ORIGINAL ARTICLE

Increased prevalence of canine echinococcosis a decade after the discontinuation of a governmental deworming program in Tierra del Fuego, Southern Chile

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Abstract

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Hydatid disease is a neglected zoonotic parasitic disease caused by cysts of the tapeworm Echinococcus granulosus. Canids, especially domestic dogs, are definitive hosts of the parasite and are the most pragmatic targets for control programs. A governmental dog deworming campaign was established in 1979 to control hydatidosis in southern Chile, which succeeded in reducing the prevalence of canine echinococcosis in Tierra del Fuego province from 68.4% (in 1978) to 1.2% (in 2002). In 2004, however, the program was dismantled to reduce costs, and since then, no follow-up echinococcosis monitoring has been conducted. We surveyed 356 domestic dogs and interviewed owners or workers at 45 ranches in Chilean Tierra del Fuego during the summer of 2015-2016. Faecal flotation was employed to detect Taeniidae eggs, and PCR was used to test faecal samples for Echinococcus granulosus. Taeniidae eggs and Echinococcus sp. DNA were detected in the faeces of 45.4% (147/324) and 6.9% (23/331) of dogs, respectively. Infrequent dog deworming and the presence of culpeo foxes (Lycalopex culpaeus) were significant predictors of the prevalence of Echinococcus sp. DNA and Taeniidae eggs. Furthermore, the presence of introduced chilla foxes (Lycalopex griseus), the municipality, and several operational characteristics of ranches (number of sheep, frequency of sheep slaughter, number of dogs, frequency of removal of dog faeces, feeding of dogs with sheep viscera) were also predictive of the prevalence of Taeniidae eggs. Our findings reveal an ongoing risk of echinococcosis with pathogen maintenance in ranch dogs in Chilean Tierra del Fuego, and in the absence of adequate control programmes, there is a tangible risk of reemergence of hydatid disease as a public health concern.

KEYWORDS

Canidae, Cestoda, cystic echinococcosis, hydatidosis, sheep, zoonosis

Jonna Ann Keener Mazet and Cristóbal Briceño should be considered joint senior authors.

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1 | INTRODUCTION

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Infection of humans by the tapeworm *Echinococcus granulosus* can lead to cystic echinococcosis, or hydatidosis, a zoonotic parasitic disease (WHO, 2013). Cystic echinococcosis is globally distributed (Savioli et al., 2013; WHO, 2013), with vast endemic areas at the southern tip of South America (Moro & Schantz, 2006; PAHO, 2007; WHO, 2013). Over 1 million people worldwide are affected with hydatidosis at any one time, and approximately 3 billion US dollars are spent globally every year in treatment costs and livestock industry compensations (Savioli et al., 2013). In humans, the disease can be expensive and complicated to treat, sometimes requiring extensive surgery and prolonged drug therapy (CDC, 2020; Moro & Schantz, 2009; WHO, 2020).

Canids, such as dogs and foxes, are the definitive hosts for adult *E. granulosus*, with adult worms reproducing in the intestine and infective eggs being shed in the host's faeces (CDC, 2020; Moro & Schantz, 2009). A number of animals, including humans and livestock, serve as intermediate hosts for *E. granulosus*, by ingesting soil, water, or food contaminated with the parasites' eggs and developing parasitic larval stages in their viscera, most commonly in liver and lungs (CDC, 2020; WHO, 2020). The cycle is completed when canids consume infected viscera from carcasses of infected intermediate hosts. In human cases, hydatidosis is characterized by asymptomatic incubation periods that can last many years until the parasite containing structures (hydatid cysts) grow, compressing viscera and triggering serious clinical signs that may ultimately cause death. In livestock, most often sheep and cattle, cases of hydatidosis are usually only detected at slaughter (WHO, 2020).

Human hydatidosis is endemic in Chile, especially in rural communities, representing the second most common cause of death from parasitic disease (OPS, 2006; PAHO, 2007). The disease also ranked as the second most common pathological finding in cattle and sheep at abattoirs in 2017 (SAG, 2018). Though human hydatidosis is a notifiable disease in Chile, it is known to be underreported (MINSAL, 2016). There were 790 discharges for human hydatidosis in 2012, which was the leading cause of hospitalization for parasitic disease in Chile (Colombe et al., 2017). Hospitalizations related to the disease have a marked regional variation, with higher rates in the southern regions of Chile, where sheep farms and rural populations predominate.

