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The association between diet of periurban wild dogs and zoonotic pathogen carriage

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Abstract. Established wildlife populations in periurban environments provide an opportunity to spread zoonotic pathogens within human-associated environments. Characteristics of prevalent pathogens harboured by periurban wild dogs suggest that dietary preference could influence their infection status; however, data comparing diet composition and pathogen presence are rarely available. We analysed the stomach contents of 170 periurban wild dogs (*Canis familiaris*) for the occurrence and biomass of prey items, and then associated this with their known infection status of key zoonotic pathogens. The staple prey items detected were mammalian prey species, most commonly swamp wallabies (*Wallabia bicolor*) (20.6 ± 6.1%), canines (*C. familiaris*) (prey) (10.6 ± 4.6%), eastern grey kangaroos (*Macropus giganteus*) (10.0 ± 4.5%), and deer (various species) (10.0 ± 4.5%). Unidentified bird species (10.0 ± 4.5%) were also common. Wild dogs that were positive for *Echinococcus granulosus* were significantly more likely to have consumed swamp wallabies. These findings demonstrate the importance of managing both the definitive and intermediate stages of *E. granulosus*, and suggest that diet correlates with pathogen presence in some cases. This information may assist the development of specific strategies to manage zoonotic pathogens of wild dogs, which are currently lacking.

Additional keywords: dingoes, ecology, parasites, predator, public health.

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Introduction

Many wildlife species have experienced increasing pressure to adapt to urbanisation (Ditchkoff *et al*. 2006). Species that can adjust and be flexible with their resource requirements generally maintain successful populations within the periurban or urban environment (Romig *et al*. 2015). Knowledge of dietary and prey resources utilised by urban-adapted wildlife can inform concerns regarding locally threatened native wildlife (Allen *et al*. 2016), and provide important ecological information that can advance management strategies to alleviate human–wildlife conflicts (Murray *et al*. 2015).

In Australia, wild dogs (*Canis familiaris*), including ancient breeds (dingoes), modern breeds (domestic dogs) and various cross-breeds (Jackson *et al*. 2017) are common across the mainland, including within periurban regions (Stephens 2011; Stephens *et al*. 2015). Human conflict with periurban wild dogs generally relates to predation or harassment of hobby farm livestock, backyard poultry and domestic pets, as well as impacts on the conservation of native wildlife (Jenkins *et al*. 2008; Allen *et al*. 2016). Wild dogs are known to prey upon large (Whitehouse 1977; Marsack and Campbell 1990; Cupples *et al*. 2011), medium-sized (Claridge *et al*. 2010) and small mammals (Corbett 2001), depending on which species are common and abundant locally (Claridge *et al*. 2010; Brook and Kutt 2011). Small to medium-sized mammals are the most frequent prey item found within scats of periurban wild dogs (Allen and Leung 2012; Allen *et al*. 2016). While scats are relatively easy to collect and allow for repeated consistent sampling across different habitats, there are some limitations with their use for assessing diet composition that only stomach sampling can overcome (Balestrieri *et al*. 2011; Klare *et al*. 2011). Analysis of stomach contents allows for more detailed methods (i.e. reporting of biomass) and provides a more accurate detection and identification of items that may be unreported from scat studies (Cavallini and Volpi 1995; Behrendorff *et al*. 2016). Human-associated food items (e.g. bread, domestic dog food) and other readily digestible foods are difficult to detect in scats, and studies may therefore give a biased representation of diet composition (Balestrieri *et al*. 2011).

Diet is known to influence wildlife host–pathogen interactions (Miller *et al*. 2003; Cross *et al*. 2007; Hegglin *et al*. 2007; Jessop *et al*. 2012). However, the relationship between diet and the presence of pathogens in wild dogs has not been investigated. Periurban wild dogs act as definitive hosts for a variety of parasites of public health significance (e.g. *Echinococcus granulosus*, hookworms, *Toxocara canis*) (Allen *et al*. 2013; Harriott 2018). The lifecycles of many of these parasites are perpetuated by the ingestion of parasite stages in intermediate or paratenic hosts that are naturally preferred prey species (Jenkins and MacPherson 2003). Hence, the relationship between wild dogs and their prey could be a key factor in understanding the transmission dynamics of infectious pathogens. Previous research suggests that wild dog populations are largely reliant on just one or two species of primary prey in any given location, with scat data from the same location in 2002 and then again in 2013 showing an almost identical degree of dietary overlap (Allen *et al*. 2016). It is also thought that staple dietary items that are reliable over time are the most important prey items (Newsome *et al*. 1983). Hence, a relatively stable dietary preference of a wild dog may indicate its potential to harbour infectious pathogens.

