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Hyperendemic *Campylobacter jejuni* in guinea pigs (*Cavia porcellus*) raised for food in a semi-rural community of Quito, Ecuador

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Summary

Domestic animals and animal products are the source of pathogenic *Campylobacter jejuni* and *C. coli* in industrialized countries, yet little is known about the transmission of these bacteria in developing countries. Guinea pigs (*Cavia porcellus*) are commonly raised for food in the Andean region of South America, however, limited research has characterized this rodent as a reservoir of zoonotic enteric pathogens. In this study, we examined the prevalence of *Campylobacter* spp. in 203 fecal samples from domestic animals of 59 households in a semi-rural parish of Quito, Ecuador. Of the twelve animal species studied, guinea pigs showed the highest prevalence of *C. jejuni* ($n = 39/40$; 97.5%). Multilocus sequence typing (MLST) was used to characterize the genetic relationship of *C. jejuni* from domestic animals and 21 sequence types (STs) were identified. The majority of STs from guinea pigs appeared to form new clonal complexes that were not related to STs of *C. jejuni* isolated from other animal species and shared only a few alleles with other *C. jejuni* previously characterized. The study identifies guinea pigs as a major reservoir of *C. jejuni* and suggests that some *C. jejuni* strains are adapted to this animal species.

Introduction

Campylobacter jejuni and C. coli are transmitted to humans from domestic animals in developed countries, yet little is known about transmission of these bacteria in developing countries where unusual animal species (such as guinea pigs) are raised for food (Dasti et al., 2010). The domestication of guinea pigs occurred more than 2,000 years ago in the Andean region (Wing, 1986); currently there is an estimated population of greater than 35 million guinea pigs (de Zaldivar, 1995). Guinea pigs are generally used for companionship or for research in Europe and North America (Pigiere et al., 2012), while in South America, the majority of guinea pigs are raised for their meat, as well as minor uses in traditional Andean rituals and medicine (Spotorno et al., 2007). In 2009, the Instituto Nacional Autónomo de Investigaciones Agropecuarias (INIAP) estimated that 710,000 Ecuadorian households raised guinea pigs, producing nearly 21 million guinea pigs that year. Demand for guinea pigs, for consumption inside and outside the country, is increasing and annual increases in production have been observed.

Research has documented a variety of zoonotic disease risks associated with guinea pigs raised under different contexts (Lutz-Wohlgroth et al., 2006; Amman et al., 2007; Fredriksson-Ahomaa, 2007; Walther et al., 2012; Gruszynski et al., 2015). Studies among laboratory research animals have found guinea pigs to carry *Campylobacter* spp. (Weber et al., 1982; Muto et al., 1983; Fakir, 1986; Bartholomew et al., 2014; Komba et al., 2014). In the Andean Region, guinea pigs have been found to carry important zoonotic pathogens such as *Fasciola hepatica* (Carolina Gonzalez *et al.*, 2011) and *Yersinia pestis*, (Gabastou et al., 2000), as well as *Trypanosoma cruzi* (Levy et al., 2006). Given that guinea pigs in South America are often raised in the home, a better understanding of their role as potential reservoirs of other zoonotic diseases is critical.

The zoonotic enteropathogen *Campylobacter* spp. is the most common cause of bacterial gastrointestinal illness globally – estimated to result in 7.5 million disability-adjusted life years in 2010 (Wagenaar et al., 2015). *Campylobacter jejuni* and *C. coli* are the species most often implicated in human disease (Wagenaar et al., 2015). In low- and middle-income countries (LMICs) the burden of *C. jejuni* and *C. coli* infections among humans is not well documented and is likely

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underestimated due to the lack of diagnosis. A recent case-control study of paediatric diarrhoea in a poor urban neighbourhood and a poor rural community of Ecuador found a small number of infections with *Campylobacter* spp. among symptomatic and asymptomatic participants (Vasco et al., 2014).