To control hydatidosis in vulnerable populations, Chile's agricultural agency (*Servicio Agrícola y Ganadero* – SAG) implemented a mandatory deworming campaign for dogs working on sheep ranches located in endemic areas in 1979 (SAG, 1979). Prior to this campaign, the prevalence of echinococcosis in dogs was estimated to be 71% and that of cystic echinococcosis in sheep was 60% in the Magallanes Region (Moro & Schantz, 2006). The treatment with praziquantel was efficacious in decreasing the prevalence of *E. granulosus* in dogs, thus reducing the prevalence of disease in susceptible secondary hosts (humans and herbivores). From 1995 to 1997, the reported prevalence of *E. granulosus* infection in the Magallanes Region was 0.35% in dogs and 1.3% in sheep (Moro & Schantz, 2006). In the

Impacts

- Cystic echinococcosis, or hydatidosis, is a zoonotic parasitic disease that affects more than 1 million people worldwide and is the second most common cause of human deaths from parasitic disease in Chile.
- A governmental dog deworming programme to control the disease in southern Chile succeeded in reducing the prevalence of canine echinococcosis in Tierra del Fuego province from 68.4% (in 1978) to 1.2% (in 2002).
- Without the control programme, which was discontinued in 2004, the prevalence of canine echinococcosis appears to have increased to 6.9% (in 2015–2016), highlighting the need to re-establish government action to reduce this public health hazard.

Tierra del Fuego province, which is dominated by sheep ranches (Iparraguirre & von der Fecht, 2000), the prevalence of canine echinococcosis decreased from 68.4% in 1978 (SAG, 1983) to 1.2% in 2002 (Alvarez et al., 2005). Though no endemic areas achieved eradication, the recorded human cases of hydatidosis in Magallanes dropped from 80 cases per 100,000 inhabitants in 1979 to 20 cases per 100,000 inhabitants in 1991 (Larrieu & Zanini, 2012). The deworming programme was dismantled in 2004 due to high costs and logistical challenges.

In this study, we aimed to estimate Taeniidae and *Echinococcus* sp. prevalence in domestic dogs at ranches in Chilean Tierra del Fuego a decade after the discontinuation of the governmental dog deworming programme, as well as assess potential risk factors for infection at the ranch level via interviews of ranch personnel. Additionally, we evaluated the prevalence of these parasites in opportunistically-collected faecal samples from wild canids in the area.

2 | MATERIALS AND METHODS

2.1 | Ethics statement

All work was conducted in accordance with the University of California, Davis (UCD) Institution Review Board Protocol 773342-2 and UCD Institutional Animal Care and Use Protocol 18815; and the Universidad de Chile Bioethics Committee Protocol 21–2015 and Biosecurity Committee Protocol #56. Informed consent was verbally obtained from all participants.

2.2 | Study site

Isla Grande de Tierra del Fuego (54°S 69°W) is located off the southernmost tip of continental South America. The island is politically administered by Chile in the west and Argentina in the east (Figure 1a).

FIGURE 1 Location of the primavera, Porvenir and Timaukel municipalities in the Chilean portion of Isla Grande de Tierra del Fuego (a) and diagnostic test results for Taeniidae in domestic dogs (b), Echinococcus sp. in domestic dogs (c), and Taeniidae in wild canids (d). Pie charts represent the proportion of samples that were positive (red) or negative (green) and their size is proportional to the number of dogs sampled at each ranch; to avoid juxtaposition, some pie charts were slightly displaced (the original position of the ranch is shown by a lead line). Blue dots represent cities and towns, blue lines represent municipality roads, and the grey-shaded background represents the altitude.



The Chilean province of Tierra del Fuego (TDF) extends over an area of 29,485 km², with the north primarily occupied by sheep ranching and scattered rural settlements and mountainous and densely forested areas in the south. The province is scarcely inhabited (0.3 inhabitants/km²), with the population distributed in three municipalities, 1158 inhabitants in Primavera municipality, 6801 in Porvenir, and 405 in Timaukel (INE, 2017a). Livestock ranching is the main local economic activity, with an estimated 848,124 sheep on 170 ranches in 2017 (INE, 2017b).

Guanacos (*Lama guanicoe*) are the most abundant native hooved herbivore (Moraga et al., 2015). In addition to the native Fuegian culpeo fox (*Lycalopex culpaeus lycoides*), the human-introduced chilla fox (*Lycalopex griseus*) and silver fox (melanistic form of *Vulpes vulpes*) are also common on the island (Valenzuela et al., 2014). Moreover, the local population of free-ranging dogs (defined as those living without direct human supervision; Lord et al., 2013) has increased in recent years (Schiavini & Narbaiza, 2015; WCS, 2019).

2.3 | Questionnaires and sample collection

From November 2015 to March 2016, we interviewed sheep ranch workers and owners using a dog and ranch management survey (Table 1). Because of the low population density in the study region, no selection criteria were used a priori to determine which ranches would participate in the study; the only selection factors therefore were (a) whether we were able to reach the ranch and (b) whether anyone was available to be interviewed at the ranch when it was visited.

