organisms (Sheppard et al., 2008; Waldenstrom et al., 2010; Lawton et al., 2018; Wei et al., 2019). For example, *C. jejuni* sequence type (ST)-137 was found to be widespread across wild bird taxa and has been implicated more recently in sporadic cases of campylobacteriosis (Wei et al., 2019). Hypervariable regions have also been discovered in *C. jejuni* that likely contribute to rapid evolutionary change, host range expansion, and antibiotic resistance (Parkhill et al., 2000).

A worrying trend is the emergence of multi-drug resistant (MDR) *Campylobacter*. In a study that took place in the United Kingdom, MDR *C. jejuni* was found to be widespread in poultry (Lopes et al., 2019). As livestock waste is considered an important reservoir of antibiotic resistance genes (ARGs; He et al., 2020), the risk of ARGs spreading to wildlife through this route is substantial. However, even in the absence of antibiotic use, high levels of resistance have been found in *Campylobacter* isolated from wild birds (Molina-Lopez et al., 2011; Du et al., 2019). Examples of this phenomenon are also observed in domestic species. For instance, 15% of *Campylobacter* isolates from a population of Australian chickens were fluoroquinolone-resistant without any history of exposure to this antibiotic class (Abraham et al., 2020). It has been demonstrated that *gyrA* mutations conferring fluroquinolone resistance are particularly stable and unlikely to incur fitness costs in *Campylobacter* (Luo et al., 2005; Luangtongkum et al., 2009). There are additional mechanisms that may allow for the persistence of antibiotic resistance genes in the absence of selective pressure, such as fitness-enhancing compensation from other regions of the genome and co-selection with genes that confer an evolutionary advantage (Melnyk et al., 2015). Monitoring antibiotic resistance in *Campylobacter* will remain key in reducing its spread and preserving the therapeutic agents available to treat disease.

While wildlife is considered an important reservoir of *Campylobacter* spp., our understanding of infection and transmission dynamics is mostly limited to avian species. The current body of evidence of *Campylobacter* among mammalian wildlife hosts is inadequate to fully

utilize a One Health approach to disease control strategies. Here, we review and summarize the literature concerning *Campylobacter* infection in wildlife hosts, identifying and expanding our current understanding of *Campylobacter* in mammalian wildlife species. Using infection detection data, we assess the potential influence of host life history traits such as trophic level, urban association, and sociality on the probability of *Campylobacter* carriage in wildlife species. We discuss these results and study limitations as well as implications to *Campylobacter* transmission dynamics and surveillance and management approaches.

Methods

Literature review

This study followed guidelines provided under the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA), a framework for the standardization of reviews and meta-analyses (Page et al., 2021). Briefly, published studies of *Campylobacter* in wildlife were retrieved from online scientific search engines (Web of Science, PubMed, Google Scholar) using the key words: 'wildlife + *Campylobacter*' and 'wild mammals + *Campylobacter*.' Only the first 300 records from each query in Google Scholar were screened, as this resource was considered a secondary database to capture articles not located on Web of Science or PubMed (Haddaway et al., 2015; Gusenbauer and Haddaway, 2020). Duplicate records were removed automatically using EndNote 20, a reference manager (The EndNote Team, 2013). Reference lists of pertinent publications were searched for additional related articles. Information was retrieved on the location of sample collection, order, genus, and species studied, animal status (captive, wild feces or wild carcass), detection of *Campylobacter* spp. and particular *Campylobacter* species identified, and method of testing used (culture and PCR or other molecular methods).

Classification of life traits

Mammals that had *Campylobacter* detection data were categorized by trophic level (herbivore, omnivore, and carnivore) and sociality using the PanTHERIA database (Jones et al., 2009) and the Animal Diversity Web (ADW; Myers et al., 2019). In cases where species are occasionally omnivores but are primarily 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 a species lived alone or within a social group (Myers et al., 2019). Mammals were also classified based on their association with urban areas. The classification system from Santini et al. (Santini et al., 2019) 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'). Per this classification system, species that are classified as urban 'dwellers' have been demonstrated to utilize urban areas for all resources, while 'visitors' may exist in urban areas for some parts of their life cycle, but still obtain most resources from natural environments. Urban association for species that were not included in the Santini et al. (Santini et al., 2019) review were searched for using 'taxon name (genus and species) + urban, urbanization or humans' (Supplementary 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. Several marine and alpine species were assumed to be avoiders

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 (IUCN, 2019) and Mildenstein et al. (2016) for some bat species.

Statistical analyses

Once data had been compiled, duplicate records were removed from the original database through an automated process using EndNote 20 (The EndNote Team, 2013). 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 1,168; *Sus scrofa*), we used a dummy categorical variable for *Campylobacter* presence in wildlife species, with 1 indicating that *Campylobacter* spp. had been detected (culture and/or polymerase chain reaction (PCR) based methods) or 0 indicating no *Campylobacter* spp. detection. This dummy variable was used to create graphs and carry out statistical analyses of the data. If at least one study of a species reported the detection of *Campylobacter* spp., it was recorded as present for the purposes of analysis. For studies that only identified *Campylobacter* to the genus level or where the authors did not attempt to detect *C. jejuni* or *C. coli*, no data was recorded at the species level and this field was left blank. All statistical analyses were conducted in R 4.1.2, an open source integrated programming environment (R Core Development Team, 2022). To investigate the effect of the categorical input variables (trophic level, urban association, and sociality) on the binary presence/absence of *Campylobacter*, *C. jejuni*, and *C. coli*, a series of logistic regression (LR) models were created in order to determine the ability of a model to predict carriage of either *Campylobacter* genus or the two species of *Campylobacter* analyzed in this study (*C. jejuni* and *C. coli*). An important assumption of LR models is that multicollinearity does not exist among the predictors. The generalized variance inflation factor (GVIF) was used to assess for multicollinearity in the predictor variables of all models used for analysis. GVIF is generally corrected by ½ degrees of freedom (df) when applied to categorical variables, and a cutoff of 1.73 following (Usio, 2020) was used, with independent variables below this threshold having little-to-no correlation. To obtain the $GVIF^{1/2df}$ value, we used the *vif* function of the *car* package (Fox et al., 2012). No independent variables in the models had $GVIF^{1/2df}$ values significantly above 1, indicating that multicollinearity was not present in this dataset.

