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Ecology of domestic dogs (*Canis familiaris*) as a host for Guinea worm (*Dracunculus medinensis*) infection in Ethiopia

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Abstract

The global programme for the eradication of Guinea worm disease, caused by the parasitic nematode *Dracunculus medinensis*, has been successful in driving down human cases, but infections in non-human animals, particularly domestic dogs (*Canis familiaris*), now present a major obstacle to further progress. Dog infections have mainly been found in Chad and, to a lesser extent, in Mali and Ethiopia. While humans classically acquire infection by drinking water containing infected copepods, it has been hypothesized that dogs might additionally or alternatively acquire infection via a novel pathway, such as consumption of fish or frogs as possible transport or paratenic hosts. We characterized the ecology of free-ranging dogs living in three villages in Gog woreda, Gambella region, Ethiopia, in April–May 2018. We analysed their exposure to potential sources of Guinea worm infection and investigated risk factors associated with infection histories. The home ranges of 125 dogs and their activity around water sources were described using GPS tracking, and the diets of 119 dogs were described using stable isotope analysis. Unlike in Chad, where Guinea worm infection is most frequent, we found no ecological or behavioural correlates of infection history in dogs in Ethiopia. Unlike in Chad, there was no effect of variation among dogs in their consumption of aquatic vertebrates (fish or frogs) on their infection history, and we found no evidence to support hypotheses for this novel transmission pathway in Ethiopia. Dog owners had apparently increased the frequency of clean water provision to dogs in response to previous infections. Variations in dog ranging behaviour, owner behaviour and the characteristics of natural water bodies all influenced the exposure of dogs to potential sources of infection. This initial study suggests that the classical transmission pathway should be a focus of attention for Guinea worm control in non-human animals in Ethiopia.

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KEYWORDS

disease ecology, disease eradication, domestic dogs, Guinea worm, Neglected Tropical Diseases, One Health

1 | INTRODUCTION

Guinea worm disease is caused by the parasitic nematode *Dracunculus medinensis* and historically has infected humans across Asia and Africa (Watts, 1986). Since the 1980s, global eradication efforts have reduced human cases from approximately 3.5 million per year to only 28 cases in 2018 (CDC, 2019). However, significant numbers of infections in non-human animals have been detected in three of the four remaining endemic countries: Chad, Ethiopia and Mali, but not South Sudan (Molyneux & Sankara, 2017). In 2018, infections were confirmed in 1,069 domestic dogs (*Canis familiaris*), 32 domestic cats (*Felis catus*) and one olive baboon (*Papio anubis*; CDC, 2019). These non-human infections, along with insecurity in the remaining endemic areas, present major obstacles for the global Guinea worm eradication programme (Al Awadi et al., 2014).

Emergent worms from human and non-human hosts are genetically indistinguishable (Thiele et al., 2018). Given the low numbers of human cases, this suggests that Guinea worm disease in humans is now effectively a zoonotic infection that is maintained by reservoirs in non-human animals. In the near absence of human cases, non-human hosts are maintaining Guinea worm in the environment, resulting in infrequent but ongoing infection in humans. The existence of a non-human reservoir could explain the apparent re-emergence of the disease in Chad, where no human cases were reported for 10 years prior to 2010, though Guinea worm surveillance at that time was also problematic (Eberhard et al., 2014). To prevent the re-emergence and resurgence of Guinea worm after its near elimination in humans, and for eradication to be completed, transmission must be interrupted in non-human hosts. However, little is known about the epidemiology of Guinea worm in any of its non-human hosts.

Classically, transmission of Guinea worm to humans is through the ingestion of water containing copepods infected with worm larvae. When male and female larvae have infected the primary host, they mate and, after a prepatent period of 10–14 months, the gravid female emerges and releases larvae into a water body, where they are ingested by copepods, completing the cycle (Greenaway, 2004). It has recently been hypothesized that a novel pathway might also contribute to ongoing infections of humans and, potentially to a greater extent, non-human animals (Eberhard et al., 2014). This hypothesized pathway requires the ingestion of the gut contents or tissues of transport or paratenic hosts, such as fish or frogs, that have themselves eaten an infected copepod (Cleveland et al., 2017; Eberhard et al., 2016).

Human cases of Guinea worm disease have been reduced by applying a number of methods, including the detection and isolation of cases, chemical treatment of water bodies to remove copepods (using the organophosphate temephos) and the provision of safe

drinking water, from pumps or by filtration (Biswas, Sankara, Agua-Agum, & Maiga, 2013). More recently, recommended but untested measures have also included thoroughly cooking fish or discarding fish entrails (Cleveland et al., 2017). Relative to implementation in people, these control strategies are much harder to implement for free-ranging animals and, although some of these measures are being applied to control dog infections, infections in dogs persist. Thus, to prioritize and target control efforts, a better insight into the ecology of non-human animal hosts, particularly dogs, in relation to Guinea worm infection is required.

Detected infections in dogs are found along major river systems in Chad and Mali, where they are distributed in riverine and wetland habitats associated with the Chari (CDC, 2017) and Niger (CDC, 2019) rivers, respectively. In contrast, infections in Ethiopia are not concentrated along a major water source and are instead localized to a cluster of villages (Beyene, Bekele, Shifara, & Ebstie, 2017), in an area dominated by forest and smallholdings (Degife, Zabel, & Mauser, 2018). The different ecology of the affected area in Ethiopia, compared to Chad and Mali, has raised questions on the similarity of risk factors for transmission in non-human hosts (Molyneux & Sankara, 2017). Our recent work in Chad (McDonald et al., 2020), using GPS tracking of dogs and stable isotope analysis of dog diets, found that dogs living in households that provided water to their animals had a lower risk of having had Guinea worm and that dogs that ate more fish had an increased risk. These findings suggested that in Chad, there is a classical route for worm transmission in dogs, via drinking contaminated water, as well as a novel route, potentially by eating fish carrying a source of infection (McDonald et al., 2020). Using similar approaches to our work in Chad, in this study we aimed to outline the ecology of dogs in this part of Ethiopia and to identify potential risk factors associated with their history of Guinea worm infections. We investigated aspects of both classical and hypothesized novel transmission pathways for Guinea worm infection. Specifically, we investigated dog husbandry, access to natural water sources and consumption of aquatic vertebrates as potential correlates of previous worm infections.

