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Research article

Subsidised by junk foods: factors influencing body condition in stray cats (*Felis catus*)

H. M. Crawford, M. C. Calver and P. A. Fleming *

Environmental and Conservation Sciences, Murdoch University, 90 South Street, Murdoch 6150, Western Australia

*Corresponding author. E-mail: t.fleming@murdoch.edu.au

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Abstract

Domestic cats (*Felis catus*) are one of the most widely distributed and successful carnivores globally. While cats are popular pets, many unowned, 'stray' cats live freely in anthropogenic environments at high densities where they make use of anthropogenic resources. These stray cats present a management challenge due to concerns about wildlife predation, pathogen transmission, public nuisance and threats to cat welfare (e.g. vehicle collisions). In Australia, there are few studies of strays compared with pet cats or feral cats (free-roaming cats in rural areas that are independent of resources provided by humans). To contribute original data about stray cat biology, the carcasses of 188 euthanised stray cats were collected from Perth, Western Australia. Cats were assessed for general health, age, reproduction, diet and gastrointestinal parasite biomass. The influence of cat demographics, collection location, season, parasite biomass, diet and history of supplemental feeding by people were tested against body condition. Overall, strays were physically healthy and reproductive, with few life-threatening injuries or macroscopic evidence of disease; however, helminths were extremely common (95% of cats) and pose a threat. Nearly 40% of strays consumed wildlife, including two species of endemic marsupial. Alarmingly, 57.5% of strays were scavenging vast amounts of refuse, including life-threatening items in volumes that blocked their gastrointestinal tracts. These findings illustrate that strays need to be removed from anthropogenic environments for their own health and welfare and to prevent continued breeding. Targeted control programmes should prioritise removal of cats from areas where refuse is common and where valued native fauna exist.

Key words: animal control, free-roaming, predation, semi-feral cat, unowned cat, cat welfare

Introduction

Unowned domestic cats (*Felis catus*) are a major management and conservation issue in many parts of the world. In cities, unowned cats ('stray') live in close association with human habitations and can roam across neighbourhoods, commercial areas, parks and bush reserves hunting wildlife (Blancher 2013; Loss, Will, and Marra 2013; Marra and Santella 2016), spreading diseases to wildlife, owned pet cats and humans (Stanek et al. 2003; Carver et al. 2016; Marra and Santella 2016), and also potentially hybridising with wild felid species (Beaumont et al. 2001). Stray cats also create considerable nuisance for people by spraying urine, defaecating or breeding on private property, and through fighting with each other, pet cats or other companion animals (Scarlett and Johnston 2012; Uetake et al. 2014; Gunther et al. 2015). In addition to their impacts on animals and people, the welfare of stray cats can also be compromised. Stray cats are vulnerable to trauma (especially collisions with cars; Childs and Ross 1986; Weary and Robbins 2019), disease and parasitic infections (Natoli et al. 2005; El-Seify et al. 2017), ingestion of poisons and inappropriate foodstuffs (Giuliano Albo and Nebbia 2004; Milewski and Khan 2006) and human persecution (Lockwood 2005; Vnuk et al. 2016). For these reasons, many countries attempt to limit or reduce urban stray cat populations using fertility control, lethal control, adoption, relocation or Trap-Neuter-Return (TNR) programmes (Natoli et al. 2006; Brickner-Braun, Geffen, and Yom-Tov 2007; Robertson 2008; Levy 2011; Crawford, Fontaine, and Calver 2017).