Campylobacter have been identified in a range of animal hosts including domestic and wild animal species (Mughini Gras et al., 2013; Wagenaar et al., 2015). Chickens are considered an important source of *C. jejuni* and *C. coli*, and several studies have analyzed household poultry production as a risk for human infection (Grados et al., 1988; Georgescourbot et al., 1990; Marquis et al., 1990; Oberhelman et al., 2003). No study to the authors' knowledge has assessed the prevalence and diversity of *Campylobacter* spp. in guinea pigs raised for food, a prevalent practice in the Andean Region. The aims of the study were to: (i) test guinea pigs and other domestic animals for the presence of *Campylobacter* spp.; (ii) compare the prevalence of *C. jejuni* and *C. coli* carriage between guinea pigs and different animal species raised for food in the study area and (iii) to study the transmission and/or host association of *C. jejuni* and *C. coli* among animal species.

Results and discussion

Twelve different species of animals, including both livestock and domestic pets, were present among the fifty-nine households studied. The range of species present among any one household ranged from one to eight. Chickens were the primary animal raised, present in 42 households (71.2%). Forty of the households (67.8%) raised guinea pigs for food, primarily for household consumption. There were 32 (54.2%) households that had both chickens and guinea pigs and eight households (13.6%) that had guinea pigs and no chickens. Dogs, pigs, and rabbits were also commonly owned by households at 66.1%, 61.0% and 33.9%, respectively. The average number of guinea pigs raised by each household was 12 (range: 2–40). All of the households housed the guinea pigs outside the home and reported to reuse the guinea pig faecal waste on their land (Supporting Information Table S1).

Using culture based methods, the prevalence of *C. jejuni* was highest in samples taken from guinea pig cages (72.5%), followed by chicken cages (59.5%) (Table 1). At much lower prevalence levels, *C. jejuni* was identified in dogs (25.0%), rabbit cages (10.0%), cows (14.0%), cats (33.3%), ducks (20.0%) and quail (50.0%). Three pigs were positive for *C. jejuni* (8.3%); pigs, however, were more often positive for *C. coli* (38.9%) and *C. hyointestinalis* (27.8%). In comparing the prevalence of *C. jejuni* among the different animal species (Supporting Information Table S2), samples from both guinea pigs and chickens had significantly higher levels of *C. jejuni* than other domestic animals. Other animal pairs were not compared due to small sample sizes. The two sheep and one cow sampled were negative for *C. jejuni*. *Campylobacter coli* was found in pigs (38.9%), chickens (16.7%), guinea pigs (5.0%), dogs (2.6%), cows (14.3%), cats (16.7%), sheep (50.0%) and ducks (20.0%). We decided to analyze further *C. jejuni* isolates because they were present in larger numbers and in most faecal samples from the animal species analyzed, whereas most *C. coli* isolates were obtained from pigs (Table 1).

Table 1. Prevalence of *Campylobacter jejuni* and *Campylobacter coli* identified in domestic animals from a semi-rural parish of Quito, Ecuador.

Source	No. Samples	*C. jejuni (%)*		*C. coli (%)*	
Guinea pigs	40	29	(72.5)	2	(5.0)
Chickens	42	25	(59.5)	7	(16.7)
Dogs	40	10	(25.0)	1	(2.5)
Pigs	36	3	(8.3)	14	(38.9)
Rabbits	20	2	(10.0)	0	(0)
Cattle	7	1	(14.3)	1	(14.3)
Cats	6	2	(33.3)	1	(16.7)
Ducks	5	1	(20.0)	1	(20.0)
Quail	3	2	(66.7)	0	(0)
Sheep	2	0	(0)	1	(50.0)
Total	265	75	(28.3)	28	(10.5)