We use the Akaike information criterion (AIC) to score and select the model with the best fit for the data balanced against the number of model parameters included (Aho et al., 2014). For this analysis we use the AICc, which is a sample size adjusted formula to calculate AIC (Bedrick and Tsai, 1994), due to the relatively low sample size ($n = 128$). AICc values were generated using *AICcmodavg* (Mazerolle and Mazerolle, 2017) and the model with the lowest AICc value was chosen as the best fit and used in additional analyses. The *predict* function in R 4.1.2 was used to estimate the probability of pathogen carriage for each level of the factors included in the in our top model. Data were visualized and graphed using *ggplot2* (Wickham et al., 2016). Summary statistics were generated using the *janitor* package (Firke, 2021).

Results

We identified 65 published papers (1985–2021) and included these in our analysis representing 128 different free-ranging mammal species

across 38 families and 9 orders. The plurality of studies was conducted on European wildlife ($n = 30$), but many world regions, including North America ($n = 11$), South America ($n = 3$), the Caribbean ($n = 4$), the Middle East ($n = 2$), Africa ($n = 6$), Asia ($n = 6$), Oceania ($n = 1$) and Antarctica ($n = 2$) were represented (See Supplementary materials S2), having at least one published study on *Campylobacter* spp. in mammalian wildlife. *Campylobacter* spp., *C. jejuni*, and *C. coli* carriage was detected by culture ($n = 56$), PCR (or other molecular methods; $n = 6$), or both ($n = 2$). One study used microarray for detection of *Campylobacter* (Jaing et al., 2015). Additionally, two of the studies that utilized culture techniques leveraged matrix-assisted laser desorption/ ionization (MALDI-TOF) mass spectrometry for species identification. Four papers were included that investigated *Campylobacter* spp. in wildlife carcasses destined for human consumption. A full list of species, references, and associated data included in our statistical analyses are listed in Supplementary Table S2. As a species was often covered by multiple studies, there were many cases of redundancy in data that were removed for the analysis. An additional 11 studies analyzed *Campylobacter* spp. presence in captive wild mammals. These studies were excluded from statistical analysis but included below due to the added value they provide in understanding *Campylobacter* spp. carriage in wildlife species.

Campylobacter spp. presence was only correlated with trophic level in the model containing the highest explanatory power (lowest AICc, ΔAICc value of 1.5; Table 1). Based on this model, omnivores are significantly more likely to carry the *Campylobacter* genus than either herbivores or carnivores (*p* value = 0.0156, Table 2). Given the breath of *Campylobacter* and host species included in the genus level analysis, this finding suggests that trophic position has an important cross-species influence on exposure dynamics for this pathogen group. Urban association and sociality life traits would appear to have a more heterogenous influence across the various *Campylobacter* pathogen-wildlife host systems.

C. jejuni presence was best predicted by urban association and trophic level (ΔAICc value of 1.17, Table 3). There was not a significant interactive effect, as the model with an interactive term performed worse than a null model (carriage predicted by 1). Based on the model containing urban association and trophic level, urban dwellers were significantly more likely to be positive for *C. jejuni* than urban avoiders (*p* value = 0.0279, Table 4). While trophic level is

included in the model with the lowest AICc value and omnivores seem to differ from carnivores in their likelihood of carrying *C. jejuni*, this effect was not quite to the level of statistical significance (*p* = 0.058, Table 4). This may be due to the relatively low sample size used in the analysis.

C. coli carriage was highly correlated with both sociality and trophic level in this analysis, as the model with the AICc included both variables (Table 5). Omnivores were significantly more likely than carnivores to carry the pathogen (*p* = 0.0282), with herbivores showing no significant difference from carnivores (*p* = 0.0977). Solitary species were less likely than social species to carry *C. coli* in our analysis (*p* = 0.0113, Table 6). Much like our analysis of *C. jejuni*, the interaction between these two variables does not appear to be significant in prediction of carriage.

Discussion

Across 65 reviewed publications meeting our criteria, infection detection was identified across a wide array and included 128 species with varying life traits and *Campylobacter* infection status. Our analysis indicates that life traits can have an important influence on the probability of *Campylobacter* carriage and transmission potential with dynamics in wildlife likely complex, involving interdependent interactions between host, pathogen, and the environment. Summary statistics by life history trait are provided in Table 7. Host factors driving infection in wildlife are multifaceted with life traits, such as sociality and trophic level appearing to influence disease transmission dynamics (Kriger and Hero, 2007; Johnson et al., 2012; VanderWaal et al., 2014). As an example, it has been demonstrated that parasite diversity is higher in bird species that utilize a wider variety of food sources (Gutiérrez et al., 2019). Host space use has been identified as an important factor influencing pathogen transmission and persistence dynamics (VanderWaal and Ezenwa, 2016). Similarly, trophic level and diet can alter pathogen exposure dynamics, with previous studies identifying an association between pathogen prevalence and carnivores in some multi-host pathogen systems (Moore et al., 2010; Hollings et al., 2013) which has recently been proposed as a form of accumulation due to the diversity of pathogen exposure from prey (Malmberg et al., 2021). Carnivores and water-associated species were shown to have a higher prevalence of antibiotic-resistant *E. coli* in a previous study (Jobbins and

TABLE 1 AICc output for *Campylobacter* genus logistic regression models.