In this study, we investigated the diet composition of periurban wild dogs in north-eastern Australia to determine whether dietary preference is associated with the parasitic and/or bacterial infection status of each wild dog. Understanding the association between diet composition and the presence of infectious pathogens will assist in determining the role that prey species have in the maintenance of infections in wild dog populations. This information could be important to future wild dog or zoonoses management programs, especially in densely populated areas.

Methods

Study area

Wild dog carcasses were supplied though pest management programs undertaken by local government or private trappers between August 2012 and May 2015. All animals were trapped, humanely euthanised, and individually bagged before being stored frozen (−20°C) on the same morning as capture. Wild dogs were sourced from south-east Queensland and a small adjacent section of northern New South Wales. The study area was divided into four regions: Greater Brisbane, North Brisbane, West Brisbane, and South Brisbane. Each wild dog was allocated to one of the four regions based on capture location (Fig. 1). All wild dogs were culled as part of routine pest management programs administered by local government agencies, and the supply of carcasses was approved for necropsy by The University of Queensland Animal Ethics Committee (approval no. SVS/145/13).

Collection of stomachs and diet composition

Whole stomachs ($n = 170$) were removed at necropsy, individually bagged and stored frozen at −20°C for bulk processing. Stomach contents were washed, air-dried and stored in paper bags before being sent for dietary composition analysis by a professional service provider (Barbara Triggs, Dead Finish, Victoria). Identification of contents was primarily based on morphological characteristics of mammalian hairs (Brunner and Triggs 2002). Dogs often ingest small amounts of hair from grooming activities. Smaller volumes of *Canis* spp. hair were classified as grooming. *Canis* spp. hair with skin and or muscle attached was classified as prey. Other items such as bones, feathers, invertebrates and anthropogenic items were recorded. All food items were identified to the lowest taxonomic level possible, and the mass (g) and volume (%) of each item was recorded for each sample.

Pathogen identification

Parasitic and bacterial pathogens were identified in wild dogs in a separate study, utilising adult worm identification, faecal flotation and egg identification, and molecular or microbiological methods (Harriott 2018). Parasites were the most commonly detected pathogens: adult *Echinococcus granulosus* worms detected within 50.7 ± 6.9% of intestines, followed by *Spirometra erinacei* (36.6 ± 6.4%); hookworms, including *Ancylostoma caninum* and *Uncinaria stenocephala* (28.8 ± 7.1%); *Toxocara canis* (5.4 ± 3.1%) and *Taenia* spp., including *T. serialis* and *T. pisiformis* (4.5 ± 2.8%). Only 18 (9.0%) periurban wild dogs were found to have a positive bacterial isolation from faeces and two dogs were infected with two species of bacteria. Bacterial pathogens detected included *Escherichia coli* (20 ± 10.1%), *Salmonella* spp. (3.7 ± 3.7%) and methicillin-sensitive *Staphylococcus aureus* (3.3 ± 2.7%).

Data analyses

To ensure that sample sizes were sufficient to describe diet composition, we randomly batched results into groups of five and compared the cumulative number of prey items and the diversity of diet to the sample size (following Gentle *et al*. 2015). The diversity of the diet was calculated using the Brillouin Index (H_B):

$$H_B = \frac{\ln N! - \sum \ln n_i!}{N}$$

where N is the total number of individuals in the sample and n_i is the number of individuals in the ith species. The Brillouin index is suggested for non-random sampling (Pielou 1975).

For each dietary item, we estimated the frequency of occurrence and the proportion of biomass. Frequency of occurrence (%) of a particular food item was calculated by dividing the number of stomachs containing each food item by the total number of stomachs analysed. Biomass (%) was estimated as a proportion by dividing the total mass of each food item by the overall mass of stomach contents. Univariate logistic regression was used to determine whether dietary composition and biomass changed across seasons. Seasons were grouped into dry (May–October) and wet (November–April) to represent potential environmental drivers in south-east Queensland, which is classified as subtropical.

To determine whether dietary composition was associated with infection status of each wild dog, we compared the presence of the main prey species consumed with the presence and absence of pathogens of interest. Data from 169 wild dogs were used for these analyses. We selected parasitic pathogens that had high prevalence, represented potential risk to human