2 | MATERIALS AND METHODS

2.1 | Study area and subject recruitment

Fieldwork was conducted in the Gog woreda (district) of Gambella region in western Ethiopia, between 28 April and 15 May 2018. With the informed verbal consent of the kebele (ward or municipality) chairman, village leaders and householders, dogs were studied in three neighbouring villages (Ablen, Atheti and Wichini, centred on 7°37'19.7"N 34°23'25.9"E; Figure 1), that are among the worst

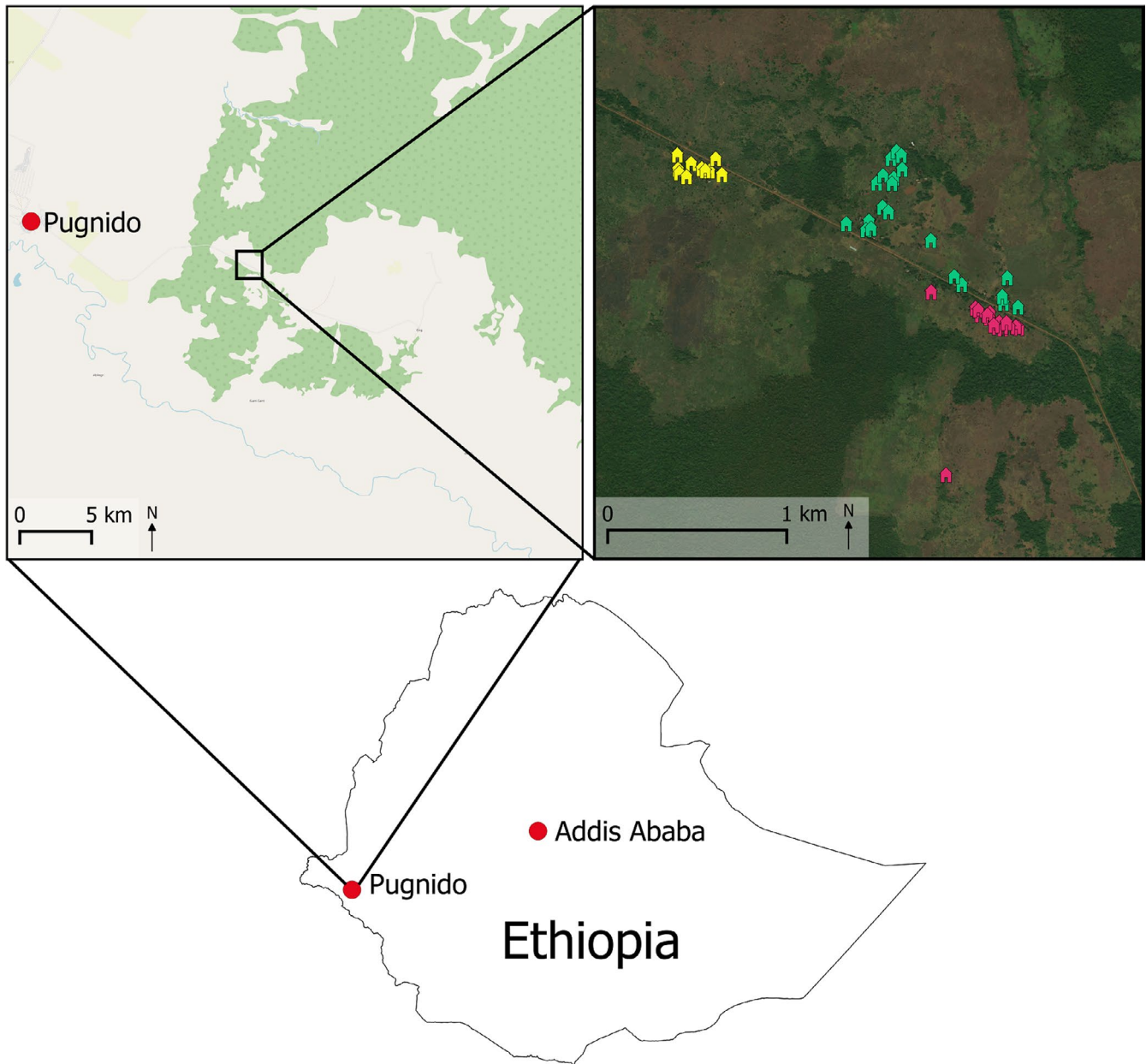


FIGURE 1 Locations of three rural villages and households in Gog woreda, Ethiopia, in which domestic dogs were studied. The house symbols represent households from Ablen (yellow), Atheti (green) and Wichini (red) from which dogs were tracked. Pugnido is the principal town of Gog woreda (district). Maps include the base map from OpenStreetMap (<https://www.openstreetmap.org>), and the satellite image was generated using the ESRI World Imagery Basemap (sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, GetMapping, AeroGRID, IGN, IGP, swisstopo and the GIS User Community)

affected by Guinea worm infections in Ethiopia. We recorded the location of all households that owned dogs using a handheld GPS (Garmin Map 64S). A questionnaire was used to gather information on whether the household members reported going hunting, the frequency of water provision for dogs (categorized as 1–3 times a day and >3 times a day), what they fed their dogs and the number of dogs in the household. For each dog, we recorded its sex, age in months (as recalled by the owner), whether the dog had ever had Guinea worm and body condition score (BCS, 1 = emaciated and 9 = obese, Laflamme, 1997). BCS was then categorized as poor (≤ 2), moderate (3) or good (≥ 4).

2.2 | Dog space use

Dogs were collared for up to 14 days with standard retail dog collars (Ancol Heritage), fitted with an i-gotU GT-600 GPS unit (Mobile Action Technology Inc.). The GPS was configured with a fix interval of 10 min. GPS data were cleaned by removing locations taken 12 hr after collar deployment and 12 hr before collar recovery. Any likely erroneous GPS fixes with speeds greater than 20 km/hr between locations were removed. GPS data were projected into the relevant coordinate reference system for Ethiopia (EPSG: 32636) using the 'sp' and 'rgdal' packages (v1.3.1 & v1.3.3, respectively).