Urban stray cat populations can reach very high densities, particularly in countries with warm, equatorial or Mediterranean climates (Mirmovitch 1995; Finkler, Hatna, and Terkel 2011). This is because cats are adapted for survival in perennially warm environments (Yamaguchi et al. 2015) and common domestic breed females have more litters and breed year-round in warm climes compared with speciality breeds or females in temperate or polar climates (Nutter, Levine, and Stoskopf 2004; Faya et al. 2011; Fournier et al. 2017). Many species of cat parasite are also tolerant of warm climates and, where cat densities are high, the prevalence of disease and parasites tends to increase (Pedersen 1988). Parasites are transmitted through fighting, breeding, grooming or consuming prey (e.g. paratenic rodents host zoonotic feline roundworm *Toxocara cati*; Beveridge and Emery 2015; Taylor, Coop, and Wall 2015). Even though cats usually cover their faeces with soil (Szwabe and Błaszkowska 2017; Vitale Shreve and Udell 2017), Szwabe and Blaszkowska (2017) rate cats as more important for contaminating the environment with potential zoonotic organisms than dogs. Health surveys of stray cats indicate that they can carry substantial mixed parasite infections (reviewed by Crawford, Calver, and Fleming 2019). For example, 74% of 568 strays in Doha, Qatar, were infected with the common feline tapeworm (*Taenia taeniaeformis*; Abu-Madi et al. 2010); and 38% of 162 strays in Lisbon, Portugal, hosted zoonotic feline roundworm (*T. cati*; Waap, Gomes, and Nunes 2014). A heavy parasite burden challenges the host's energetic balance and can cause poor body condition and death, particularly in juveniles (Lopate 2012; Beugnet, Halos, and Guillot 2018). Ectoparasites, stress and ill health can also degrade coat condition (Little 2012; Arhant, Wogritsch, and Troxler 2015). Poor body and coat conditions may therefore indicate long-term or heavy parasite burdens in stray cats (Serrano and Millãn 2014).

The body condition of cats can also reflect food quantity and quality. Cats are relatively opportunistic in their diet, readily swapping between food types in response to local availability (Turner and Bateson 2000). Stray cats living in urban areas do hunt prey (Hernandez et al. 2018); however, human refuse can also be a regular supplementary food (Spotte 2014), particularly when refuse is nutritious (e.g. fish scraps in dockyards; Izawa, Doi, and Ono 1982), easily accessible (e.g. open tips, dumpsters and street litter; Brickner-Braun, Geffen, and Yom-Tov 2007) or available year-round (Campos et al. 2007). It many countries, it may also be common practice to deliberately feed stray cats with house scraps, raw/cooked meat, and commercial cat food (Natoli et al. 1999; Gunther et al. 2016; Hwang et al. 2018), and provision of regular food can increase population density through increased reproductive rate or juvenile survival (Finkler, Hatna, and Terkel 2011; Little 2012) as well as attracting more cats to locations with food (Centonze and Levy 2002; Hwang, et al. 2018; Swarbrick and Rand 2018).

The health and welfare of stray cats is therefore influenced by their environment and season, parasite load and diet, as well as the care that they may receive from humans (Little 2012). It is important to understand the relative impacts of each of these factors on cat welfare if stray cats are to be managed appropriately (i.e. whether cats should be trapped and euthanised or rehomed). Physical health assessment is an obvious way to test the welfare of stray cats, where the animals can be inspected closely (Castro-Prieto and Andrade-Nunez 2018). Comparison of body mass with body size also provides a valuable measure of body condition (Schulte-Hostedde et al. 2005).

To increase knowledge about stray cat health in Australia, we examined health and welfare-relevant measures using the carcasses of animals euthanised as part of trapping programs around the city of Perth, Western Australia (WA). Controlling for the sex and age of animals, we tested whether the body condition of stray cats was influenced by:

1. Source location—we predicted that stray cats would be in better physical condition in urban and peri-urban locations and worse condition at commercial and rural refuse tip locations where food resources would be available but of low quality.
2. Seasonal differences—we predicted that strays would be in better condition in summer compared with winter when food resources may be less available.
3. Biomass of gastrointestinal helminth parasites—we predicted that there would be some cost of high parasite biomass, and therefore animals with the smallest mass of gastrointestinal helminth parasites would be in the best condition.
4. Diet—we predicted better body condition for stray cats that had consumed fauna, and worse condition for those feeding on refuse.
5. Whether or not strays were deliberately fed—we predicted that strays receiving supplemental feeding by people would be in better condition than those that were not fed.