Model	K	AICc	Delta_AICc	AICcWt	*Cum*.Wt	LL
Campy ~ trophic	3	175.1983	0	1	0.390461	−84.5024
Campy ~ trophic sociality + interaction	6	176.6988	1.500488	0.472251	0.574856	−82.0023
Campy ~ trophic + sociality	4	177.2206	2.0223	0.3638	0.716906	−84.4477
Campy ~ 1 (null)	1	177.9431	2.744766	0.253502	0.815889	−87.9557
Campy ~ urban + trophic	6	179.6512	4.45285	0.107914	0.858025	−83.4785
Campy ~ urban + trophic + interaction	12	179.7306	4.532233	0.103714	0.898521	−87.8173
Campy ~ urban	4	179.8723	4.673984	0.096618	0.936247	−85.7736
Campy ~ sociality	2	180.0615	4.86314	0.087899	0.970568	−76.6742
Campy ~ urban + trophic + sociality	7	181.8307	6.632329	0.036292	0.984738	−83.4487
Campy ~ urban + sociality	5	181.982	6.783648	0.033647	0.997876	−85.7451
Campy ~ urban + sociality + interaction	8	185.6265	10.42812	0.00544	1	−84.2082

Note that the model with the lowest AICc value (delta AIC of 1.36) contains only trophic level as an explanatory variable. The next best model contains sociality and trophic level as well as an interaction term.

Alexander, 2015), further reinforcing the importance of life history traits in the evaluation of infectious disease dynamics.

Life history traits

Trophic level

Diet can provide a critical influence on infectious disease exposure and transmission (Fischer et al., 2005) with results from our meta-analysis indicating that they may influence *Campylobacter* spp. transmission patterns in wildlife as well. Omnivores are more likely to carry *Campylobacter* than herbivores or carnivores (Figure 1), which may be related to differences in host foraging behavior or bacterial survival rates in different environments. Trophic level did not seem to be as important in the transmission of *C. coli*, although the best performing model in the prediction of *C. jejuni* carriage included this variable, suggesting that it may be important for this species or that there is an interaction between trophic level and urban association. A model including an interactive term, however, did not reveal a significant interaction between these variables and did not perform as well in model comparison as the model without the interactive term (Table 2).

Urbanization

Urbanization did not appear to predict carriage of the *Campylobacter* genus, based on our analysis. However, wildlife species that utilize the urban landscape (urban dwellers) were significantly more likely using logistic regression to carry *C. jejuni* than urban avoiders (Figure 2).

TABLE 2 Logistic regression output for the best explanatory model (*Campylobacter* ~ trophic).

Factor level	Estimate	Std. Error	z Value	Pr(>|z|)
Carnivore	−0.6931	0.3273	−2.118	0.0382*
Herbivore	0.1967	0.4712	0.417	0.6793
Omnivore	1.1558	0.4506	2.565	**0.0156**

Significant results are bolded. Note that omnivores are significantly more likely to carry *Campylobacter* than carnivores and herbivores. Please also note that the significant value for carnivores indicates only that the estimate (logit) is significantly different from zero.

C. jejuni is considered an important zoonotic human pathogen and is ubiquitous in domestic poultry. Urban dwellers are more likely than avoiders to ingest waste from humans and domestic animals infected with *C. jejuni*. This has been demonstrated in wild birds, with those feeding on refuse more likely to carry *Campylobacter* than those that forage on natural food sources (Kapperud and Rosef, 1983). Additionally, *C. jejuni* has been found in raccoons and civets inhabiting urban centers (Lee et al., 2011), rodents overwintering in human dwellings (Lõhmus and Albihn, 2013) and even in wildlife feces on playgrounds (French et al., 2009; Abdollahpour et al., 2015). However, the occurrence of *C. jejuni* in wildlife species is not exclusively dependent on transmission from human sources. Wild birds are also known carriers of *C. jejuni*, having their own distinct *C. jejuni* subtypes (Ramonaite et al., 2014), and may act as a reservoir for other wildlife species in these environments. Wild-bird associated *C. jejuni* is also commonly found in water sources (Mughini-Gras et al., 2016) and may be responsible for a small fraction of human campylobacteriosis cases annually (Cody et al., 2015). In a recent study, 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 exposure to water sources used by migratory birds thought to be the primary source of infection (Khoshbakht et al., 2015). Interestingly, *C. coli* carriage was not associated with how an organism utilizes the urban environment, with no difference found between urban avoiders and dwellers or visitors/ dwellers. *Campylobacter coli* is primarily associated with swine production systems, and previous studies have identified an overall reduced risk of *C. coli* infection in humans who live in urban areas (Roux et al., 2013) consistent with the limited number of swine expected in these environments.

Sociality

Sociality did not appear to be important in the carriage of *Campylobacter* at the genus level or in the carriage of *C. jejuni*. Interestingly, from our analysis it has demonstrated importance in the carriage of *C. coli*, with social species more likely to carry this pathogen (Figure 3). A study of *C. coli* prevalence in feral pigs found a significant difference between males and females, with males more likely to carry the bacteria (Cummings et al., 2018). It was postulated that this was due to the social structure of pigs, as males are more likely to

TABLE 3 AICc values for logistic regression models with *C. jejuni* presence/absence as the output variable.