The dogs' home and core ranges were calculated using autocorrelated kernel density estimates (AKDE) from continuous-time movement models. Models were fit using the 'ctmm' package (v0.5.5) following procedures set out by Calabrese, Fleming, and Gurarie (2016). Variograms were used to check the autocorrelation structure of each individual's movement data. Individuals were excluded from home range analyses if there was no asymptote in the variogram, suggesting the individual had not been monitored for long enough, or was exhibiting non-range-resident behaviours, for example range expansion or dispersal. Movement models were fitted using maximum likelihood, and model selection was determined on the basis of Akaike's information criterion (AIC). Once the models were selected, the 95% AKDE ($AKDE_{95}$) and core AKDE ($AKDE_{core}$) were calculated. To calculate the core range for each individual, an exponential regression was used to identify the isopleth where the estimated home range area begins to increase more rapidly than the relative frequency of use (slope = 1; Van der Wal & Rodgers, 2012). For comparability with earlier studies only, we also calculated the 100% minimum convex polygon (100% MCP) as a measure of total range and the 60% kernel density estimate (60% KDE) as a measure of core range, using the 'adehabitatHR' package (v0.4.18). To estimate the probability of finding each dog around their respective household, the number of relocation points within a 50 m radius of the household's location was divided by the total number of relocation points. In addition, the same was done for relocation points within 100 m of any household with tracked dogs, and this was used to estimate the probability of finding the dogs around the village.

DigitalGlobe satellite imagery of the field site was obtained for October 2018, red, green, blue and near-infrared bands from WorldView-3 and WorldView-2 satellites. Natural water sources were identified and vectorized using the QGIS platform by manually searching an area of 1365 km² centred on the villages of interest and buffered with radius corresponding to the largest ranges reported for free-ranging dogs in Ethiopia (Atickem, Bekele, & Williams, 2010). To ground-truth the location of vectorized water bodies, GPS locations of water sources around villages were taken in the field. For each dog, we determined the number of relocation points within 100 m of a natural water body and water pumps, the number of separate visits to water bodies (defined by an interval of 30 min between fixes) and the number of unique water bodies visited. For each water body, we measured area, distance to the nearest household with tracked dogs, whether it had been visited by a dog across the monitoring period, the number of individual dogs that had visited and the number of relocation points within 100 m of the water source for all dogs and for those dogs with a history of Guinea worm infection.

Variation in the size of the dogs' ranges was analysed using linear models (LMs). Only $AKDE_{95}$ was used in analysis as $AKDE_{core}$ was highly correlated ($\rho = 0.99$; $p < .01$). $AKDE_{95}$ was \log_e -transformed to normalize its distribution, and explanatory variables were village, sex, age, body condition, whether the dog was from a hunting household, frequency of water provision, number of days monitored and the distances of the nearest water pump and natural water body to the household.

Variation in the activity of dogs around natural water bodies was analysed using general linear models (GLMs). The first model used a binomial error structure and considered whether or not dogs had visited a water source or not. Explanatory variables were village, sex, age, body condition, $AKDE_{95}$, whether the dog was from a hunting household, frequency of water provision, days monitored and the distances of the nearest natural water body and nearest pump to the household. Two additional models, with negative binomial error structures, were used to investigate activity around water for those individuals that visited water bodies. The response variables for these models were the number of relocation points around water bodies and the number of unique water bodies visited. Explanatory variables were the same as in the previous model, but with the addition of the \log_e -transformed number of days for which a dog had been monitored included as an offset.

To investigate predictors of whether or not a water source was visited by dogs, a binomial model was fitted. Explanatory variables included the \log_2 area of the water body and the \log_2 distance of the water body to the nearest known household with dogs. To identify predictors of the variation in dog activity around water bodies for those visited by dogs, a negative binomial GLM was fitted. The number of relocation points around the water body was used as the response variable, and the explanatory variables were the same as in the previous model. A generalized additive model (GAM) was used to relate the cumulative total of dog visits per water body to the \log_2 -transformed distance of the water bodies from households with tracked dogs and then to identify the threshold in distance of water bodies from households below which 95% of dog visits to all water bodies occurred. The smoothing parameter of the GAM was restricted ($k = 4$) to prevent overfitting and to derive a simple curve reaching an asymptote. The cumulative count of visits was made after ordering the water bodies by number of visits in descending order.

2.3 | Dog diets

To identify the principal food items, owners were asked: (a) What did they feed their dogs? (b) What did they feed their dogs yesterday? And (c) what had they seen other people's dogs eating? Where possible, samples of principal food items were sampled from the households and were otherwise sourced from the market in the nearby town of Pugnido (Gog) or opportunistically from local hunters and fishers. For each dog, one whisker was plucked during collar collection. On the day of collection, food samples and whiskers were dried and stored in ambient conditions. All samples were sterilized in a sterilizing oven for 6 hr at 140°C before, and in an autoclave after, importation to the UK under licence.

Prior to analysis, food samples were freeze-dried and homogenized, and approximately 0.7 mg (± 0.1 mg) was weighed in a tin cup. For nitrogen-depleted plant samples, 10 mg (± 0.1 mg) was weighed out and analysed in order to produce enough nitrogen for accurate isotopic characterization. Whiskers were rinsed in distilled water, scraped to remove surface contaminants, sterilized and dried for

TABLE 1 Summary of characteristics of the free-ranging domestic dog population in three rural villages in Gog woreda, Ethiopia. Reported for each village are numbers of households owning dogs, number of resident adult dogs, mean numbers of dogs per household, their sex, age (mean \pm standard error), body condition in categories, the numbers and proportion of the resident population with a history of Guinea worm infection and the numbers of dogs collared and as a proportion of the resident adult dog population. Two resident adult dogs were not collared; one of these, from a household in Ablen village, had a history of Guinea worm infection, while the other, from Wichini village, did not. Numbers of dogs with missing data or where the variable was not recorded are indicated

Village	No. of households with dogs	No. of resident adult dogs	No. of dogs per dog-owning household	Sex F:M (No. not recorded)	Age in months (No. not recorded)	Body condition Poor:Moderate:Good (No. not recorded)	No. of dogs with history of Guinea worm infection (proportion of resident adult dogs)	No. of dogs collared
Ablen	10	24	2.4	14:10 (0)	28 \pm 5 (0)	8:6:9 (1)	2 (8.3%)	23 (95.8%)
Atheti	21	68	3.2	37:31 (0)	34 \pm 3 (1)	16:30:19 (3)	12 (17.6%)	68 (100%)
Wichini	16	39	2.4	19:19 (1)	29 \pm 4 (2)	3:26:8 (2)	5 (12.8%)	38 (97.4%)
Total	47	131	2.8	70:60 (1)	32 \pm 2 (3)	27:62:36 (6)	19 (14.5%)	129 (98.5%)

24 hr. They were then cut into 0.4–0.8 mg sections and sealed in a tin cup for analysis.