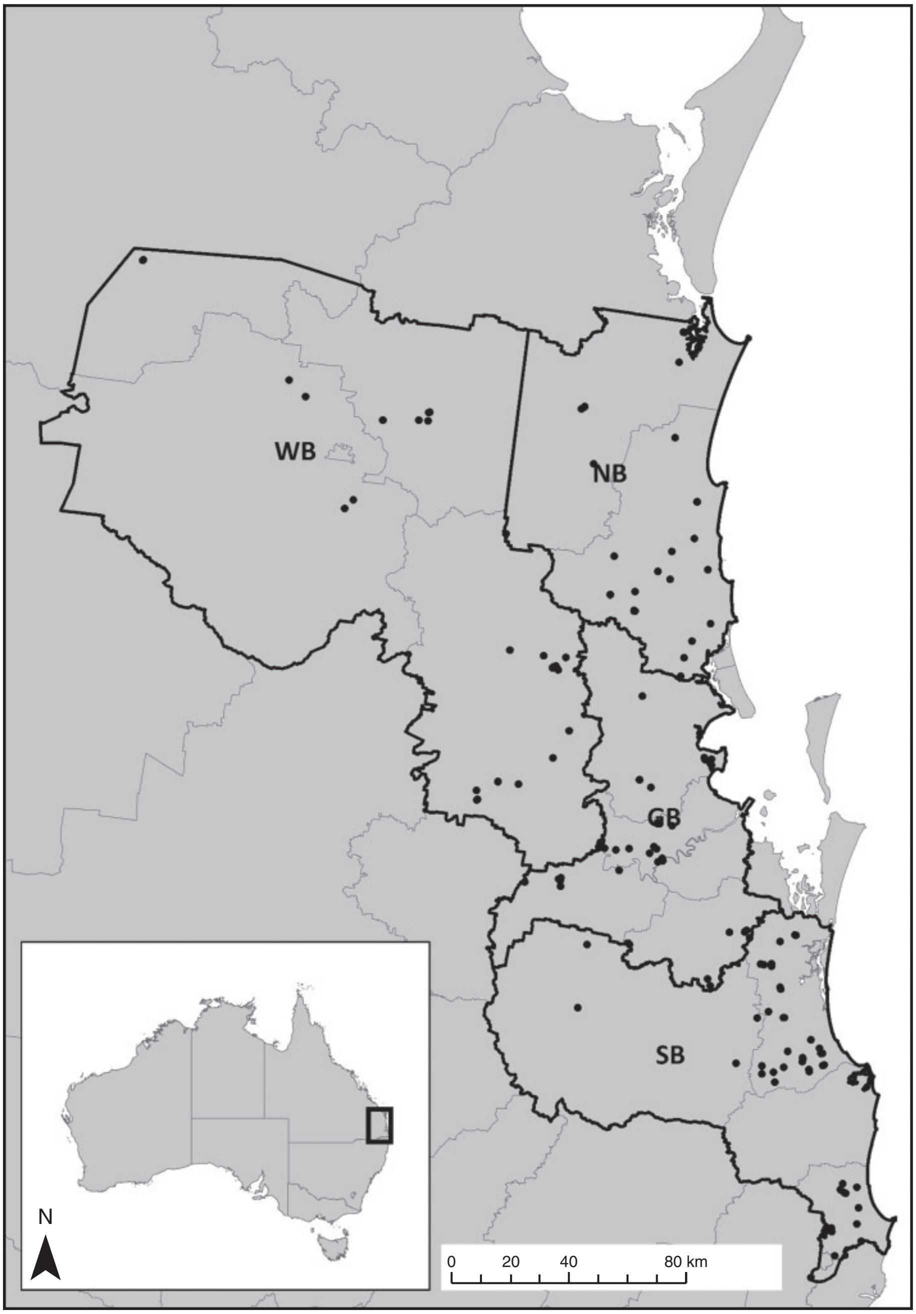

Fig. 1. Geographical location of the study area showing wild dog capture locations (•) within each region. Regions are labelled WB (West Brisbane), NB (North Brisbane), GB (Greater Brisbane) and SB (South Brisbane).

health, and involved an intermediate host where ingestion can be a transmission method. On the basis of these criteria, the pathogens of interest were: *E. granulosus*, *S. erinacei* and hookworms (including *A. caninum* and *U. stenocephala*). Individual factors (e.g. dog age and sex) that may influence feeding behaviour were also examined. First, univariate logistic regression models (Family, Bernoulli) were constructed including *E. granulosus* infection as the response variable and individual factors (age and sex) and diet items as univariate predictors. Macropods are a known intermediate host for *E. granulosus*, therefore grouped macropod species (*Notamacropus rufogriseus* (formerly *Macropus rufogriseus*), *Macropus giganteus*, *Wallabia bicolour* and unidentified macropod species) were compared with other prey species (non-macropod) as the reference category. Reference categories for age and sex were >6 months and males respectively. Variables displaying at a $P < 0.20$ were then considered for a full multivariate model. Second, a final multivariate logistic regression model accounting for animal age, sex and a random effect for region was fitted by backwards stepwise regression (McDonald 2014). The same analytic approach was conducted for other pathogens of interest (hookworms and *S. erinacei*). Due to the lower prevalence of infection for these pathogens, dietary items were classified into general categories including: macropods, canines, bandicoots, other mammals, vegetation and birds. *S. erinacei* has an important aquatic stage in its lifecycle (Lee *et al*. 1990). To determine whether distance to natural water sites influenced infection, we measured the distance (km) from point of capture to the closest natural water site utilising geographical information systems (GIS) and included these data in the logistic regression for *S. erinacei* only. All statistical analyses were conducted in STATA/IC 13.1 (StataCorp, College Station, TX, USA) and spatial data management and maps were conducted in ArcGIS Desktop 10.5.1 (ESRI Inc., Redlands, CA, USA).