After obtaining consent, a veterinarian examined and sampled all ranch dogs available at the time of the visit. Estimated age (puppy <6 months, adolescent 6–12 months, adult >12 months), sex, reproductive status (intact, neutered), and breed were recorded, and a 9-point body condition scale was assessed (Laflamme, 1997). Approximately 5–10 g of faeces were collected from each dog and preserved in airtight vials. Whenever possible, a sample was taken from the environment after visualization of defecation, but digital sampling from the rectum was commonly performed. Exceptionally, when no faeces were extractable from the rectum, a fresh sample was picked up from the ground within 2 m of the dog's unique shelter. Faeces from culpeo and chilla foxes were opportunistically collected whenever found. Appropriate personal protection equipment was employed during all sampling procedures.

2.4 | Laboratory procedures

For biosafety, each dog faecal sample was inactivated using a hot incubation bath (70–80°C) for 5 min. Then, each sample was divided: 2 g for Taeniidae screening procedure and the remainder stored in 95% ethanol at -18°C for subsequent molecular analyses.

TABLE 1 Summary of responses collected through
uestionnaires provided to the workers or owners of 45 ranches in
Tierra del Fuego. Chile in 2015–16

Questions and multiple-choice answers	Responses (%)		
1. In the last 12-months period, what is the maximum number of dogs that lived or worked on this ranch at any one time?			
Less than 5	13		
From 6 to 15	69		
From 16 to 25	13		
More than 25	4		
2 How often are deworming products given to the dogs that you			

own? (Note: this question does not necessarily apply to all dogs at the ranch)

More than twice per year	38
Twice per year	20
Once per year	16
Never	27

3. Can you show the medication(s) given to the dogs at the ranch to prevent tapeworms?

Yes	38
No or shows incorrect medication/product	62
4. How often are dog faeces collected and discarded ranch?	l from the
Once per day	9
Once per week or at the end-of-shift	18
Once per month	20
Once per year	7
Never	47
5. Approximately how many sheep are maintained o	n this ranch?
None/do not know	4
Less than 500	7
From 501 to 1000	4
More than 1000	84
6. How frequently are sheep slaughtered at this rand	ch?
Never	16
Once per month	4
Twice per month	7
Once per week	7
Twice per week	58
7. Are dogs fed with or allowed to eat sheep viscera	at this ranch?
Yes	20
No	80
8. Are dogs fed with or allowed to eat guanaco meat this ranch?	or viscera at
Yes	51
No	49
9. Do you ever see free-ranging dogs on this ranch?	
Yes	51
NI-	10

TABLE 1 (Continued)

Questions and multiple-choice answers	Responses (%)
10. Do you ever see culpeo foxes on this ranch?	
Yes	16
No	84
11. Do you ever see chilla foxes on this ranch?	
Yes	91
No	9

A non-specific Taeniidae screening procedure modified from Mathis et al. (1996) was performed in the field on the 2 g of fresh sample. The sample was reduced to a uniform consistency and transferred into a 15 ml plastic tube, adding four times the volume of physiological saline (0.9% NaCl). Samples were vortexed for 1 min and then centrifuged at 1000g for 10 min. Supernatant was discarded, and the pellet loosened in the tube. The same volume of flotation solution (ZnCl₂ at specific gravity = 1.45) was added and contents vortexed for 30 seconds, then centrifuged at 3000 rpm for 30min. Supernatant was poured through a 44µm filter fabric (Lanz-Anliker AG; egg diameter \sim 35 μ m). The filtered contents were poured through a 21 µm filter (Lanz-Anliker AG) into a clean receptacle. Filtrate was disposed and the filter was flushed with distilled water and allowed to sediment overnight. Using a disposable Pasteur pipette, the supernatant was drawn, leaving about 1.5 ml which was allowed to sediment for at least 1 h. Supernatant was removed, leaving only 500µl remaining. Finally, a 100µl of homogeneous sample was placed on a slide, covered and examined systematically under light microscopy at 10x and 40x magnification. Taeniidae eggs were counted and recorded as number of eggs/100µl of sample (quantification was right-censored at 100 eggs/100 µl). Egg abundance (average egg density per individual examined) and intensity (average egg density per individual with eggs) were calculated.

Since *E. granulosus* eggs cannot be reliably distinguished from other Taeniidae eggs under light microscopy (Eckert & Deplazes, 2004), polymerase chain reaction (PCR) of faecal samples was performed. Prior to processing, the 95% ethanol aliquots were stored at -80°C for \geq 72 h to suppress cyst infectivity. A 200 mg stool sample was placed in a 2 ml microcentrifuge tube containing 200 mg glass beads and 540 µl of buffer, then vortexed at maximum speed for 10 min using the Mini-Beadbeater-96 (Bio Specs Products Inc.). Additionally, and to increase DNA yield, each sample was subjected to five freeze-thaw cycles; placed in liquid nitrogen for 5 s to allow for rapid freezing, followed by thawing by incubation at 65°C for 1 min (modified from Klein et al., 2014). DNA was then extracted using *E.Z.N.A.®* Stool DNA Kits (Omega Bio-teak Inc.) following the manufacturer's instructions.