To conduct stable isotope analyses of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), samples were analysed in a Sercon 2020 elemental analyser isotope ratio mass spectrometer. Stable isotope ratios are expressed as δ values in ‰, the ratio of heavy to light isotope relative to the isotopic ratios of an international standard for each element: the Vienna Pee Dee Belemnite (VPBD) for $\delta^{13}\text{C}$ and atmospheric N_2 for $\delta^{15}\text{N}$. Estimated mean precision between sample runs was $\pm 0.10\%$ (± 0.01) for $\delta^{15}\text{N}$ and 0.08% (± 0.01) for $\delta^{13}\text{C}$, based on standards run within sample batches. A lipid normalization model was applied to $\delta^{13}\text{C}$ values of samples with a high lipid content (Kiljunen et al., 2006; Post et al., 2007).

The relative contributions of food source groups to dog diets were estimated using the package 'SIMMR' v.0.3 (Parnell, Inger, Bearhop, & Jackson, 2015), and isotope ratios were averaged across all whisker sections for each dog. This was done initially to estimate the diets of the whole dog population and then to estimate the diets of individual dogs. Population-level estimates of diet composition provide a more accurate representation of overall dog diets, whereas estimates of individual diet should instead be viewed as a means of ranking individual dogs based on the relative importance of food sources, due to the increased influence of uninformative priors in models with low numbers of observations (Swan et al., 2020). Models were run for 1,000,000 iterations, with a burn-in of 50,000 and thinning rate of 50. Gelman diagnostics were used to check model convergence. The package 'SIDER' v.1.0.0 (Healy et al., 2018) was used to generate trophic discrimination factors for dogs for $\delta^{15}\text{N}$ (3.68‰ SD 1.36) and $\delta^{13}\text{C}$ (2.82‰ SD 1.78), based on their diet type and phylogenetic position. Since dogs are omnivores, concentration dependence values (mean N/C) were added to the model (Phillips & Koch, 2002).

2.4 | Guinea worm infection

Field records of owner-reported Guinea worm histories were cross-checked with records of emergent adult worms from

Ethiopian Dracunculiasis Eradication Program (EDEP). There was agreement in all but three records: two owner-reported infections were not in the EDEP database, and for these, the owner-reported records were used as they could represent undetected infections. The third discrepancy was an infection recorded by the EDEP that was missing in the owner-reported records. We included the EDEP Guinea worm record as it was based on the collection of an emergent worm. Any EDEP records of emergent worms within the 14 months after our fieldwork were also included, as transmission may have occurred at or around the time of the study.

A GLM with a binomial error structure was used to explore the correlates of individual-level factors with the dogs' history of Guinea worm infection. Explanatory variables were sex, age, body condition, estimated proportion of aquatic vertebrates in the diet from stable isotope analysis, range ($AKDE_{95}$), number of relocation points within 100 m of a water body, water provision frequency, village and whether the dog was from a hunting household. A staged analysis was conducted in order to maximize sample size. The model was run first for all predictors (requiring the removal of data for individuals with missing data). All variables that had summed weights across the top model set of >0.5 for any of the three sets of Guinea worm infection records (EDEP, owner-reported and combined records) in this initial analysis were then included in the final model. This ensured that any potentially important explanatory variables were retained for further analysis.

To identify the characteristics of water sources that might be more likely to be visited by dogs with a history of Guinea worm infection, a binomial GLM was conducted. Explanatory variables were the \log_2 -transformed area of the water body and the \log_2 distance of the water body to the nearest known household with dogs. A GLM with a Poisson distribution and offset for total number of visits was used to identify predictors for the variation in the activity of dogs with a history of Guinea worm around water bodies. The number of relocation points within 100 m of the water body was used as the response variable, and the explanatory variables were the same as in the previous model.

TABLE 2 Summary of ranging behaviour and measures of activity around natural water sources for free-ranging dogs from three rural villages in Gog woreda, Ethiopia. Data are from collared dogs ($n = 129$) with successful GPS data downloads ($n = 127$) that were determined to be range-resident ($n = 125$). A summary of the home range estimates for the 95% and core autocorrelated kernel density estimates (AKDE₉₅ and AKDE_{core}, respectively) is provided for each village. 100% minimum convex polygon (MCP) and 60% kernel density estimates (KDE_{60%}) are provided only for comparison with other studies. Summary statistics are also reported for the number of individuals with relocation points within 100 m of a water source, the number of unique water sources visited, proportion of time spent around water sources and the distance of households to the nearest water source. For the number of unique water sources visited and time at water sources, summary values exclude individuals that were not active around water sources. Where relevant, the median and inter-quartile ranges are provided for each parameter

Village	No. of dogs with successful data downloads	No. of range-resident dogs	AKDE ₉₅ (km ²)	AKDE _{core} (km ²)	100% MCP (km ²)	KDE _{60%} (km ²)	No. of dogs to visit water sources (%)	No. of unique water sources visited	Time at water sources (%)	Distance of household to nearest natural water source (km)
Ablen	22	22	0.14 (0.01–0.32)	0.03 (<0.01–0.07)	0.63 (0.19–1.03)	0.03 (<0.01–0.06)	7 (31.8%)	1 (1–2)	<1 (<1–<1)	1.12 (1.06–1.17)
Atheti	67	65	0.08 (0.02–0.46)	0.01 (<0.01–0.08)	0.29 (0.10–0.76)	0.01 (<0.01–0.06)	53 (81.5%)	6 (4–8)	3 (1–6)	0.34 (0.28–0.37)
Wichini	38	38	0.12 (0.03–0.69)	0.02 (<0.01–0.16)	0.38 (0.17–0.80)	0.02 (<0.01–0.13)	17 (44.7%)	6 (4–7)	1 (<1–2)	0.45 (0.41–0.48)
Total	127	125	0.10 (0.02–0.44)	0.02 (<0.01–0.07)	0.36 (0.13–0.84)	0.02 (<0.01–0.07)	77 (61.6%)	5 (4–8)	2 (1–5)	0.39 (0.32–0.48)

An information-theoretic approach was used for model selection in all LMs and GLMs, using ranked comparison of corrected AIC (AICc) values. The top model set was selected using a difference in AICc (Δ AICc) of < 2 from the top model, and model averaging was conducted over the top model set (Burnham & Anderson, 2002). Results are expressed as full model-averaged coefficients for specific explanatory variables and 95% confidence intervals. For binomial epidemiological models, results are expressed as the odds of having had Guinea worm and as relative risks, with 95% confidence intervals from bootstrapping 10,000 times with replacement. Correlations between explanatory variables were investigated prior to analyses using Spearman's rank correlation tests, and correlated variables were not entered into the same models. In all models, village and distance from natural water bodies and from water pumps were highly covariable and so were precluded from appearing together in models. Analyses were undertaken in R version 4.0.0 (R Core Team, 2020) and QGIS v2.18.1. The package 'MASS' (v7.3-51.5) is for negative binomial GLMs, 'MuMIn' (v1.43.17) for model selection and 'mgcv' (v1.8.12) for GAMs. Additional model checks were performed using 'DHARMA' (v0.3.2.0).