Wild dogs that exhibited bacterial infections of any kind were also examined in terms of their dietary items. The small sample size of wild dogs with bacterial infections precluded formal statistical analyses to be conducted.

Results

Diet composition

In total, 170 periurban wild dog stomachs were collected and analysed for dietary composition (Table 1). Overall, the most frequent prey species identified was swamp wallaby, occurring in 20.6% of periurban wild dogs. This was followed by canines (*Canis* spp. (prey)) and bird feathers, both present in 10.6% of samples. The eastern grey kangaroo and unidentified deer species were both also present in 10.0% of stomachs. Mammals also dominated the consumed biomass (82.4%), with unidentified deer, canines (prey) and macropods accounting

Table 1. The occurrence of food items (mammals and other) in wild dog stomachs from the four regions within the study area

The overall occurrence (%) and overall biomass (%) for each dietary item are also shown

Common name	Scientific name	Greater Brisbane ($n = 49$) (%)	North Brisbane ($n = 39$) (%)	South Brisbane ($n = 51$) (%)	West Brisbane ($n = 31$) (%)	Overall occurrence ($n = 170$) (%)	Overall biomass (%)
Mammals							
Antechinus sp.	*Antechinus* sp.	2.04	0.00	0.00	0.00	0.58	Trace
Australian swamp rat	*Rattus lutreolus*	2.04	0.00	0.00	0.00	0.58	0.41
Black rat	*Rattus rattus*	0.00	2.56	0.00	0.00	0.58	0.47
Cattle	*Bos taurus*	6.12	7.69	0.00	0.00	3.53	4.11
Common ringtail possum	*Pseudocheirus peregrinus*	0.00	0.00	0.00	3.22	0.58	0.58
Deer	Various	22.44	5.12	5.88	3.22	10.00	14.30
Dingo/dog (grooming)	*Canis* sp. (grooming)	6.12	2.56	0.00	6.45	3.53	Trace
Dingo/dog (prey)	*Canis* sp. (prey)	12.24	12.82	1.96	19.35	10.60	20.37
Eastern grey kangaroo	*Macropus giganteus*	8.16	20.51	1.96	12.90	10.00	6.82
European rabbit	*Oryctolagus cuniculus*	0.00	5.12	1.96	3.23	2.35	1.54
Feral pig	*Sus scrofa*	4.08	0.00	0.00	0.00	1.18	0.11
Greater glider	*Petauroides volans*	0.00	0.00	0.00	3.23	0.58	0.43
Long nosed bandicoot	*Perameles nasuta*	0.00	0.00	1.96	0.00	0.58	0.11
Northern brown bandicoot	*Isoodon macrourus*	8.16	5.12	7.84	12.90	8.23	5.52
Mammal bones	–	0.00	10.26	9.80	0.00	5.29	6.48
Possum species	*Trichosurus* sp.	0.00	2.56	3.92	3.23	2.35	0.94
Red necked wallaby	*Macropus rufogriseus*	4.08	0.00	1.96	0.00	1.76	2.33
Sheep	*Ovis aries*	2.04	5.12	0.00	0.00	1.76	2.38
Squirrel glider	*Petaurus norfolcensis*	2.04	0.00	0.00	0.00	0.58	0.09
Swamp wallaby	*Wallabia bicolor*	14.29	10.26	41.18	6.68	20.58	14.98
Unknown macropod species	*Macropus* sp.	0.00	0.00	0.00	19.35	3.53	6.23
Total mammals		81.63	73.47	76.47	90.32	82.35	88.21
Other							
Beetle		2.04	0.000	1.96	0.00	1.18	0.02
Birds		12.24	10.26	11.76	6.45	10.60	6.61
Bone fragments		0.00	0.00	0.00	3.23	0.58	0.23
Eggshell		2.04	0.00	1.96	0.00	1.18	0.16
Emasculation ring		2.04	0.00	0.00	0.00	0.58	Trace
Fish bones/scales		2.04	0.00	0.00	0.00	0.58	0.54
Human hair		0.00	0.00	0.00	3.23	0.58	Trace
Net/mesh/wire/string		6.12	5.12	0.00	0.00	2.35	0.07
Paper		6.12	7.69	11.76	3.23	7.06	0.17
Reptile		0.00	5.12	0.00	0.00	1.18	0.05
Sponge		0.00	5.12	1.96	6.45	2.94	0.09
Stones		0.00	0.000	1.96	3.23	1.18	0.16
Vegetation		67.35	69.23	74.51	74.19	71.18	3.70