Model	K	AICc	Delta_AICc	AICcWt	*Cum*.Wt	LL
C. jejuni ~ urban + trophic	6	138.4256278	0	1	0.331347	−62.7798
C. jejuni ~ urban + sociality	5	139.6037136	1.178085794	0.554858087	0.515198	−66.6819
C. jejuni ~ urban + trophic + sociality	7	140.0756225	1.64999462	0.438236171	0.660406	−64.7317
C. jejuni ~ trophic	3	140.5290637	2.103435884	0.349337092	0.776158	−62.6812
C. jejuni ~ trophic + sociality	4	141.3321862	2.906558327	0.233802353	0.853628	−66.4641
C. jejuni ~ 1 (null)	1	142.343611	3.91798318	0.141000536	0.900348	−70.1522
C. jejuni ~ urban + sociality + interaction	8	143.6562944	5.230666526	0.073143409	0.924584	−65.3952
C. jejuni ~ trophic + sociality + interaction	6	143.8500115	5.424383616	0.066391131	0.946582	−69.8656
C. jejuni ~ urban + trophic + interaction	12	143.8500115	5.424383616	0.066391131	0.968581	−69.8656
C. jejuni ~ urban	2	144.2745202	5.8488924	0.05369442	0.986372	−63.3794
C. jejuni ~ sociality	2	144.8077785	6.382150621	0.041127622	1	−58.6896

Note that the model with the input variables urban association and trophic level has the lowest AICc value, although the delta AIC value is under the 2 that is usually indicated as a significant difference in the explanatory power of models. However, the models with the lowest AICc all contain urban association as a predictor variable, suggesting that it is important in the transmission dynamics of *Campylobacter*.

be solitary. Our results indicate that solitary species are less likely to carry *C. coli*, but there may exist heterogeneity across species, geographic areas, and a host of other factors. Different risk factors have been associated with *C. coli* and *C. jejuni* in human infections, including age, season and location (Gillespie et al., 2002; Roux et al., 2013), which implies that different risk factors could also be associated with *C. coli* in wildlife. Similar differences in transmission pathways may also explain why *C. coli* was more common in social than solitary species.

Public health implications

Consumption of wild game/bush meat

Overall, we found that almost 50% of wildlife species used as human food resources were positive for *Campylobacter* spp., with 31% positive for *C. jejuni* and 26% positive for *C. coli*, highlighting an important public health concern. This is a concern that is not entirely restricted to the developing world, however, with many developed countries having high prevalence of the pathogen group. For example, it was found that 9.1% of diarrheic patients in Alberta over a one-year period were positive for *Campylobacter* (Inglis et al., 2021). Additionally, some

TABLE 4 Summary statistics for the logistic regression model (*C. jejuni* ~ urban + trophic).

Factor level	Estimate	Std Error	z	Pr(>|z|)
Avoider	−2.9386	1.1202	−2.623	0.00871*
Dweller	2.4765	1.1266	2.198	**0.02793**
Visitor	1.9762	1.1027	1.792	0.07310
Visitor/ Dweller	2.2451	1.1463	1.959	0.05016
Herbivore	0.3161	0.5900	0.536	0.59210
Omnivore	1.0254	0.5416	1.1893	0.05834

Significant results are bolded. Note that urban dwellers and dwellers/visitors are significantly more likely to carry *C. jejuni* than urban avoiders. Please also note that the significant value for urban avoiders only indicates that the estimate of effect is significantly different from zero.

wildlife species consumed by humans contained antimicrobial resistant (AMR) strains of *Campylobacter* spp., which may have important implications to AMR transmission dynamics and public health (Sasaki et al., 2013).

Although there is an association between *Campylobacter* spp. presence and wildlife consumed by humans, there is not strong evidence from the literature implicating game meat as a significant public health threat. *Campylobacter* spp. were only rarely detected in moose (*Alces alces*; 6%) and deer (*Odocoileus virginianus*; 2%) carcasses in Finland (Sauvala et al., 2019), hares (*Lepus timidus*; 4.3%) in Norway (Rosef et al., 1983), and were not detected in any deer carcasses (*Capreolus capreolus* and *Cervus elaphus*) in Germany (Atanassova et al., 2008). Pyrenean chamois (*Rupicapra pyrenaica*) a game species harvested was also not found to harbor *Campylobacter* spp. (Espunyes et al., 2021) in a study conducted in Spain. *Campylobacter* was not detected in monkey, porcupine, duiker or river hog muscle meat (n = 104) in Gabon (Bachand et al., 2012). Results from wild boar studies have been more varied, with some detecting no or low *Campylobacter* spp. prevalence (Atanassova et al., 2008; Wacheck et al., 2009; Cummings et al., 2018), and others detecting high *Campylobacter* spp. prevalence (Jay-Russell et al., 2012; Díaz-Sánchez et al., 2013; Sasaki et al., 2013). 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* (Díaz-Sánchez et al., 2013). 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 (Navarro-Gonzalez et al., 2014), and found that it was significantly higher (*p* < 0.01) in wild boar than free-ranging cattle (Navarro-Gonzalez et al., 2014). *Campylobacter lanienae* has primarily been isolated from livestock and slaughterhouse workers, and its pathogenicity and role as a human gastrointestinal pathogen is not well understood (Guévremont et al., 2008; Oporto and Hurtado, 2011). Other species commonly isolated from wild boar include *C. hyointestinalis* (Sasaki et al., 2013), while *C. coli* and *C. jejuni* have been consistently less common (Jay-Russell et al., 2012; Cummings et al., 2018).

If there is a public health concern from wild game, it looks to be associated with cross-contamination during butchering and

TABLE 5 AICc output for *C. coli* logistic regression models.

Model	K	AICc	Delta_AICc	AICcWt	*Cum*.Wt	LL
C. coli ~ trophic + sociality	4	96.03855	0	1	0.499323	−43.8065
C. coli ~ sociality	2	98.01888	1.980333	0.371515	0.684829	−46.9469
C. coli ~ trophic + sociality + interaction	6	98.07086	2.032305	0.361985	0.865576	−42.5789
C. coli ~ trophic	3	100.812	4.773411	0.091932	0.91148	−45.0834
C. coli ~ urban + sociality	5	100.9031	4.864507	0.087839	0.955339	−42.8361
C. coli ~ urban + trophic + sociality	7	102.0795	6.040953	0.048778	0.979695	−47.9134
C. coli ~ 1 (null)	1	104.3584	8.319898	0.015608	0.987489	−51.1586
C. coli ~ urban + trophic	6	104.6789	8.64037	0.013297	0.994129	−43.5395
C. coli ~ urban + sociality + interaction	8	106.0756	10.03703	0.006614	0.997431	−46.5813
C. coli ~ urban	4	106.6288	10.59029	0.005016	0.999936	−49.1017
C. coli ~ urban + trophic + interaction	12	113.9627	17.92412	0.000128	1	−43.1674

The model with the lowest AICc includes trophic level and sociality as predictor variables, the only *Campylobacter* species examined for which sociality seems to be important in the prediction of carriage.

processing as in most food systems. For example, Stella et al. (2018) 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 (Mpalang et al., 2013). Although the risk of infection from consuming wild game meat is lower than that from poultry, communities who rely heavily on this food source should exercise caution during butchering to reduce exposure.