The gene *pgm* was amplified and sequenced from all recovered *C. jejuni* isolates (this gene is the most variable of the seven in the MLST set); all isolates which shared an identical DNA sequence with at least another isolate, were further analyzed using the following two loci, *glyA* and *tkt* (44 out of 65). Finally, the samples with the same *glyA-pgm-tkt* profile were sequenced for the remaining four MLST loci (44 out of 48). Among 44 *C. jejuni* isolates analyzed using MLST, we identified 21 sequence types (STs) (Table 2 and Fig. 1). Ten STs were identified in isolates from guinea pigs; 9 of which were novel (i.e. not described previously). Guinea pig STs formed three clusters (potential clonal complexes, i.e. STs that matched the central genotype at four or more loci). Cluster 1 comprised ST 7775 ($n = 4$), ST7777 ($n = 1$), ST7778 ($n = 1$), ST7781 ($n = 3$) and ST7789 ($n = 1$); cluster 2 was formed by ST7779 ($n = 2$) and ST7780 ($n = 2$); and cluster 3 comprised ST 7759 ($n = 6$), ST 7775 ($n = 1$) (Table 2 and Fig. 1). Remarkably, all STs from cluster 1 and most STs from clusters 2 and 3 seemed to have exchanged alleles only with strains isolated from guinea pigs (Fig. 1), which may indicate genetic isolation; allele similarity is indication of horizontal gene transfer rather than the emergence of independent mutations (Sheppard and Maiden, 2015).

Table 2. *Campylobacter jejuni* sequence types (STs) and clonal complexes (CCs) identified in guinea pigs (*Cavia porcellus*) and other domestic animals in a semi-urban community close to Quito.

CC	ST[a]	Animal	No. of isolates	Allele[b]						
				aspA	*glnA*	*gltA*	*glyA*	*pgm*	*tkt*	*uncA*
Unassigned	**7759**	Guinea pigs	6	4	7	**455**	62	**731**	25	104
	7760	Guinea pigs	1	4	7	**455**	62	**733**	25	104
	7775	Guinea pigs	4	**394**	**538**	**454**	**601**	**729**	**582**	**462**
	7777	Guinea pigs	1	**394**	**537**	**454**	**601**	**729**	**582**	**463**
	7778	Guinea pigs	1	**394**	**538**	**454**	**601**	**729**	**582**	**464**
	7779	Guinea pigs	2	**393**	**536**	**454**	62	**734**	**583**	104
	7780	Guinea pigs	2	**393**	**536**	**454**	62	13	25	104
	7781	Guinea pigs	3	**394**	**538**	**454**	**601**	**730**	**582**	**462**
	7789	Guinea pigs	1	**394**	**538**	**454**	**601**	**729**	**582**	**463**
	7671	Dogs	1	8	113	5	121	11	25	6
	7672	Cats	1	2	114	5	298	13	61	460
	7672	Dogs	1	2	114	5	298	13	61	460
464	464	Chickens	1	24	2	2	2	10	3	1
	464	Rabbits	1	24	2	2	2	10	3	1
45	137	Rabbit	1	4	7	10	4	42	7	1
353	1233	Chickens	2	7	17	5	10	10	177	6
	1233	Guinea pigs	1	7	17	5	10	10	177	6
	3515	Chickens	1	7	17	2	2	10	3	6
	7643	Quail	1	7	17	5	2	10	3	54
	7643	Dogs	1	7	17	5	2	10	3	54
354	354	Chickens	1	8	10	2	2	11	12	6
	7662	Quail	1	390	2	2	2	11	5	6
	7662	Chickens	1	390	2	2	2	11	5	6
	7669	Chickens	1	8	10	95	2	11	12	6
607	607	Chickens	2	8	2	5	53	11	3	1
	607	Dogs	2	8	2	5	53	11	3	1
	1212	Chickens	1	8	2	5	53	11	3	105
	1212	Cattle	1	8	2	5	53	11	3	105
	1212	Pigs	1	8	2	5	53	11	3	105

a. Sequence types and alleles in bold are new.