3 | RESULTS

3.1 | Ranging behaviour

Collars were deployed on 129 of 131 (98.5%) resident adult dogs from 47 households (Table 1). Data were successfully downloaded from 127 collars, and, from these, 125 dogs were identified as range-resident. The mean number of days that dogs were tracked was 10 days, with a minimum observation period of 3 days and a maximum of 13 days. Median AKDE₉₅ was 0.10 km², and median AKDE_{core} was 0.02 km² (Table 2). The median proportion of time that dogs spent around their household was 77% (inter-quartile range 61%–89%) and around the village was 94% (IQ range 83%–99%). Range size was significantly larger in older dogs (26.6% larger for every year older; 95% confidence interval 4.0%–54.2%, $n = 114$). Range sizes did not differ between villages. Dog sex, body condition, and whether the dog was from a hunting household, or from a household that provided water more frequently, did not significantly affect range size. A summary of the top model sets for all analyses is provided in Supplementary Information.

3.2 | Activity around natural water sources

A total of 359 water bodies were identified. Of the water bodies with known GPS locations, 60 of 99 (61%) were detected in the satellite imagery. Households with tracked dogs were a median of 406 m (IQ range 312–513 m; Table 2) from the nearest natural water body. Of all the water bodies identified, 50 (14%) were visited by tracked dogs during the study. The visited water bodies

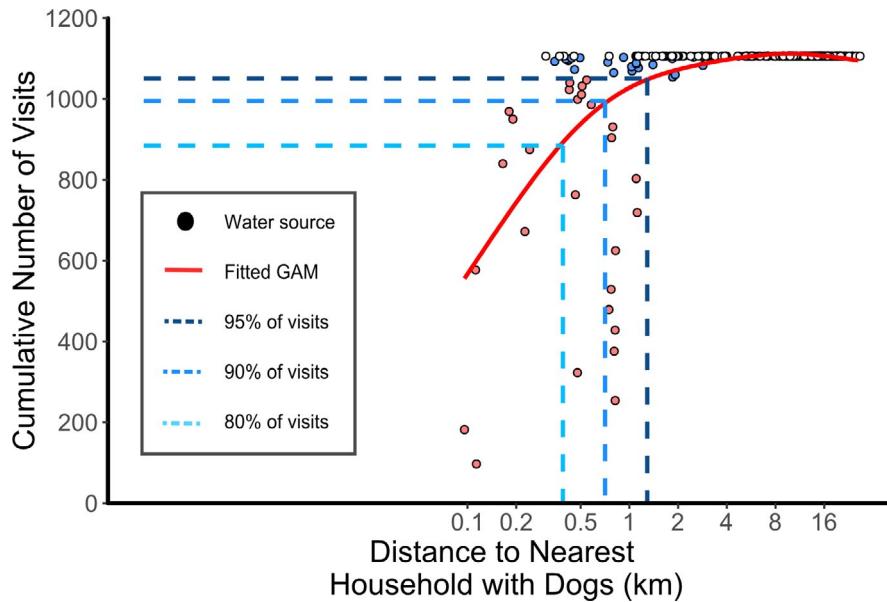


FIGURE 2 Free-ranging domestic dog activity around water bodies in three rural villages in Ethiopia, showing the cumulative total of all dog visits to water bodies plotted against the distance of the water body to the nearest household with tracked dogs. The dashed lines indicate the distance from a household with dogs at which 80%, 90% and 95% of all dog visits are captured. Points represent water bodies that account for 95% of visits (red), which have been visited but are not within the 95% threshold (blue) and those not visited by dogs (white). The red line represents the predictions from a generalized additive model relating the cumulative number of dog visits to the distance of water bodies from a household with a tracked dog

were a median of 742 m (IQ range 426–1,086 m) from a household with tracked dogs and had a median area of 77 m² (IQ range 43–223 m²). The relationship between dog visits to water bodies and distance from households with dogs (GAM: $r^2 = .37$, $t = 200.1$, $k = 3$, $p < .001$) identified that 27 water bodies accounted for 95% of all dog visits and these were all <1.5 km from a household with tracked dogs (Figure 2).

Natural water bodies that were further from a household were less likely to be visited by dogs than those that were closer (odds ratio = 0.20 as distance from a household doubles, 95% CI 0.13–0.32, $n = 359$). Of the water bodies that were visited by dogs, those further from households experienced less dog activity (odds ratio = 0.59 as distance from a household doubles, 95% CI 0.40–0.86, $n = 50$), while larger water sources experienced less dog activity (odds ratio = 0.74 as size doubles, 95% CI 0.61–0.92).

Dogs in Atheti village were more likely to have visited a natural water source than dogs in Ablen (odds ratio = 13, 95% CI 3–55, $n = 114$). Dogs with larger ranges were more likely to have visited a water body (Figure 3a; odds ratio = 48, 95% CI 6–373), though dogs from a hunting household were less likely to have visited a water body (odds ratio = 0.13, 95% CI 0.03–0.62).

Of those dogs that had visited a natural water source ($n = 68$), dogs in poor body condition spent less time (proportionally 0.55 of GPS fixes, 95% CI 0.38–0.81) around natural water bodies than dogs in better condition. Dogs in different villages spent different amounts of time near natural water bodies. Those in villages nearer natural water source systems spent more time near water bodies: dogs in Atheti and Wichini were predicted to have 7.6 (95% CI 4.4–13.2) and 2.8 (95% CI 1.5–5.2) times more fixes near water bodies, respectively, when

compared to Ablen. All households reported providing water for dogs on at least a daily basis, but dogs from households that provided water more frequently (>4 times a day) spent less time near standing water (proportionally 0.65 of GPS fixes, 95% CI 0.47–0.90) than those dogs provided water 1–3 times a day (Figure 3b). There were significant differences in the number of unique water bodies dogs had visited between different villages, with dogs in Atheti (4.2 times the number of water bodies, 95% CI 2.7–6.6) and Wichini (3.5, 95% CI 2.2–5.6) visiting more water bodies than dogs in Ablen. Dogs with larger ranges also visited 1.3 (95% CI 1.1–1.5) times the number of water bodies.