Wildlife transmission to livestock and humans

As *Campylobacter* is primarily a foodborne pathogen, a pressing concern is the role of wildlife in pathogen transmission to domestic species commonly consumed by humans. There is conflicting evidence regarding the role of wildlife in *Campylobacter* transmission to livestock and poultry species. In one study from Spain, *Campylobacter* spp. from

TABLE 6 Logistic regression output for the model with the highest explanatory power (*C. coli* ~ sociality + trophic).

Factor level	Estimate	Std. Error	z value	Pr(>|z|)
Carnivore	−2.1227	0.7507	−2.827	0.0047
Herbivore	1.4183	0.8564	1.656	0.0977
Omnivore	1.8371	0.8376	2.193	**0.0282**
Solitary	−1.7356	0.6848	−2.534	**0.0113**

Significant results are bolded. Note that omnivores and solitary species are significantly more likely to carry *C. coli*. An interactive term did not increase the explanatory power of the model and was therefore not considered further.

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 (Navarro-Gonzalez et al., 2014). 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 (French et al., 2005; Jensen et al., 2006; Meerburg et al., 2006; Sippy et al., 2012; Olkkola et al., 2021). When wildlife-specific strains were compared to generalist strains, there were genetic regions missing from wildlife-specific strains that may explain why they are unable to colonize a wide host range (Hepworth et al., 2011). Although Viswanathan et al. (2017) found most *C. jejuni* isolates phylogenetically grouped into distinct wildlife and livestock clusters, 31.25% (5/16) of dairy cattle isolates and 17.6% (3/17) of beef cattle isolates clustered with small mammal (raccoons, skunks and mice) isolates collected from farms, suggesting that transmission is occurring between wildlife and livestock in this landscape type. 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 United Kingdom found little genetic overlap between cattle and wild birds, but rabbit isolates were genetically similar to cattle isolates (Kwan et al., 2008).

Additional studies have identified identical *Campylobacter* spp. clones from rodents, sparrows, flies and livestock (Adhikari et al., 2004), and high genetic similarity between *Campylobacter* spp. isolated from wild birds, mice and poultry (Hiett et al., 2002). This genetic similarity across isolates can create increased transmission risk to poultry flocks, as an environment contaminated with feces from other animals is a risk factor for poultry infection with *Campylobacter* spp. (Ellis-Iversen et al., 2012). An increased transmission risk to poultry flocks may also increase risk to humans, as demonstrated by a study in England which found significant overlap of *Campylobacter* sequence types between animals and humans (Wilson et al., 2008). It is also worth noting that *Campylobacter* has been demonstrated to form distinct genetic clusters that differ in pathogenicity

TABLE 7 Summary statistics by organism and life history trait.