for much (65.0%) of the biomass. Nearly all (93.5%) wild dog stomachs featured only one prey species. Accordingly, most prey items represented a high biomass percentage within each individual stomach. Additional (i.e. a second) prey species was present in only 6.5% of stomachs, generally in only trace amounts. The presence of vegetation (grass and/or leaves) was common (71%); however, it accounted for only trace or very low amounts within the stomach (71% contained <1 g). In 11 stomachs, grass was the sole item consumed; most contained only minimal amounts (<2 g) but one stomach contained 58 g of vegetative matter. There was no detection of the mesopredators red fox (*Vulpes vulpes*) or feral cat (*Felis catus*) in any of the samples. Human-associated food items (commonly food product wrappers) were detected in 7% of stomachs.

The occurrence (%) and overall biomass (%) of the eight most common dietary items were calculated (Table 2). Vegetation occurred the most frequently; however, it presented the least biomass. Macropods (including swamp wallaby) dominated the biomass consumed in both wet and dry seasons. There were no significant differences in occurrence of all major dietary items across the wet and dry seasons. However, there was a significantly higher biomass of bird species consumed in the wet season compared with the dry (Odds ratio = 3.7, 95% CI = 1.0–13.8, $P < 0.05$).

Sample size

The sample size used for this study was sufficient for describing the composition and diversity of periurban wild dog diet. Brillouin's Index reached an asymptote at ~70 stomachs and no new food groups were recorded after sampling of 50 stomachs, confirming that our sample size ($n = 170$) exceeded that required to sufficiently describe diet.

Table 2. The occurrence and biomass (±standard error of the mean) of the seven major dietary items of periurban wild dogs in the wet and dry seasons of south-east Queensland

$n = 93$ (wet), $n = 71$ (dry)

	Occurrence (%)		Biomass (%)	
	Wet season	Dry season	Wet season	Dry season
Birds	18.3 ± 7.1	5.6 ± 5.4	10.8 ± 3.2	0.4 ± 0.7
Deer	16.9 ± 6.8	2.8 ± 3.8	19.5 ± 4.1	8.7 ± 3.3
Dingo/dog	18.3 ± 7.1	14.1 ± 8.1	12.8 ± 3.5	22.5 ± 5.0
Northern brown bandicoot	4.2 ± 3.6	11.3 ± 7.4	1.4 ± 1.2	10.7 ± 3.7
Other macropods	16.9 ± 6.8	16.9 ± 8.7	16.6 ± 3.9	16.3 ± 4.4
Swamp wallaby	26.8 ± 8.2	19.7 ± 9.3	15.6 ± 3.8	14.1 ± 4.1
Vegetation	90.1 ± 9.4	76.1 ± 9.9	4.9 ± 2.2	4.3 ± 2.4

Association between *Echinococcus granulosus* carriage and diet

Our results indicate that 25.0% (±4.6) of *E. granulosus*-positive wild dogs in our study area had swamp wallaby in their stomach (Table 3). After accounting for age, sex and clustering of samples by region (Table 4), multivariate analysis showed that dogs with *E. granulosus* infection were 1.79 times more likely to have consumed swamp wallaby (Diet 1) ($P < 0.05$), and 4.18 times more likely to have consumed unidentified *Macropus* species (Diet 4) ($P < 0.01$) than dogs without *E. granulosus* infection.

Association between hookworm carriage and diet

After accounting for age, sex and clustering of samples by region (Table 5), periurban wild dogs that were positive for hookworm carriage were 3.09 times more likely to have consumed northern brown bandicoots (*Isoodon macrourus*) ($P < 0.01$) and 7.80 times more likely to have consumed unknown bird species ($P < 0.01$) than wild dogs that were negative for hookworm infection.