All DNA samples were analysed by PCR using the primers Eg1f and Eg1r, which were designed to amplify a 255 bp fragment (210 bp without primers) of the mitochondrial 12S rRNA gene from *E. granulosus* (Štefanić et al., 2004) but which may cross-amplify other

Echinococcus species (Boufana et al., 2008). This primer pair was chosen because of the reported 100% sensitivity compared to other established protocols (Boufana et al., 2008). Amplification reactions were conducted in 25 µl wells containing 12.5 µl of ReadyMix PCR Kit (Kapa Biosystems). Forward primer (Eg1f) and reverse primer (Eg1r) were added at 0.4 μ M each, plus 5.0 μ l of the template and double-distilled water to complete 25 µl. All samples underwent an initial denaturation at 95 °C for 3 min followed by 40 amplification cycles (15s at 95°C, 15s at 55°C, 20s at 72°C) and a final extension at 72°C for 5 min. Amplicons were detected through 1.5% agarose gel electrophoresis of 5 µl of PCR products stained with ethidium bromide (0.8 µg/ml). All reactions included positive (purified E. granulosus DNA) and negative controls (double-distilled water). Samples that yielded amplicons of 255 bp were sequenced at Macrogen Inc. to confirm the presence of Echinococcus sp. DNA. Nucleotide BLAST search was used to compare sequences obtained in this study to publicly-available sequences in GenBank (McGinnis & Madden, 2004).

2.5 | Statistical analyses

Within-ranch prevalences (no. positive individuals/no. individuals tested) were calculated for Taeniidae and Echinococcus sp. The 95% confidence interval (CI) for estimated prevalence was calculated at the overall and municipality levels. Cohen's Kappa coefficient (κ) was calculated to assess the agreement between the test results for the two parasites at the individual level, and linear regression analysis was used to evaluate the relationship between the ranchlevel prevalence of the two parasites. Binary logistic general linear models (GLM) were used to determine whether the municipality (3 categories: Primavera, Porvenir, Timaukel) and responses to 11 questions (see Table 1) were predictive of within-ranch prevalence of Taeniidae eggs and Echinococcus sp. DNA. The stepwise procedure was used to select the variables that significantly contributed to each model. Statistical analyses were performed with R 4.1.2 (R Foundation for Statistical Computing) with the packages DescTools 0.99.44 (Signorell, 2021) and stargazer 5.2.3 (Hlavac, 2022).

3 | RESULTS

Ranch workers and owners were interviewed at 45 ranches within three municipalities: Primavera (7), Porvenir (25), and Timaukel (13). Questionnaire responses are summarized in Table 1. Interviewees at two Porvenir ranches also reported knowing a co-worker who had been diagnosed with hydatidosis in the last 10 years: one reported knowing two men (ages 50 and 60 years old at diagnosis) and the other reported knowing one man (72 years old).

A total of 356 dogs were evaluated at these ranches, with an average 9.7 \pm 6.1 domestic dogs per ranch (range = 2-30). At the ranch level, the proportion of male dogs was typically high (71.2% \pm 22.9%, range = 0%-100%). In total, 258 males (7 puppies, 14 adolescents,

236 adults, 1 age not determined) and 98 females (5 puppies, 4 adolescents, 89 adults) were evaluated. Average age was 4.0 ± 3.0 years (range 0.3–13). At the ranch level, 15 ranches (33%) had only adult dogs; 28 ranches (62%) had mostly adult dogs, and two ranches (4%) had mostly puppies and adolescent dogs. All dogs were intact except for 8 adult females that had been neutered (9% of adult females). Average body condition score (1–9) was 4.7 ± 1.1 (range = 1–8) at the individual level and 4.7 ± 0.8 (range = 2.5–6.4) at the ranch level.

Faecal samples from 324 dogs were tested for Taeniidae (7.2 \pm 3.9 dogs per ranch, range = 1–14); faecal samples could not be obtained or were insufficient from the remaining dogs. The overall prevalence of Taeniidae eggs was 45.4% (Cl: 39.9%–51.0%), with a municipality prevalence of 26.7% (Cl: 12.3%–45.9%) for Primavera, 44.1% (Cl: 34.3%–54.3%) for Timaukel and 49.0% (Cl: 41.7%–56.3%) for Porvenir (Figure 1b). At the ranch level (*n* = 45), the prevalence of Taeniidae eggs ranged from 0% to 100%, with an average of 38.3% \pm 28.9% (mean \pm SD) and a median of 35.7% (first quartile = 20.0%, third quartile = 63.1%). Seventeen samples from domestic dogs had too many Taeniidae eggs to count (>100 eggs per 100 µl of filtered and concentrated sample). The remaining 307 dog samples had an average abundance of 5.7 \pm 14.4 eggs per 100 µl and an average intensity of 13.4 \pm 19.6 eggs per 100 µl.