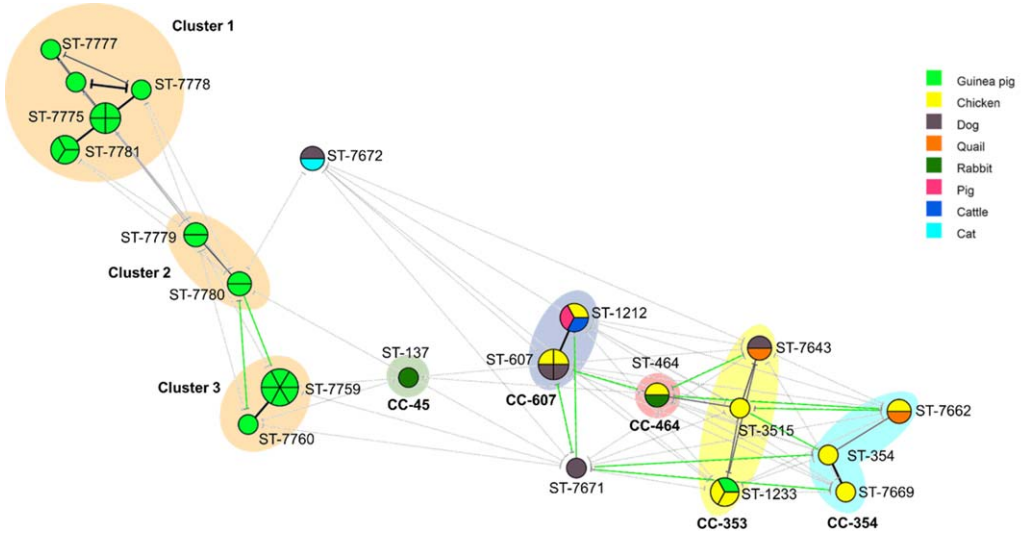

Fig. 1. Minimum spanning tree analysis of 44 *C. jejuni* isolates (from a semi-rural parish of Quito, Ecuador) based on MLST profile and according to animal source. Each circle represents the sequence type (ST), the size of the circle and circle divisions indicate the number of isolates within any given ST. Line colours indicate the following information: black = 5-6 shared alleles; grey 3-4 shared alleles; and gree *n* = 1-2 shared alleles. The colour of the circle indicates the animal species.

Campylobacter jejuni STs can be either adapted to one animal species or generalists (i.e. equally able to infect different animal species) (Sheppard et al., 2013). Our data (Fig. 1) seem to show that *C. jejuni* isolates from guinea pigs belong to STs adapted to this animal species.

Seven STs were present in multiple animal species: quails and chickens (ST 7662); dogs and chickens (ST 607); cattle, chickens and pigs (ST 1212); guinea pigs and chickens (ST 1233); quails and dogs (ST 7643); rabbits and chickens (ST 464); and cats and dogs (ST 7672). Twenty-three strains (46.9%) from animals other than guinea pigs belonged to four major clonal complexes (CC) previously described: CC-607, CC-353, CC-354, CC-464 and CC-45 (Fig. 1). Seven isolates (16%) belonged to ST-607, the founder sequence type of CC-607; 6 isolates (13.6%) to CC-353, 4 isolates (9%) to CC-354, 2 isolates (4.5%) to CC-464 and 1 isolate (2.2%) to CC-45 (Fig. 1). Unlike guinea pigs, isolates from other animal species seemed to share alleles with STs and CCs previously described. The complete description of alleles from all isolates is shown in (Table 2; Supporting Information Fig. S1), all nucleotide sequences are available at Genbank, accession numbers are: KU728723 to KU728740.