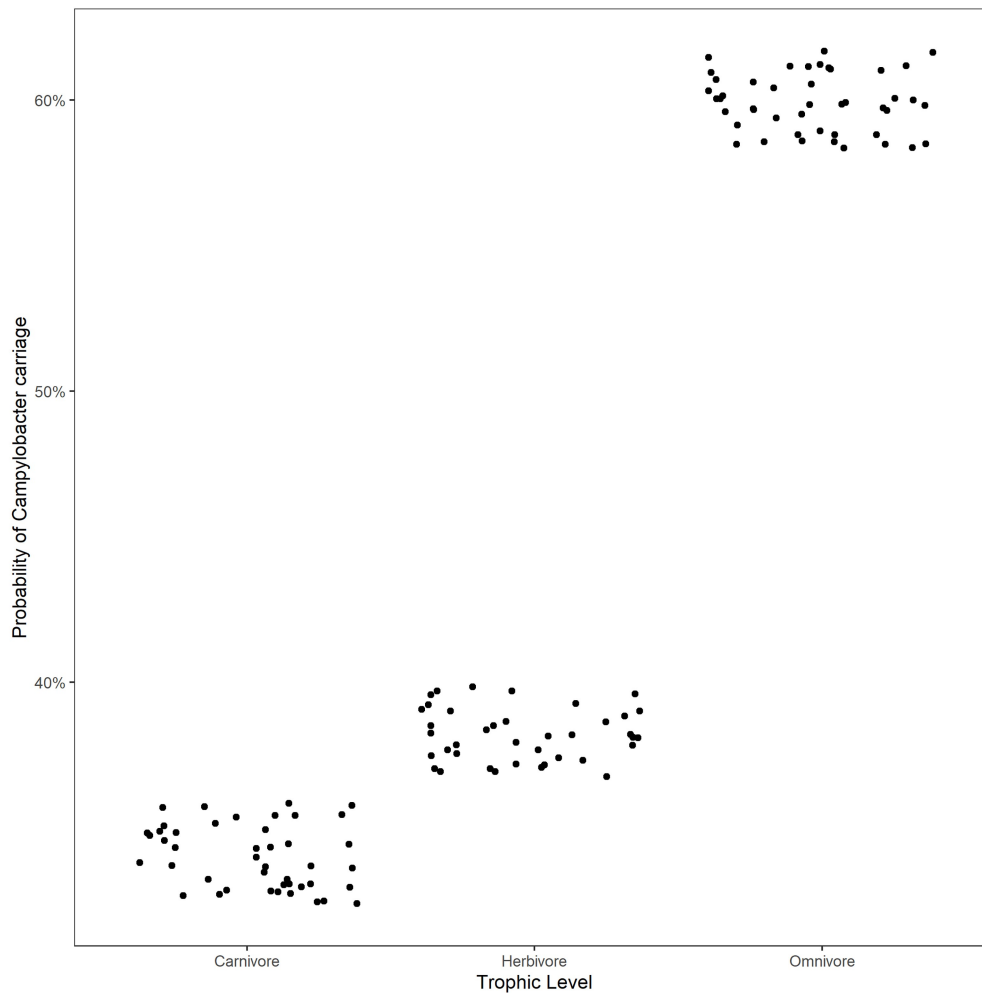| *Campylobacter*	Urban Association				Trophic level			Sociality		
	Avoider	Dweller	Visitor	Visitor/Dweller	Carnivore	Herbivore	Omnivore	Social	Solitary	Total
Absent	18% (12)	25% (18)	31% (22)	26% (19)	41% (29)	34% (24)	25% (18)	68% (45)	32% (2\3)	71
Present	11% (6)	35% (20)	39% (22)	16% (9)	26% (15)	26% (15)	47% (27)	63% (36)	37% (21)	57
Total	16% (18)	30% (38)	34% (44)	20% (28)	34% (44)	30% (39)	35% (45)	66% (84)	34% (44)	128
C. jejuni										
	Avoider	Dweller	Visitor	Visitor/Dweller	Carnivore	Herbivore	Omnivore	Social	Solitary	Total
Absent	21% (13)	24% (15)	35% (22)	19% (12)	34% (21)	37% (23)	29% (18)	61% (38)	39% (24)	62
Present	2% (1)	43% (18)	36% (15)	19% (8)	21% (9)	21% (9)	55% (23)	57% (24)	43% (18)	42
Not detected	17% (4)	21% (5)	29% (7)	33% (8)	58% (14)	25% (6)	17% (4)	85% (17)	15% (3)	24
Total	16% (18)	30% (38)	36% (44)	18% (28)	34% (44)	30% (39)	35% (45)	64% (79)	36% (45)	128
C. coli										
	Avoider	Dweller	Visitor	Visitor/Dweller	Carnivore	Herbivore	Omnivore	Social	Solitary	
Absent	16% (13)	32% (25)	32% (25)	19% (15)	36% (28)	29% (23)	35% (27)	53% (41)	47% (37)	78
Present	5% (1)	29% (6)	52% (11)	14% (3)	10% (2)	38% (8)	52% (11)	86% (18)	14% (3)	21
Not detected	21% (6)	24% (7)	28% (8)	28% (8)	48% (14)	28% (7\8)	24% (7)	86% (25)	14% (4)	29
Total	16% (18)	30% (38)	34% (44)	20% (28)	34% (44)	30% (39)	35% (45)	66% (84)	34% (44)	128

FIGURE 1
Probability of *Campylobacter* carriage at different trophic levels.

([Carvalho et al., 2001](#)). If such clusters are found circulating in animal species, they may represent a heightened risk to associated humans.

It is unclear whether wildlife may acquire *Campylobacter* spp. infections from livestock and/or the environment. In a study of wild rodents across chicken and pig farms, *Campylobacter* species in rodents varied between farm type, with *C. jejuni* more common on poultry farms and *C. coli* more common on pig farms ([Backhans et al., 2013](#)). A survey of omnivorous mesopredators in Canada (skunks, raccoons, and opossums) associated with swine farms revealed the presence of *C. jejuni* and *C. upsaliensis*, but not *C. coli* which is typically associated with swine ([Bondo et al., 2019](#)). Further analysis of mammalian wildlife and livestock species that incorporates both behavior and phylogenetic analysis of *Campylobacter* spp. is necessary and has demonstrated value in wild bird studies ([Taff et al., 2016](#)). It is difficult to make broad conclusions on the role of wildlife in agricultural *Campylobacter* transmission dynamics as most studies have been limited to the United States and Europe. Food production systems are increasingly globalized, so it will be important to understand the role of the various wildlife species across landscapes ([Van Nierop et al., 2005; Suzuki and Yamamoto, 2009; Adzitey et al., 2012; Perdoncini et al., 2015](#)).