Faecal samples from 331 dogs were tested for *Echinococcus* sp. (7.4 \pm 3.9 dogs per ranch, range = 1-15). The overall prevalence of *Echinococcus* sp. DNA was 6.9% (Cl: 4.5%-10.2%), with a municipality prevalence of 3.2% (Cl: 0.1%-16.7%) for Primavera, 5.1% (Cl: 2.5%-9.2%) for Porvenir and 11.4% (Cl: 6.1%-19.1%) for Timaukel (Figure 1c). At the ranch level (n = 45), the prevalence of *Echinococcus* sp. DNA ranged from 0% to 100%, with an average of 8.6% \pm 17.2% and a median of 0% (first quartile = 0%, third quartile = 14.3%). Sequencing of amplicons was successful for 10 out of 23 PCR-positive samples; all sequences obtained (ranging from 70 to 182 bp due to varying chromatogram quality) were identical. A representative sequence was deposited in GenBank (accession code ON511391); BLAST revealed that this sequence is identical to publicly-available 12S rRNA sequences of *Echinococcus*.

A total of 320 faecal samples were tested for both Taeniidae (faecal flotation) and *Echinococcus* sp. (PCR). Of these, 14 samples (4.4%) were positive by both methods, 8 samples (2.5%) were positive for *Echinococcus* sp. only, 130 samples (40.6%) were positive for Taeniidae only, and 168 samples (52.5%) were negative for both parasites. There was no significant correlation in the prevalence of these parasites at the ranch level (p = 0.733, $R^2 = 0$). Taeniidae positive samples that were positive for *Echinococcus* sp. DNA had an average intensity of 29.0 ± 34.3 Taeniidae eggs per 100µl, whereas Taeniidae-positive samples that were negative for *Echinococcus* sp. DNA had an average intensity of 22.4 ± 33.0 Taeniidae eggs per 100µl.

Stepwise GLM produced a model that predicted Taeniidae prevalence based on the municipality and the answers to all interview questions except 3, 8 and 9 (Table 2). Ranches in Timaukel tended to present higher Taeniidae prevalence (z = 3.133,

TABLE 2 Coefficient estimates [z-value] for the linear model results for the detection of Taeniidae and Echinococcus sp. in faecal samples from domestic dogs at ranches in Tierra del Fuego, Chile in 2015–16

		Taeniidae		Echinococcus sp.	
Variable	Category	All variables	Stepwise	All variables	Stepwise
Constant		-8.55 [-4.18]**	-7.66 [-4.25]**	27.36 [†]	16.16 [†]
Municipality ^a	Porvenir	1.18 [1.72]	0.96 [1.47]	-1.85 [-0.45]	
	Timaukel	2.99 [3.28]**	2.5 [3.13]**	-1.54 [-0.33]	
(1) Number of dogs ^b	6-15 dogs	2.56 [2.34]*	2.27 [2.25]*	-1.48 [-0.54]	
	16-25 dogs	5.04 [3.74]**	4.42 [3.86]**	0.09 [†]	
	>25 dogs	6.17 [4.26]**	5.89 [4.19]**	16.29 [†]	
(2) Frequency of dog deworming ^c	$1 \times$ per year	0.99 [1.73]	0.97 [1.77]	-17.39 [†]	-18.80 [†]
	$2 \times$ per year	0.08 [0.13]	0.4 [0.76]	-1.85 [-0.82]	-0.12 [-0.19]
	>2× per year	-1.2 [-1.95]	-0.98 [-2.05]*	-4.10 [-1.87]	-1.72 [-2.37]*
(3) Able to show deworming drugs ^d	Yes	0.31 [0.60]		0.97 [0.94]	
(4) Frequency of dog faeces collection ^e	1× per week or EOS	3.36 [2.87]**	3.56 [3.50]**	0.85 [0.45]	
	1× per month	1.62 [2.10]*	1.61 [2.11]*	-1.17 [-0.66]	
	≤1× per year	1.95 [2.47]*	1.82 [2.66]**	-0.25 [-0.18]	
(5) Number of sheep ^f	≤500 sheep	2.67 [2.58]**	2.44 [2.41]*	-9.92 [†]	
	501-1000 sheep	-4.92 [-2.75]**	-4.92 [-2.74]**	-11.47 [†]	
	>1000 sheep	-1.29 [-1.22]	-1.36 [-1.31]	4.38 [†]	
(6) Frequency of sheep slaughter ^g	1× or 2× per month	1.89 [2.71]**	1.55 [2.40]*	-31.86 [†]	-18.30 [†]
	1× per week	1.90 [3.12]**	1.70 [2.90]**	-30.3 [†]	-17.37 [†]
	$2 \times per week$	-1.60 [-1.53]	-1.72 [-1.66]	-51.04 [†]	-19.16 [†]
(7) Dogs allowed to eat sheep viscera ^d	Yes	-3.37 [-3.42]**	-3.45 [-4.34]**	-1.57 [-0.97]	
(8) Dogs allowed to eat guanaco meat ^d	Yes	0.67 [1.89]	0.68 [1.95]	1.24 [0.86]	
(9) Free-ranging dogs at ranch ^d	Yes	-0.54 [-1.16]		33.1 [†]	18.43 [†]
(10) Culpeo foxes at ranch ^d	Yes	-2.02 [-3.17]**	-1.89 [-3.05]**	1.24 [0.93]	1.29 [2.03]*
(11) Chilla foxes at ranch ^d	Yes	2.64 [3.19]**	2.29 [2.96]**	-31.62 [†]	-18.46 [†]
Observations		324	324	331	331
Log Likelihood		-187.288	-188.075	-61.278	66.527
Veall-Zimmermann pseudo-R ²		0.313	0.307	0.353	0.278
Akaike information criterion		422.576	420.151	170.556	153.055