Association between *Spirometra erinacei* carriage and diet

After accounting for age, sex and clustering of region (Table 6) periurban wild dogs that were positive for *S. erinacei*

Table 3. Number and percentage (in parentheses, with standard error of the mean) of species of macropods found in the stomachs of periurban wild dogs, and infection status (positive or negative) for *Echinococcus granulosus*

Average worm burdens are shown for *E. granulosus*-positive dogs

	Echinococcus +ve ($n = 88$) N (%)	*Echinococcus* –ve ($n = 81$) N (%)	Average worm burden in wild dogs (*n* worms)
M. giganteus	7 (7.9 ± 2.9)	10 (12.3 ± 3.6)	9300
M. rufogriseus	1 (1.1 ± 1.1)	2 (2.5 ± 1.7)	140
W. bicolor	22 (25.0 ± 4.4)	12 (14.8 ± 3.6)	12 800
Unidentified *Macropus* sp.	4 (4.5 ± 2.1)	2 (2.5 ± 1.7)	35 500

Table 4. Univariate and multivariate analyses of age, sex and diet on intestinal *Echinococcus granulosus* infection in periurban wild dogs

CI, confidence interval

Variables	Univariate			Multivariate		
	Odds ratio	95% CI	*P*	Odds ratio	95% CI	*P*
Female (vs male)	0.70	0.46–1.07	0.104	0.72	0.48–1.08	0.109
Age 6–12 months (vs <6 months)	0.67	0.34–1.35	0.266	0.68	0.35–1.28	0.232
Age 1–2 years (vs <6 months)	1.01	0.39–2.63	0.988	0.87	0.35–2.16	0.771
Age >2 years (vs <6 months)	1.51	0.65–3.50	0.338	1.06	0.50–2.25	0.866
Diet 1: *W. bicolor* (vs non-macropod)	1.74	1.02–2.99	0.003	1.79	1.12–2.85	0.015
Diet 2: *M. giganteus* (vs non-macropod)	0.67	0.17–2.61	0.562			
Diet 3: *N. rufogriseus* (vs non-macropod)	0.89	0.06–13.26	0.934			
Diet 4: all macropods (vs non-macropod)	3.70	1.64–8.37	0.002	4.18	1.80–9.74	0.001

Table 5. Univariate and multivariate analyses of age, sex and diet on hookworm infection in periurban wild dogs
CI, confidence interval

Variables	Univariate			Multivariate		
	Odds ratio	95% CI	*P*	Odds ratio	95% CI	*P*
Female (vs male)	1.00	0.25–3.95	1.000	1.19	0.19–7.28	0.850
Age 6–12 months (vs <6 months)	0.61	0.27–1.37	0.230	0.47	0.25–0.89	0.020
Age 1–2 years (vs <6 months)	2.03	1.21–3.38	0.007	2.00	0.60–6.67	0.261
Age >2 years (vs <6 months)	0.65	0.23–1.85	0.421	0.38	0.07–1.98	0.249
Diet 1: northern brown bandicoot (vs macropods)	1.87	0.77–4.53	0.164	3.09	1.43–6.70	0.004
Diet 2: *Canis* spp. (vs macropods)	1.79	0.86–3.74	0.220			
Diet 3: other mammals (vs macropods)	0.89	0.54–1.49	0.673			
Diet 4: vegetation (vs macropods)	0.85	0.73–0.99	0.466			
Diet 5: bird (vs macropods)	5.63	0.99–32.22	0.052	7.80	5.42–11.21	0.000

Table 6. Univariate and multivariate analyses of age, sex and diet on *Spirometra erinacei* infection in periurban wild dogs
CI, confidence interval

Variables	Univariate			Multivariate		
	Odds ratio	95% CI	*P*	Odds ratio	95% CI	*P*
Female (vs male)	0.74	0.33–1.68	0.479	0.87	0.35–2.19	0.782
Age 6–12 months (vs <6 months)	0.57	0.39–0.84	0.124	1.02	0.39–2.68	0.957
Age 1–2 years (vs <6 months)	2.10	1.31–3.34	0.059	2.71	0.83–8.87	0.100
Age >2 years (vs <6 months)	1.40	0.89–2.21	0.148	1.98	0.79–4.99	0.145
Diet 1: northern brown bandicoot (vs macropods)	0.88	0.33–2.34	0.801			
Diet 2: *Canis* spp. (vs macropods)	0.75	0.49–1.12	0.155	0.72	0.38–1.29	0.268
Diet 3: other mammals (vs macropods)	0.85	0.32–2.21	0.737			
Diet 4: vegetation (vs macropods)	2.18	1.39–3.40	0.001	2.37	1.62–3.46	<0.001
Diet 5: bird (vs macropods)	1.13	0.46–2.75	0.788			
Distance to water	1.04	0.69–1.56	0.861			

Table 7. Bacterial pathogens present in periurban wild dogs including their dietary items