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 and did not include *Campylobacter* prevalence data, removing some of the complexity of the original datasets. Prevalence often varied greatly between species and studies, ranging between 1 to 87.5%. These differences in prevalence likely create differential transmission risks, a potential area of future research. Culture and detection methods also varied greatly between the studies which can have a significant impact on the prevalence, species and genotypes isolated ([Williams et al., 2012; Hetman et al., 2020](#)). Detection methods often are biased toward *C. jejuni* and *C. coli* isolation which can skew the representation of *Campylobacter* species present ([Lastovica and le Roux, 2000](#)). Importantly, there have been relatively few studies about *Campylobacter upsaliensis*, especially in free-ranging wild mammals. This species is suspected to be an emerging human pathogen and has been isolated from domestic animals such as dogs with some frequency ([Bourke et al., 1998; Man, 2011; Couturier et al., 2012](#)). The age and storage of feces also impacts *Campylobacter* isolation, with fresh fecal samples significantly more likely to likely to be positive for *Campylobacter* spp. than older feces using culture methods
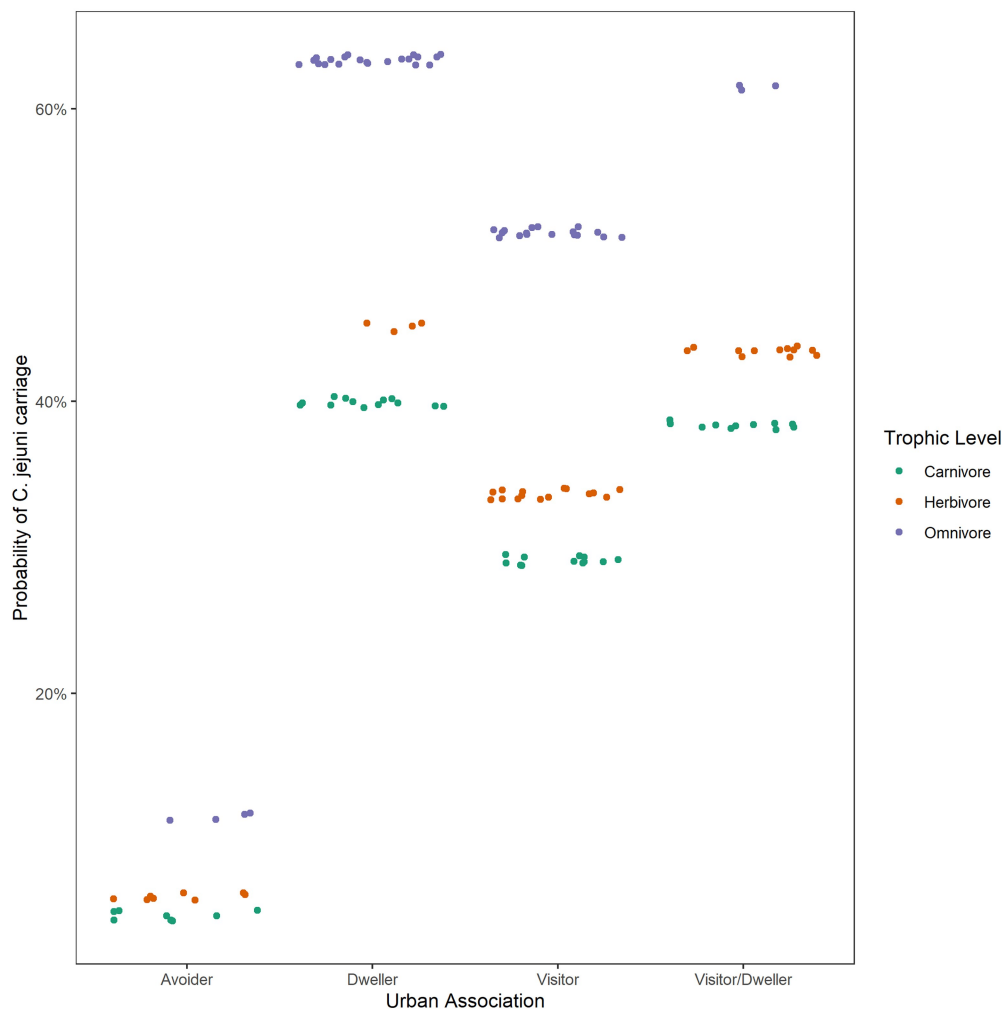
FIGURE 2
Probability of *C. jejuni* carriage at different trophic levels and degrees of urban association.

([Abdollahpour et al., 2015]). In a study performed using sheep feces sampled and placed back into the environment ([Jackson et al., 2009]), the authors found that *Campylobacter* died rapidly. Another phenomenon in *Campylobacter* spp. that complicates isolation is the progression to a viable but non-culturable (VBNC) state under harsh conditions ([Moriarty et al., 2011]). This may be particularly relevant for *Campylobacter* isolation from wildlife samples, especially if samples are taken from remote sites. Culture methods have also been found to be inferior to immunoassay and molecular methods for sensitivity and specificity of *Campylobacter* detection ([Buss et al., 2019]).

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 have occurred in developing countries where *Campylobacter* burden is highest ([Troeger et al., 2017]), transmission dynamics may differ ([Platts-Mills and Kosek, 2014]), and limited resources may increase the dificulty of investigations. There is also a lack of phylogenetic information on *Campylobacter* spp. in mammalian wildlife. *Campylobacter* spp. possess the ability to evolve rapidly ([Wilson et al., 2009]) which suggests that the relationship between wildlife-associated *Campylobacter* and human-associated *Campylobacter* may be obscured. Most papers that incorporate genetic or phylogenetic information rely on MLST techniques which

have been the gold-standard for defining clonal groups but have been shown to be inferior at establishing epidemiological dynamics ([Llarena et al., 2017]). Only two recent papers incorporate WGS on free-ranging wildlife and both papers found human-associated *Campylobacter* genotypes in their respective wildlife species ([Baily et al., 2015]; [Hazeleger et al., 2018]). Future research should incorporate WGS methods into targeted studies of species at the human-wildlife interface that are most likely to contribute to *Campylobacter* transmission and human disease.