Note: **p* < 0.05, ***p* < 0.01, ****p* < 0.001, [†]|*z*| < 0.05.

^aReference category is 'Primavera'.

^bReference category is '≤5 dogs'.

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^cReference category is 'Never or not reported'.

^dReference category is 'No'.

^eReference category is 'Never or once per year.

^fReference category is 'None or not informed'.

^gReference category is 'Never or less than once per month'.

p = 0.002) relative to ranches in Primavera (reference category). The number of dogs at the ranch (question 1) showed a consistent positive association with the Taeniidae prevalence, with incremental positive effects. Frequency of dog deworming (question 2) only had a significant effect when interviewees responded 'More than twice per year' (z = -2.051, p = 0.040). Frequency of dog faeces removal (question 4) also showed a significant effect, with a

higher Taeniidae prevalence when interviewees responded other than 'Once per day' (reference category; Table 2). For the number of sheep (question 5), Taeniidae prevalence was generally higher when interviewees reported 'Less than 500 sheep' (z = 2.413, p = 0.016) but lower when interviewees answered 'From 501 to 1000 sheep' (z = -2.739, p = 0.006) or 'More than 1000 sheep' (z = -1.310, p = 0.190) relative to ranches where interviewees

responded 'None/do not know' (reference category). The frequency of sheep slaughter (question 6) had a significant effect on Taeniidae prevalence, which was generally higher when interviewees responded 'Once or twice per month' (Z = 2.397, p = 0.017) or 'Once per week' (Z = 2.899, p = 0.004) compared to the response 'Never' (reference category). Taeniidae prevalence was generally lower when interviewees responded 'Yes' to whether the dogs were fed with or allowed to eat sheep viscera (question 7; z = 4.340, p < 0.001) and whether culpeo foxes were seen on the ranch (question 10; z = -3.046, p = 0.002). In contrast, when interviewees responded 'Yes' to whether chilla foxes were seen on the ranch (question 11) the Taeniidae prevalence tended to be higher (z = 2.959, p = 0.003). Although the question of whether dogs were fed with or allowed to eat guanaco meat or viscera (question 8) was included in the final model, its positive coefficient was not significant by a small margin (z = 1.953, p = 0.051).

Stepwise GLM produced a model that predicted *Echinococcus* sp. prevalence based on the answers to interview questions 2, 6, 8, 9, 10 and 11 (Table 2). Frequency of dog deworming (question 2) only had a significant effect when interviewees responded 'More than twice per year' (z = -2.370, p = 0.018). Additionally, the *Echinococcus* sp. prevalence was generally higher when interviewees responded 'Yes' to whether culpeo foxes were seen on the ranch (question 10; z = 2.026, p = 0.043). Questions 6, 8, 9 and 11 were included as variables in the final model; however, their coefficients were not significant (all with |z| < 0.012 and p > 0.98).

Thirty-one faecal samples from wild canids (culpeo or chilla foxes) were collected; all were tested for *Echinococcus* sp., and 25 were tested for Taeniidae. Five samples (20%; Cl: 6.8%-40.7%) were positive for Taeniidae, with an average abundance of 0.3 ± 0.7 eggs per 100µl and an average intensity of 1.4 ± 0.9 eggs per 100µl. Taeniidae-positive samples were found only in the Timaukel municipality (Figure 1d). All samples from wild canids were negative for *Echinococcus* sp. DNA (prevalence CI: 0%-11.2%).