Bacterial infection	Predatory dietary item	Vegetation
Salmonella spp. ($n = 3$)	Deer ($n = 1$) Dingo/dog (prey) ($n = 1$) No diet data ($n = 1$)	Vegetation ($n = 1$)
Staphylococcus aureus ($n = 5$)	Swamp wallaby ($n = 2$) Northern brown bandicoot ($n = 2$)	Vegetation ($n = 4$)
Escherichia coli ($n = 12$)	Dingo/dog (prey) ($n = 1$) Northern brown bandicoot ($n = 2$) Mammal bones ($n = 3$) Swamp wallaby ($n = 1$) Greater glider ($n = 1$) Dingo/dog (grooming) ($n = 1$)	Vegetation ($n = 11$)

infections were 2.37 times more likely to have consumed vegetation than wild dogs that were negative for *S. erinacei*. There was no difference in the average distance to natural waterways (creeks) for *S. erinacei*–infected dogs with and without vegetation in their stomachs as well for the non-infected dogs.

Bacterial pathogen infection and diet

A higher percentage (82.4%) of wild dogs infected with the targeted bacterial pathogens had consumed vegetative material than dogs without bacterial infections (70.6%), but only trace and/or low amounts of vegetation were recorded. Predatory dietary items appeared to be random; with no common themes (Table 7). Formal analyses were not completed given small sample size.

Discussion

Our results confirm that periurban wild dogs predominantly consume mammalian prey, particularly macropods, which is consistent with scat analysis from periurban wild dogs in north-eastern Queensland (Allen *et al*. 2016). Together with the assessment of pathogen presence, this study offers the opportunity to assess potential relationships between diet composition and pathogen presence. Similar to the results reported by Allen *et al*. (2016), both the swamp wallaby and the northern brown bandicoot appeared to be two of the most important prey items for periurban wild dogs. However, our study had a higher representation of dingo/wild dog and eastern grey kangaroo as prey, and a lower representation of birds. The high presence of invasive deer species in the diet of periurban wild dogs in the greater Brisbane region corresponds with known populations of feral deer of various species (red (*Cervus elaphus*), chital (*Axis axis*), sambar (*Rusa unicolor*) and fallow (*Dama dama*)). Red deer were historically concentrated within the Brisbane Valley, although more recent introductions of other species have established wild populations and expanded distribution (Stuart *et al*. 2013). The occurrence of deer as a dietary resource for wild dogs throughout periurban south-eastern Queensland mirrors the situation in south-eastern Victoria (Forsyth *et al*. 2014, 2018; Davis *et al*. 2015).

Periurban wild dogs are known to travel into suburban backyards (Allen *et al*. 2013), with several anecdotal reports suggesting that they opportunistically consume domestic pet food. Domestic pet food was not detected in this study, suggesting that it is not a significant food resource. Human-associated food resources are often utilised by urban vertebrate pests (Contesse *et al*. 2004; Newsome *et al*. 2015). Coyotes (*Canis latrans*) were found to utilise anthropogenic sources of food when they exhibited signs of illness (Murray *et al*. 2015), dingoes in the Tanami desert often consume human-provided rubbish (Glickman and Schantz 1981), and dingoes on Fraser island consume human-sourced foods such as pasta and bread (Behrendorff *et al*. 2016). However, in periurban areas where waste disposal systems are relatively predator proof, the opportunity for wild dogs to access sources of anthropogenic food may be reduced. Despite evidence of contact with these resources (e.g. paper, food product wrappers), such items do not make a significant contribution to the diet. The provision of anthropogenic food resources has been shown to have neutral, positive and negative effects on pathogen infection rates in wildlife (Becker *et al*. 2015). Rock iguanas (*Cyclura cychlura*) fed supplementary dietary items by tourists presented with increased hookworm infections (Knapp *et al*. 2013). In addition, decreased consumption of intermediate hosts (due to reduced exposure) and an increased reliance of anthropogenic food items led to a decrease in the prevalence of *Echinococcus multilocularis* in urban foxes (Hegglin *et al*. 2007). The lack of consumption of anthropogenic resources by periurban wild dogs suggests that there is a greater opportunity for predator–prey interactions and hence greater dietary exposure to pathogens found in prey species.

The occurrence of birds in wild dogs' diet was greater in the wet season than in the dry season, and was also positively associated with the presence of hookworms. The lifecycle of hookworms exhibits seasonal variation where eggs shed in canine faeces develop in suitably moist and warm environments. *A. caninum*, the most common species of hookworm present in wild dogs (Harriott 2018), undergoes hypobiosis during the dry season (Gibbs 1982), which ensures that maximum egg output coincides with the onset of the wet season. Birds have been shown to be paratenic hosts of hookworm (Agarwal and Johri 1980; Agarwal and Agarwal 1983) and patent infections can develop in pups that had consumed infected chickens (Mittra and Sasmal 1985). This suggests that an increased consumption of birds during the wet season may increase the risk of hookworm infection in periurban wild dogs. Alternatively, birds may be secondarily associated with hookworm where they act as an indicator of risk within environments that provide ideal survival of hookworm larvae. More research is needed to investigate the potential role of small mammals and birds in the transmission route of hookworms to wild dogs.