These data are relevant to decisions on cat management in Australia, as well as internationally where populations of stray cats are a concern.

Materials and methods

Collection of stray cat specimens

Enforced from 2013, the Western Australian Cat Act (Government of Western Australia 2011) requires that, by the age of 6 months, all pet cats must be: (1) desexed, (2) microchipped with sub-dermal ID tag, (3) registered with a local municipal council and (4) wearing a collar with ID and registration tags. Any cat not identifiable as an owned pet that is trapped because of nuisance or welfare concerns, and/or surrendered to a shelter, is therefore considered a stray cat. The stray cat population in Perth has not been estimated; however, in 2017–8 the Cat Haven shelter (CH) and WA Royal Society for the Prevention of Cruelty to Animals (RSPCA) shelter processed 8919 and 824 cats, respectively (Cat Haven 2017; RSPCA 2017), which included surrendered pets, unwanted kittens and stray cats. Where their behaviour is suitable for rehoming, these cats are offered for adoption (WA shelters have an excellent rehoming rate; in 2017–8 the CH rehomed 7176 cats and RSPCA rehomed 514; 79% of intakes rehomed overall). However, cats are euthanised if they have temperaments that are not amenable to re-homing (as assessed by trained personnel) or have untreatable medical issues (e.g. severe trauma from vehicle collision; 14.5% of cat intakes were euthanised in 2017, CH total $n = 965$; RSPCA $n = 149$).

The carcasses of 188 stray cats euthanised for these reasons were obtained opportunistically from licenced animal controllers, government councils and an animal shelter over three years (four cats in 2010, three in 2015 and 181 in 2016). The protocols for carcass and data collection were reviewed and approved by the Murdoch University Animal Ethics Committee

Table 1: Categories and sample sizes of stray cats included in this study, shown by location and supplemental feeding history

Feeding history	Deliberately fed			Not fed			All cats	
Location cat sex	Female	Male	Total	Female	Male	Total	Total	%
Urban—suburbs within metropolitan area, e.g. residential streets, urban bush reserves, private businesses.	13	14	27	12	16	28	55	29.2
Commercial—on the premises of commercial businesses, light to heavy industrial suburbs within metropolitan area.	19	19	38	15	18	33	71	37.8
Peri-urban—suburbs on periphery of metropolitan area, e.g. private small-holdings, peri-urban bush reserves.	6	6	12	5	4	9	21	11.2
Rural tip—trapped at three open refuse tips in rural agricultural locations.	0	0	0	21	20	41	41	21.8
Total	38	39	77	53	58	111	188	100.0
% of 188	20.2	20.7	41.0	28.2	30.8	59.0	100.0	

(W2266/09) and complied with the Australian Code for the Care and Use of Animals for Scientific Purposes (NHMRC 2013). The dates on which cats were trapped were recorded for interpretation of seasonal effects. The physical location of cats was provided (i.e. GPS coordinates or physical address where cats were trapped/found) and mapped using Google Earth Pro® to classify cat origin by location as urban, commercial, peri-urban or rural tip locations (Table 1). We recorded all available details about the sourced animals including: how long cats had lived at a location, why animal controllers were contacted by the public about the cats (nuisance behaviour, welfare concerns, abandonment), and why cats were ultimately euthanised (injury, disease, aggressive temperament). Some cats were being deliberately provided with food by caretakers for a period preceding trapping ($n = 77$); these cats were classified as 'deliberately fed', and the pre-trapping feeding periods, food types (commercial cat food, tinned tuna or roast chicken) and frequency of feeding (once per day, once per week etc.) were noted. Cats with no known history of feeding by caretakers were classified as 'not fed' ($n = 111$; Table 1). Additional cats were removed from refuse tips (i.e. garbage sites, refuse dumps; $n = 53$) and because these cats were not intentionally fed by people they were pooled under 'not fed'.