4 | DISCUSSION

We estimated the prevalence of echinococcosis in the ranch dog population of Chilean Tierra del Fuego for the first time since the governmental programme for controlling canine echinococcosis was discontinued in 2004. We found that 6.9% of dogs were PCRpositive for *Echinococcus* sp., demonstrating a persistent risk of exposure and disease. Prior to our study, the last survey conducted in TDF in 2002 showed a prevalence of 1.2% (Alvarez et al., 2005). Because diagnostic methods have advanced dramatically in the intervening period, the prevalence in our study cannot be directly compared to previous estimates. The survey reported by Alvarez et al. (2005) used the arecoline hydrobromide purgation method, which has an estimated sensitivity of 55% for *Echinococcus multilocularis* and 76% for *E. granulosus* (assuming 100% specificity; Hartnack et al., 2013). In contrast, faecal PCR has an estimated sensitivity of 89% for *E. multilocularis* and 93% for *E. granulosus* (specificity of 93% and 83%, respectively; Hartnack et al., 2013). If the 1.2% prevalence estimated by Alvarez et al. (2005) is adjusted based on these sensitivity and specificity values, the prevalence in 2002 may have been between 1.4% and 2.3% had a faecal PCR been employed. This suggests that the variation between our results and those from Alvarez et al. (2005) cannot be explained solely by differences in diagnostic methods, and therefore our study provides compelling evidence that there was a substantial increase in the prevalence of *Echinococcus* sp. in dogs from TDF between 2002 and 2015–2016.

The importance of a deworming programme is highlighted by the fact that the frequency of deworming was one of the main drivers of Echinococcus sp. prevalence in ranch dogs. Governmental surveys showed that only 13% of the interviewees dewormed their dogs in 1979, a number that increased to 98% in 1982 during the control programme (SAG, 1983). At that time, veterinarians from the government agency attempted to deworm all sheep dogs every 45 days, which is the approximate length of the pre-patent period of E. granulosus (Cook, 1989). In this study, interviewees from only 38% of ranches indicated that dogs were dewormed more than twice per year, and the same proportion were able to show deworming drugs when prompted by the interviewer. This suggests that with no control programmes in place, the geographic isolation of the ranches on the island and the costs associated with continued treatment have led most ranchers to stop deworming their dogs at the recommended frequency. Of relevance, lower frequencies of deworming (once or twice per year) did not have a significant effect on the prevalence of E. granulosus relative to ranches where interviewees reported never deworming their dogs, emphasizing the need for a deworming programme that is both consistent and intensive. Deworming more than twice per year also had a significant effect in reducing the prevalence of Taeniidae, which underscores its broader benefits to canine and public health.

Our results show that Echinococcus sp. prevalence in ranch dogs was generally higher in ranches where the interviewee reported seeing culpeo foxes on the property. Both culpeo and chilla foxes are known to be competent hosts of Echinococcus sp. (Schantz et al., 1972, 1976; Scioscia et al., 2013; Zanini et al., 2006), but chilla foxes seem to be less susceptible to infection under experimental conditions (Schantz et al., 1976). We did not detect Echinococcus sp. DNA in the faeces of wild canids (unidentified to species). However, our sample size was limited (n = 31), sampling was opportunistic (and therefore subject to bias), and samples were collected from the field (potentially with greater DNA degradation than the dog samples). Thus, these negative results are not sufficient to dismiss the possibility that culpeo foxes play a role in the epidemiology of Echinococcus sp. in TDF. Previous studies have documented E. granulosus infection in one chilla fox shot by hunters (n = 81) on the Argentinean portion of TDF (Zanini et al., 2006). Moreover, although we did not find an association between Taeniidae or Echinococcus sp. prevalence and whether or not dogs were fed or allowed to feed on guanaco meat, abattoir inspections reveal that Taenia hydatigena and E. granulosus are present in 0.8% and 3.1%, respectively, of guanacos harvested in Chilean TDF (n = 619; Swanhouse, 2015).