The high reliance on macropod species as a staple dietary item has been hypothesised to be a significant factor in the high prevalence of *E. granulosus* within wild dog populations (Coman 1972). Macropods with hydatid cysts experience massive loss of lung volume and severe respiratory conditions, thus exposing them as easy prey for predators (Jenkins and MacPherson 2003; Jenkins *et al*. 2005). The prevalence of hydatid cysts in swamp wallabies is known to be higher than in other macropods (Jenkins and Morris 2003). In addition to this, 100% of hydatid cysts present in swamp wallabies have been shown to be viable. Because of this, they present a greater risk as an intermediate host, in comparison to eastern grey kangaroos that have displayed, in some animals, the ability to initiate an immune response that results in unviable cysts (Jenkins and Morris 2003). Cattle and sheep can also be intermediate hosts to the hydatid tapeworm (*E. granulosus*), but domestic stock is rarely recorded in periurban dog diets (Allen *et al*. 2016). Our results support the hypothesis that the sylvatic cycle has significant impacts on infection of periurban wild dogs with *E. granulosus* sourced through consumption of macropod species such as the swamp wallaby. However, there could be other factors responsible for *E. granulosus* presence that could influence infection risk (e.g. environmental conditions: Thevenet *et al*. 2005); further research is required to address this.

The association between *S. erinacei* infection and the presence of vegetation in the diet is unexpected and unclear. The lifecycle of *S. erinacei* requires an aquatic cycle involving copepods as intermediate hosts (Lee *et al*. 1990). Infection in dogs requires consumption of an infected intermediate and/or subsequent paratenic host such as amphibians, reptiles, and feral pigs, which do not frequently occur in their diet (Allen *et al*. 2016). The distance to water sources was not significant for dogs infected with *S. erinacei* that had consumed vegetation. However, wild dogs could travel extended distances as part of daily activities, including use of watering points, and thus the distance to the nearest natural water source may not adequately represent exposure to such environs. The limited public health significance of *S. erinacei* from wild dogs suggests a low priority for further research into this topic.

Our results should be interpreted in light of some limitations. Due to the small sample size, the bacterial results are likely inconclusive to suggest that dietary items are influencing the presence of bacterial pathogens within wild dogs. Nevertheless, diet remains an obvious and likely influence on infection. Bacteria can be transmitted through environmental contamination; however, both dogs with and without bacterial infections had high prevalence, but little biomass, of vegetative matter within their stomachs. It is highly likely that bacterial infections in periurban wild dogs are sporadic. Although, diet may be the initial route of infection, a larger sample size of periurban wild dogs with bacterial infections is required to more reliably determine potential causal factors. Another limitation is that, without multiple samplings of each individual, dietary studies can only provide a 'snapshot' of the diet at each sampling period. Multiple stomach samplings to examine the diet composition are not possible for wild-living individuals, and using other sampling techniques (such as scats) are problematic given the requirement to link to the individual over time. It is likely that variation in dietary composition between seasons is influenced by the availability and distribution of prey items, rather than dietary preference (Corbett and Newsome 1987). However, this cannot be confirmed without knowledge of seasonal fluctuations in prey densities and distribution, which are unknown at the scale of this study. Wild dogs have been shown to rely on staple dietary items over time (Newsome *et al*. 1983; Corbett and Newsome 1987) and swamp wallabies are known to be staple dietary items of periurban wild dogs (Allen *et al*. 2016). As a result, the associations presented here, particularly between swamp wallaby consumption and *E. granulosus* infection are epidemiologically significant, support hypotheses generated from previous studies, and provide an insight into potential linkages between diet and infection status. Given the public health implications of *E. granulosus* infection (Deplazes *et al*. 2017), these initial findings warrant further detailed study into factors that drive prevalence in periurban areas.

In summary, our findings are epidemiologically significant and suggest that consumption of prey is an important transmission pathway for wild dog zoonosis infection. Densities of prey species, as well as knowledge of environmental sources and risk factors for pathogens, are required to further elucidate linkages. Research pertaining to periurban wildlife, and periurban wild dogs in particular, is of increasing importance given the rapid population growth in such areas, urban habitat expansion, and increasing focus on one-health approaches to disease management.

Conflicts of interest

The authors declare no conflicts of interest

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