Conclusion

Multi-host pathogens, such as *Campylobacter,* have complex interdependent transmission dynamics that can be altered by landscape changes and host life traits. Our understanding of *Campylobacter* spp. in mammals at the human-wildlife interface is limited, but it is important to understand these dynamics to effectively model and predict transmission risk and public and animal health needs. As large-scale surveillance of *Campylobacter* is economically unfeasible, this study may optimize efforts by identifying the wildlife species most likely to contribute to *Campylobacter* infections in humans. In this study, we found that life traits significantly influenced the presence of *Campylobacter* spp. in free-ranging wildlife. Most
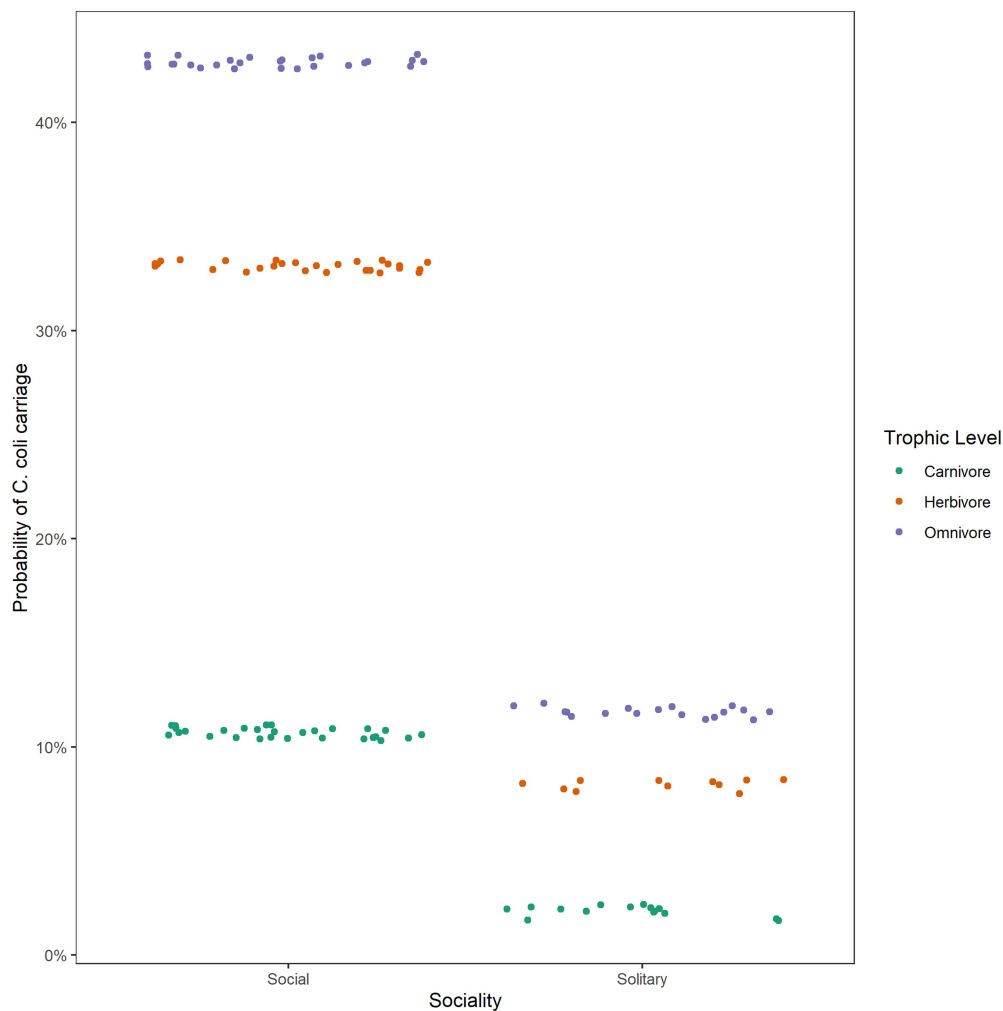
FIGURE 3
Probability of *C. coli* carriage at different levels of sociality and urban association.

importantly, urban association is strongly correlated with *C. jejuni* presence (Figure 4) and trophic level was important across all pathogens, with omnivores more likely to carry *Campylobacter* spp. Additionally, sociality is strongly correlated with *C. coli* presence. These results demonstrate that life traits must be leveraged as a powerful tool for identifying points of increased zoonotic spillover risk across the landscape. *Campylobacter* is a rapidly evolving pathogen at the human-animal interface; therefore, targeted monitoring of urban-associated species will be important for understanding transmission dynamics and protecting public health.

Author's note

As demonstrated with the recent emergence of SARS-CoV-2 and the ensuing global pandemic, our ability to predict pathogen emergence remains extremely limited, influenced strongly by the complexity of interdependent factors that drive these processes. Using published literature and *Campylobacter* spp. infection detection in wild mammalian species, we identify the potential usefulness of key life traits that may predict a heightened risk of infection with this multi-host pathogen. Across host-pathogen systems, this approach may provide a useful framework for identifying host factors that influence pathogen transmission potential.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

KA: conceptualization, funding acquisition, project administration, and resources. MB, SM, and KA: data curation, methodology, software, visualization, and validation. MB and SM: formal analysis and Investigation. KA and MP: supervision. KA, MB, SM, and MP: writing – original draft preparation. KA, MB, and MP: writing – reviewing and editing. All authors contributed to the article and approved the submitted version.
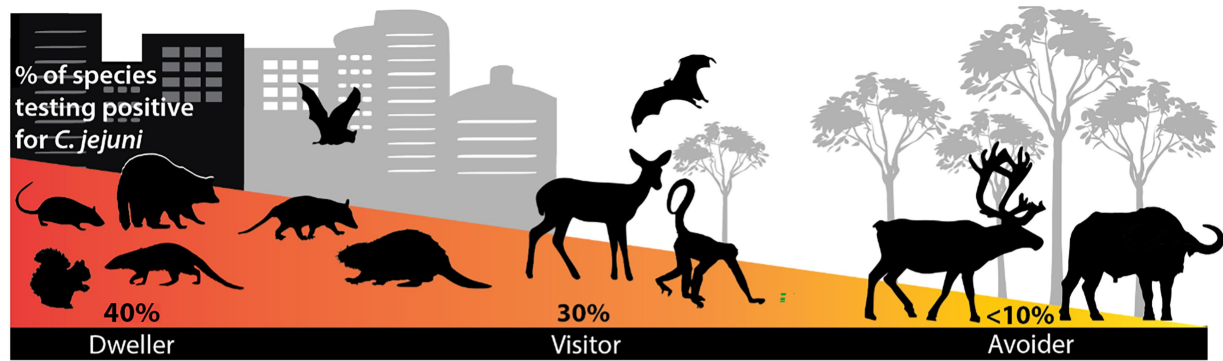
Funding

FIGURE 4
Difference in *C. jejuni* detection among wild mammalian species based on urban behavior. Urban dwellers had a higher probability of carrying *C. jejuni* than urban avoiders.

Conflict of interest

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

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Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1070519/full#supplementary-material

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