Interestingly, the presence of culpeo foxes was associated with a decrease in Taeniidae prevalence while the presence of chilla foxes was associated with an increase in the prevalence of these parasites. Coproparasitological surveys in Chile have shown that Taenia hydatigena and Spirometra sp. are more prevalent in culpeo foxes, whereas Mesocestoides sp. are more prevalent in chilla foxes (Oyarzún-Ruiz et al., 2020). It is plausible that the positive effect of chilla foxes on Taeniidae prevalence in ranch dogs is driven by different rates of foxto-dog transmission according to the species involved. Alternatively, there may be a spurious correlation due to habitat selection and resource partitioning. Epidemiological studies have shown that land cover may have a significant effect on the parasite prevalence of wild canids, with a pattern of increased prevalence of Taeniidae in grassland areas; this is thought to be secondary to the differences in intermediate hosts that are consumed by canids in each habitat type (Bouchard et al., 2021; Watts et al., 2015). Culpeo foxes (native species) are usually associated with denser thicket or matorral vegetation, whereas chilla foxes (human-introduced species) usually show a preference towards open grasslands and scrublands in plains (González del Solar & Rau, 2004; Jiménez & Novaro, 2004; Johnson & Franklin, 1994). Thus, the positive effects on the prevalence of Taeniidae attributed to the presence of chilla and to the absence of culpeo foxes may be instead related to differences in community structure driving parasite transmission across habitats. Although free-ranging dogs can play an important role in the epidemiology of Echinococcus sp. and other parasites in urban settings in Argentina (Flores et al., 2017; Soriano et al., 2010), we found that whether or not interviewees reported seeing free-ranging dogs at the ranch was not a significant predictor of the prevalence of these parasites.

Ranches where interviewees reported that dogs were fed or allowed to eat sheep viscera tended to present substantially lower prevalence of Taeniidae. This suggests that sheep may not be the main source of Taeniidae infection in ranch dogs and that the consumption of sheep viscera has a protective effect on ranch dogs, presumably because it makes them less likely to hunt wildlife that may serve as intermediate hosts of canid-infecting Taeniidae, such as rabbits and hares (Allan et al., 1999; Schantz et al., 1972). Several other characteristics of the ranches, as accessed through interviews, were also associated with Taeniidae prevalence in ranch dogs. Ranches located in Timaukel municipality with 500 sheep or less and where sheep were slaughtered less frequently tended to present greater Taeniidae prevalence in their dogs. These differences could be related to socioeconomic factors, with smaller ranches having less access to resources necessary to provide adequate veterinary care and food to their dogs (leading them to rely more on wildlife for nutrition). Additionally, ranches with larger number of dogs also tended to present higher Taeniidae prevalence, which is consistent with dog-to-dog transmission playing a role in the epidemiology of these parasites. Unexpectedly, ranches where dog faeces were removed more frequently showed a trend towards greater Taeniidae prevalence. This could be due to ranchers being more inclined to collect the faeces of their dogs when the dogs are kept in kennels or fenced areas at night, with increased Taeniidae transmission

occurring under conditions of confinement and in the absence of adequate deworming. While these results provide interesting grounds for speculation, further studies are needed to clarify how the epidemiology of different species of Taeniidae is driven by the nutrition and husbandry of dogs in Patagonian sheep ranches.

Although the prevalence of *Echinococcus* sp. could be argued to have been relatively low in this study (compared to the 68.4% prevalence recorded in 1979; Moro & Schantz, 2006), the fact that the prevalence of *Echinococcus* sp. has nearly tripled since the control programme was discontinued in 2005 is acutely concerning. Furthermore, the finding that 45.4% of ranch dogs tested positive for Taeniidae suggests that, at present, TDF sheep farms provide favourable conditions for the transmission and persistence of canid-infecting tapeworms. While other canid-infecting Taeniidae are generally of lower public health concern than *E. granulosus*, humans can occasionally serve as intermediate hosts (Spickler, 2020). Furthermore, Taeniidae can also cause economic losses in sheep farms due to mass condemnation of meat (Oryan et al., 1994).

While the PCR protocol employed in this study was initially thought to be 100% specific to *E. granulosus* (Štefanić et al., 2004), later studies found that the method did cross-amplify other species of *Echinococcus* (Boufana et al., 2008). To confirm the species involved, we attempted sequencing the amplicons of all PCR-positive samples, yet only succeeded for 10 samples (out of 23), due to partial sequences of insufficient quality in the remaining samples. Nevertheless, the fact that all sequences obtained were identical to publicly available sequences of *E. granulosus* confirms that this was indeed the main – if not the only – species of *Echinococcus* parasitizing ranch dogs in the study area.

In conclusion, our findings point to a persistent risk of echinococcosis in domestic dogs at ranches in Tierra del Fuego and provide convincing evidence that Chile's hydatidosis control programme, which was once considered to be successful, should be re-established and maintained to prevent the re-emergence of this disease as a significant public health problem. Additionally, it would be valuable to establish educational programmes aimed at improving local awareness about hydatidosis risk factors and the husbandry and hygiene practices that reduce the risk of human exposure. Furthermore, ethical management of free-ranging dogs would also contribute to reducing the potential propagation of *Echinococcus* sp. and other parasites on the island.

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CONFLICT OF INTEREST

The authors declare no competing or conflicting interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at https://zenodo.org/badge/DOI/10.5281/ze-nodo.6287410.svg, reference number 10.5281/zenodo.6287410.

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