This study identified high levels of *Campylobacter jejuni* in guinea pigs raised for food in Ecuador, however *C. jejuni* infection (worldwide) has been attributed to chickens (50–80%), cattle (20–30%) and to a lesser extent sheep, pigs, wild animals, water and unpasteurized milk (Michaud et al., 2004; Wagenaar et al., 2015). Detecting *C. jejuni* from 97.5% of guinea pig fecal samples tested, using PCR, contrasts with the results of studies looking at other domestic and wild animals: 19.4% - 72.5% in poultry; 16-90% in cattle (Kaakoush et al., 2015), 7.9–90.0% in dogs (Marks et al., 2011; Gras et al., 2013; Ramonaite et al., 2014), 35.4% in free-living birds (Ramonaite et al., 2014). The difference in the prevalence of *C. jejuni* was not statistically significant between guinea pigs and chickens. Both of these animal species, however, had significantly higher levels than those of dogs, pigs and rabbits. There were no differences in the prevalence of *C. jejuni* in guinea pigs raised with chickens versus guinea pigs raised without chickens and these two animal species did not share STs except in the case of ST-1233 in guinea pigs and chickens from the same household.

Surveillance programs that track *C. jejuni* are limited (Scallan et al., 2011) and control measures have focused on poultry because they are generally considered the primary reservoir of *C. jejuni* and cause outbreaks in humans in industrialized countries (Kaakoush et al., 2015; Wagenaar et al., 2015). Little is known about the epidemiology of *C. jejuni* infections in humans living in developing countries where unusual animal species are used as food and where other domestic animals are raised under different conditions. In this case, the risk of *C. jejuni* infection may include not only households raising guinea pigs but the whole community who consumes crops raised in the area. The use of domestic animal faecal waste to fertilize crops could potentially be affecting the microbiological safety of strawberries, the primary edible crop raised in the area. More research is needed to understand how the use of guinea pig feces as a fertilizer could result in transmission of *C. jejuni* through contaminated crops.

It is unclear why guinea pigs in this region have such a high prevalence of *C. jejuni*. In this study, many of the households applied fresh guinea pig faecal waste directly to the crops (including alfalfa used for feeding guinea pigs) (Supporting Information Table S1); this practice may favour the cycling of *C. jejuni* in guinea pigs if the fertilized alfalfa is then fed back to local guinea pigs. Although *Campylobacter jejuni* is considered fragile in contrast to many other bacterial pathogens, research has found *Campylobacter* to survive in the environment between three to ten months, especially under wet conditions, including faecal slurries, contaminated waters and stored manure (Inglis et al., 2010). It will be important to determine the prevalence of *C. jejuni* in guinea pigs in other parts of Ecuador and in guinea pigs kept as pets in other parts of the world.

In this study, isolates from chickens belonged to 8 STs which were present in other animal species or have been described previously in other animal species (STs: 607, 1212, 464, 3515, 1233, 354, 7662 and 7669) (Fig. 1). This finding underscores the importance of avian species as reservoirs of genetically diverse and generalist *C. jejuni*.

Given the limited scope of the study – 59 households, 40 of which raised guinea pigs – it is important to treat the uncertainties in a transparent manner. First, the generalizability of the findings is limited and it will be important for future research to determine how *C. jejuni* varies in guinea pigs across ecologically separate niches in Ecuador. Second, only a subset of the *C. jejuni* isolates – 44 of the 65 (67.7%) – were analyzed using MLST due to resource limitations. Furthermore, this study was not able to assess seasonal variation or the variation stemming from animal management practices, such as housing, diet and crowding. We did not investigate the relationship between five large-scale poultry operations in the area and the high rate of *C. jejuni* colonization in guinea pigs.

This study highlights the complexity of *C. jejuni* transmission in the environment where not only local agricultural practices but also *C. jejuni* genetics are involved. It will be important to study the temporal patterns of ST

distribution (in different animal species) which may indicate how stable different STs are overtime in one region. These type of studies may show the potential transient emergence of *C. jejuni* STs with different aptitude to cross-infect different animal species (Boes et al., 2005).

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Descriptive information of the forty study households that raised guinea pigs for food in a semi-urban parish of Quito, Ecuador.
Table S2. Prevalence ratio of *Campylobacter jejuni* carriage among domestic animals from a semi-rural parish of Quito, Ecuador
Fig. S1. Guinea pigs contained six alleles (aspA 4, glnA 7, glyA 62, pgm 13, uncA 104 and tkt25) that were previously reported in other animal species (based on the pubMLST database).