3.3 | Dog diets

Dog owners reported that they had either fed or had seen their dogs eat a range of items, from maize, wild meat, livestock, vegetables and grain foods. C4 plant foods, specifically a maize or maize-based porridge, were reported from all 47 household respondents. The next most commonly reported items were C3 plant foods (cabbage, beans, squash, rice and papaya; 17 respondents) and livestock meat (beef, goat and pork; 10 respondents). These were followed by wild meat (baboon, wild bovid (antelope) species, rats, frogs, felid and unspecified; 8 respondents) and fish (4 respondents). Most people reported that they did not know what dogs from other households ate (27 respondents) or that they ate maize (13 respondents), with a range of other items that were only identified on single occasions. Only three respondents reported that their own dog, or others' dogs, ate human faeces.

Owner reports of principal dietary items, together with previous studies of dog diets in Chad (McDonald et al., 2020),

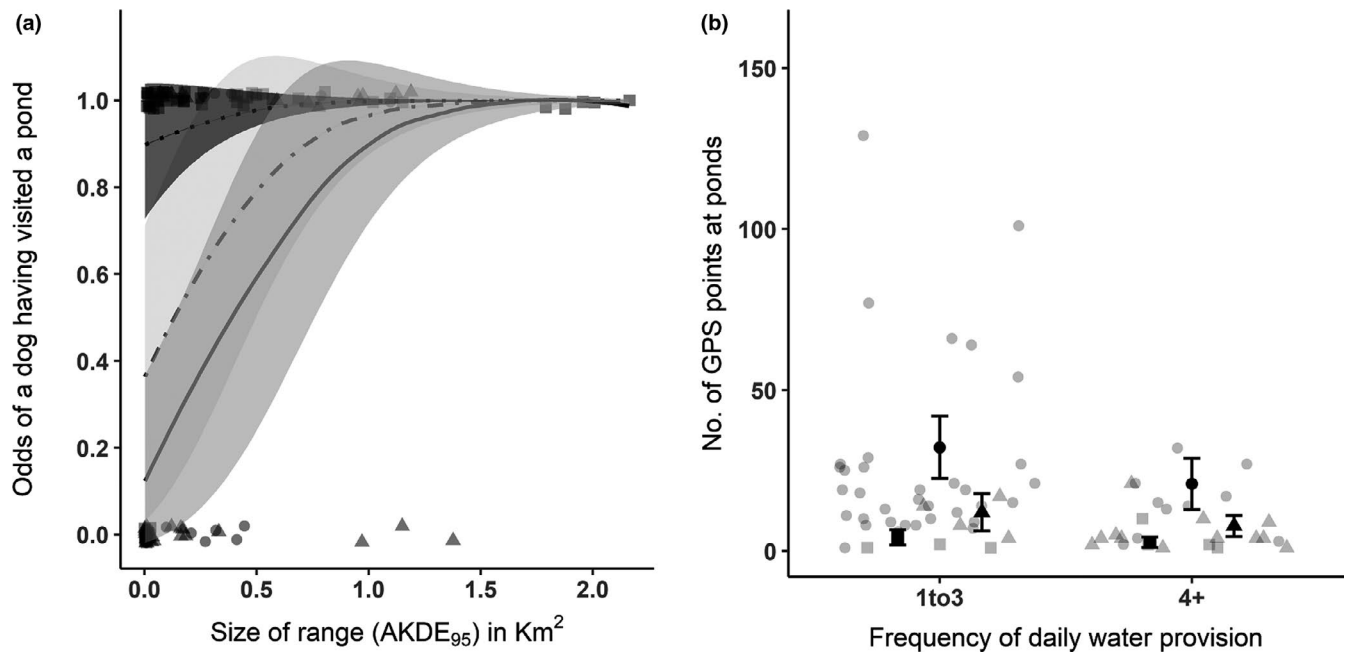


FIGURE 3 Domestic dog ranging behaviour and exposure to potential sources of Guinea worm infection in three rural villages in Ethiopia. (a) The relationship between dog home range size and the likelihood of a dog having visited a natural water body (pond). Odds are predicted from the model of factors explaining whether a dog had visited a water body over the course of the study. (b) The relationship between frequency of water provision and the amount of time spent near natural water bodies (based on the number of relocation GPS fixes). Predictions are from the model of factors explaining the number of fixes within 100 m of water body for those dogs that had visited a natural water body. The predictions are shown for dogs in the three villages: Atheti (dotted line, circles), Wichini (solid line, triangles) and Ablen (dashed line, squares). Other factors are held constant

determined the initial collection of putative food items. Once the stable isotope ratios were compared, these food items were formed into six food source groups: C3 plant foods, C4 plant foods, human faeces, livestock, terrestrial wild vertebrates and aquatic vertebrates (comprising fish and frogs; Figure 4; Table 3).

Whiskers of 119 dogs were analysed. Based on an estimate of dog whisker growth rate of 0.42 mm per day (McDonald et al., 2020), these whiskers represented dog diets over a time span of a little over 3 months (98 days; SD 21 days). Isotopic analysis of dog whiskers and food sources corresponded with dog diet composition as reported by owners. The majority of the diet of the dog population was composed of C4 plant sources (62%, 95% credible intervals 59%–66%). This was followed by faeces (17%, 95% CI 11%–22%) and livestock meat (11%, 95% CI 8%–14%) making up between 10% and 20% of the diet, and then C3 plants (4.2%, 95% CI 1.1%–8.3%), terrestrial wild vertebrates (3.7%, 95% CI 1.5%–6.1%) and aquatic vertebrates (2.6%, 95% CI 1%–4.3%) each constituting <5% of the dogs' diets (Figure 4).

3.4 | Correlates of Guinea worm infection

Of the 129 collared dogs, 18 had some history of Guinea worm infection (Table 1). One of the two uncollared dogs also had history

TABLE 3 Numbers of samples collected of each putative food source group and their constituent food items

Found source group	Food item	Sample count	Group total
C3 plants	Pulses	11	52
	Grains	9	
	Vegetables	18	
	Fruit	14	
C4 plants	Maize	19	29
	Sorghum	5	
	'Mash'	5	
Faeces	Human faeces	2	2
Livestock	Chicken	5	12
	Beef	1	
	Goat	6	
Terrestrial wild vertebrates	Reptile	1	10
	Mammal	7	
	Bird	2	
Aquatic vertebrates	Lake fish	3	39
	River fish	7	
	Stream fish	19	
	Frogs (various species)	10	

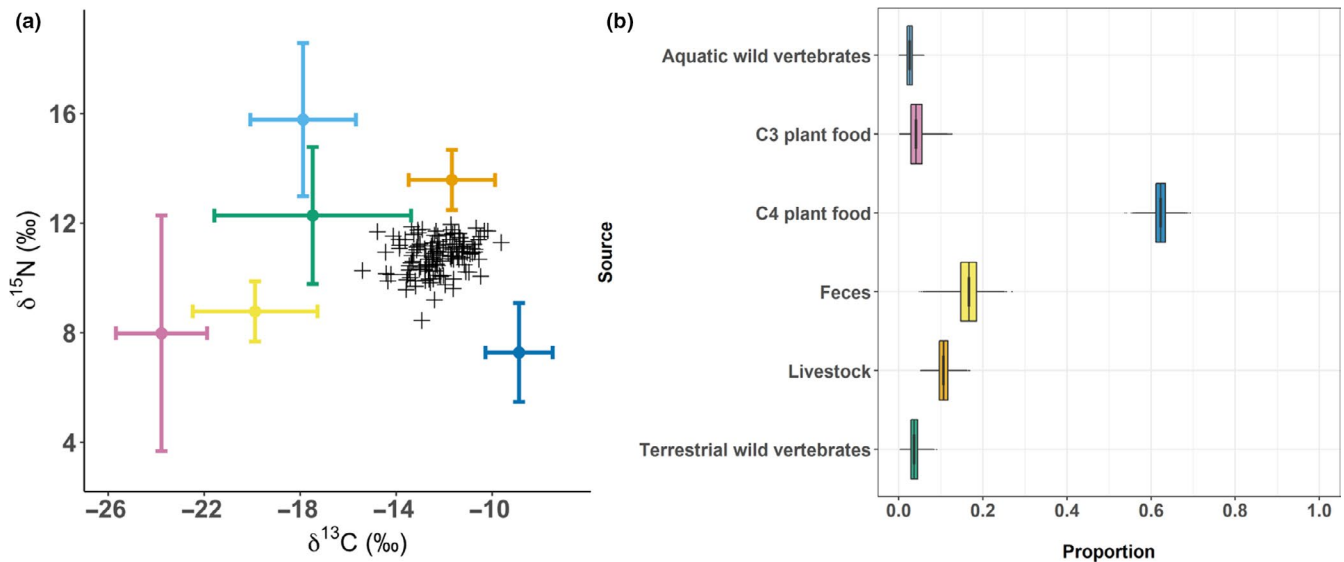


FIGURE 4 Estimates of the composition of the diets of free-ranging domestic dogs in three rural villages in Ethiopia, as determined by stable isotope analysis of dog whiskers and putative foods. (a) The isospace of dogs and their putative food source groups: the mean \pm standard deviation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for the food source groups; and the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for individual dogs, averaged across all whisker sections (black crosses). Trophic discrimination factors have been applied to adjust the relative position of food sources upwards for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. (b) Estimates of the proportional contribution of each putative food source group to the diets of the sampled dog population, as calculated by stable isotope mixing model analysis

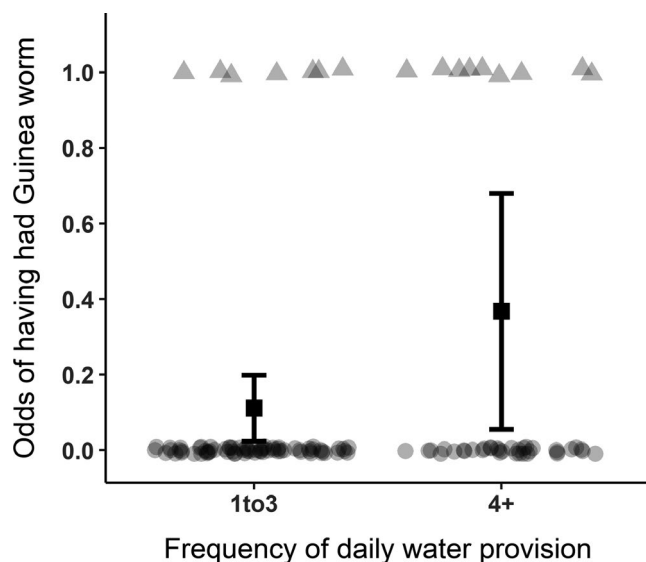


FIGURE 5 The effect of the frequency of water provision on Guinea worm infection histories of free-ranging dogs in three villages in Ethiopia. The odds, with 95% confidence intervals, of having had Guinea worm are shown for dogs which are reported by owners to be provided with water from 1 to 3 times a day and at least four times a day. Odds are predicted from the model looking at the relationship between the history of Guinea worm infection and with other predictive factors held constant. Results are presented for Atheti village but are similar in the other two villages

of infection. In initial models of the risk factors in predicting the history of Guinea worm infection ($n = 107$ dogs), the frequency of water provision, the number of visits to natural water bodies, the age of a dog, and its village all had a sum of weights >0.5 across

one of the top model sets and so were retained for further analysis. The proportion of aquatic vertebrates in the diets of dogs had a sum of weights of 0.26, 0.13 and 0.04 of the respective top model sets for the three Guinea worm record datasets and hence did not contribute significantly to variation in infection history. Dogs that were reported to be provided water at least 4 times a day had a higher chance of having had Guinea worm than those provided with water with less frequency (relative risk = 4.0, 95% confidence interval 1.8–28.8; Figure 5). Older dogs had slightly higher chances of having had Guinea worm (relative risk = 1.02 with each additional month of age, 95% CI 0.98–1.04, $n = 121$), although this effect was marginal.

Of the natural water bodies that were visited by dogs over the course of the study ($n = 50$), a water body was less likely to have been visited by a dog with a history of Guinea worm if it was further away from households (odds ratio = 0.23 as distance doubles, 95% CI 0.08–0.50). Dogs with a history of Guinea worm infection spent more time around larger water bodies, compared to the general dog population (dogs with a history of infection were located proportionally 1.22 times more frequently around natural water sources as the area doubled, 95% CI 1.12–1.33).

4 | DISCUSSION

We have provided a detailed account of the ranging behaviour and diets of free-ranging domestic dogs in this area of rural Ethiopia, with the aim of understanding the potential pathways for transmission of Guinea worm infection and therefore potential ways in which transmission might be interrupted. In this initial, short-term

study in this disease system in Ethiopia, we found no evidence to support the hypothesized novel transmission pathway involving paratenic or transport hosts (Cleveland et al., 2017; Eberhard et al., 2016). There was a general lack of dietary variation among dogs in this population at this time, and the contribution of aquatic vertebrates (frogs and fish) to dog diets was small and variation among dogs was uncorrelated with infection history. This is not to say that any putative novel transmission pathway, via transport or paratenic hosts, is not salient in this system, but suggests that either transmission via such hosts is not a major pathway, or that it is confined to very rare events, or that it arises from consumption of very low mass items that do not contribute significantly to the mass of dog diets. This is in contrast to Chad, where the risk of a history of Guinea worm infection was related to between-dog variation in the proportion of fish in their diet, over the range of about 10–20% (McDonald et al., 2020).

We found that variations in dog body condition, dog husbandry and the range sizes of dogs were related to their exposure to water bodies, as potential sources of infection. These results identify factors affecting exposure to such water bodies and might be used to frame further investigations and measures in mitigation of potential risks of dogs in rural Ethiopia acquiring Guinea worm infection through the classical transmission pathway (Greenaway, 2004). Management efforts in both Ethiopia and Chad, where primary studies of dog ecology in relation to Guinea worm infection have now been conducted, need to be tailored to the ecology of the affected areas, and, in Ethiopia, there is more support for links between the classical transmission pathway and dog infections.

The positive effect of dog age on history of infection is likely a simple function of the duration of exposure. While this effect is intuitive, reflecting the fact that older dogs have had longer to acquire an infection, due to the relative infrequency of infection, this effect was marginal. It was also the case that older dogs had larger home ranges, which was associated with a greater probability of having visited a natural water body. Therefore, the increased ranges of older dogs could lead to increased exposure risk. Overall, dogs in these villages had small home ranges at this time of year and the majority of their time was spent around the village. Although seasonal differences in ranging behaviour are expected (Atickem et al., 2010), the ranges in this study are representative of dog movements at the start of the Guinea worm transmission season and when infection is thought most likely to occur (CDC, 2019).

Against a background of reports of near-universal provision of pumped groundwater to dogs, we identified an increase in the likelihood of a history of infection with respect to increasing frequency of water provision. This is counterintuitive, given that in Chad household water provision to animals was associated with reduced risk of infection in dogs (McDonald et al., 2020), and dogs given water more frequently would be less reliant on potentially contaminated natural sources of water. The water provided to dogs comes from groundwater (aquifers) that cannot, at the time of collection, be contaminated with copepods or worm larvae. One possible explanation for the current result is that households reporting their current practice of providing water more

frequently were doing so in response to owning a dog that had previously had an emergent worm. The Guinea worm eradication campaign has clearly had some success in educating rural communities in this region of Ethiopia on how to reduce risks of infection. Therefore, it is reasonable that the owners would respond to having had an infected dog by ensuring that clean water is readily available, thereby reducing the chance of reinfection. This response seems appropriate, given that dogs provided with water more frequently were also found to spend less time around standing water bodies.

The distance of natural water sources from households was an important correlate of variation in the amount of dog activity they experienced, much of which is explained by the different locations of villages in relation to areas with the greatest concentration of water bodies. Water bodies closer to a household with dogs were both more likely to be visited by a dog and a dog with a history of Guinea worm. Both the general dog population and infected dogs spent more time around natural water bodies that were closer to households; however, the wider dog population more frequently visited smaller water bodies, while dogs with a history of Guinea worm infection spent proportionally more time around larger water bodies. This correlation with infection history could be due to the fact that larger water bodies will persist for longer during dry periods and therefore have a greater potential to support copepod populations that could be infected with Guinea worm. From a management perspective, this knowledge of how dogs interact with water bodies can help tailor strategies for the control of copepod populations, initially targeting efforts towards systematic treatment of those experiencing the most dog activity. In this case, water bodies within 1.5 km of a household with tracked dogs accounted for the overwhelming majority of interactions between dogs and natural water bodies. In our use of satellite imagery to identify water sources, there was some difficulty in detecting small ephemeral water bodies, which were identified in the land-based survey. While this may not substantially affect results, as it appears that larger water bodies are used most by dogs with a history of Guinea worm infection, improved detection rates might be achieved through the use of additional spectral bandwidths and/or machine learning techniques.

This study occurred during the onset of the rainy season in Gambella region (Berhanu, Seleshi, & Melesse, 2014), which corresponds to the apparent beginning of the Guinea worm transmission season (CDC, 2019); thus, the observed behaviour and diets of the dogs are reflective of the period in which infection likely occurs. However, if dog behaviour changes later in the season, different emphasis might be placed on alternative transmission pathways. It is also worth noting that, due to the current lack of a prepatent live diagnostic test for dogs, Guinea worm infections are only detected through the emergence of an adult worm, meaning individuals will be overlooked if they had genuinely been exposed and infected but had not successfully facilitated the completion of the parasite's life cycle. In addition, the eradication programme requires the containment of every case and, although necessary, this prevents the characterization of dog behaviour during, or shortly after, worm

emergence, which might more directly identify the water bodies that are at greater risk of becoming sources of infection.

This study has identified correlates for the history of Guinea worm disease in free-ranging dogs in this badly affected area of rural Ethiopia. It was found that dog owners might have responded to dog infections by taking positive measures to prevent further reinfection by providing safe drinking water for dogs. In turn, the provision of safe water, as well as better body condition, was associated with reduced time spent at natural water bodies. These findings suggest that there are multiple elements of owner behaviour, dog ranging behaviour and the characteristics of natural water bodies that can influence potential exposure through the classical pathway of transmission (ingesting water containing infected copepods) and that these could be targeted for more effective disease control.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

The authors confirm that the ethical policies of the journal, as noted on the journal's author guidelines page, have been adhered to. This study was approved by the Ethiopian Public Health Institute Institutional Review Board (081-2018) and by the University of Exeter College of Life and Environmental Sciences (Penryn Campus) Ethics Committee (2016/1488). The project adhered to the 'Guidelines for the treatment of animals in behavioural research and teaching' of the Association for the Study of Animal Behaviour.

AUTHOR CONTRIBUTIONS

RM and JZ conceptualized the study. ZT, DG and HM supported project administration and resources. RM, JW-A, GS, HF, AO, AA and JZ conducted the investigation. JW-A, CG and GS led formal analysis and data curation, developed software and contributed to visualization. JW-A, CG and RM wrote the manuscript, and other authors reviewed, edited and approved the manuscript.

DATA AVAILABILITY STATEMENT

Data are available at Dryad Digital Data Repository, <https://doi.org/10.5061/dryad.s4mw6m94p> (Wilson-Aggarwal et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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