All cats were necropsied in the same manner by the same team of researchers. Each cat was weighed (± 0.01 kg) and a tape measure used to measure head length, head–body length and pes length (in millimetres, mm). The general health of cats was determined by macroscopically examining external features (e.g. nostrils, ears, genitalia) and major organs (e.g. kidney, liver, heart) for signs of abnormality, inflammation, infection or injury. The body condition of strays was scored subjectively based on costal and mesenteric fat deposits: 1 = 'poor condition' cat ribs visible and limited mesenteric fat; 2 = 'optimal condition', cat ribs could be palpated but were not visible; and 3 = 'heavy', cats had substantial costal, subcutaneous and mesenteric fat deposits. Coat condition was also scored subjectively (1 = 'poor condition' with missing fur, lesions, parasite scarring; 2 = 'normal condition' with no fur or skin issues but fairly dull fur, and 3 = 'excellent condition' no issues and lustrous, shiny fur) and presence and species of ectoparasites were noted.

We removed heads and macerated the skulls ($n = 161$; 27 cats had damaged or irretrievable skulls). Cats were then aged using incremental lines of their canine cementum (Grue and Jensen 1979). Males were classified as adult if >12 months (puberty at 8–10 months; Root Kustritz 2009). Females were scored as reproductive and adult through examination of mammillae (current or previous lactation) and uterine horns (enlarged/engorged or foetuses present and counted) or were identified as having bred previously via scarred ovaries.

Stomachs and intestines ('gastrointestinal tract' or GI) were removed and stored frozen for later analysis in the laboratory. For each cat, the stomach, small intestine and large intestine were individually processed. Each GI section was weighed, the contents scraped onto 1 mm sieves, and the GI section then reweighed (content mass was calculated as the difference between full and empty sections). GI contents were rinsed with water and identified (e.g. trap bait, pet food, fauna to species-level where possible, green grass, refuse, helminth parasites; for the complete list see Supplementary Table S1). Consumed animals were classified as fresh or carrion using tissue friability, smell and the presence/absence of maggots. Ingested meat was classified as refuse if it was consumed with other refuse items (e.g. ham slice in bread) or if recognisable as a processed product (e.g. cooked prawns in plastic bag, roast chicken in foil). The proportional mass of each category was approximated and specimens for identification were stored in 70% ethanol solution (e.g. parasites, reptiles etc.) or air-dried for one week (e.g. fur and bones). Mammals were identified using microscopic hair analysis (Brunner and Triggs 2002), and other groups, including endo- and ectoparasites, were identified using taxonomic manuals (Bush et al. 2007; Simpson and Day 2010; Beveridge and Emery 2015) and expert knowledge (see Acknowledgements section).

Statistical analyses

General health, sex and age of stray cats

We tested whether reproductive status of females was associated with season using Pearson's χ^2 analysis, with expected values calculated assuming an equal proportion of the total numbers of females sampled were categorised as breeding (pregnant, lactating, or with evidence of previous breeding) across all four seasons. Male reproductive status could not be similarly tested because while spermatogenesis is generally complete by 8–10 months of age, the actual age at which mating begins varies with physical condition, body size and season (Little 2012). We compared the age of male and female cats (dependent variable) with sex, location and history of supplemental feeding as predictor variables using multiple regression (Statistica 7.1; StatSoft Inc. 2007). We also compared the age structure of these stray cats with published data describing the age structure of pet cats from Sydney, Australia (Toribio et al.

2009) using a three-way log-linear analysis [factors of age, sex and study (our data or Sydney cats)] carried out in VassarStats (http://vassarstats.net/) for three age categories (<5 years, 5–10 years and >10 years).

Factors determining body condition index in stray cats

We used the morphometric measurements to calculate a body condition index (BCI)—reflecting how much heavier-than-average each cat was, accounting for its body size. Due to sex differences, BCI values were calculated for each sex separately as the residual of body mass (minus mass of GI contents) against body size indicators (head length and head–body length; pes measurements were included in initial tests, but they showed least correlation with body mass and were excluded from further analyses). We used generalised linear modelling (GLM) (Statistica 7.1; StatSoft Inc. 2007) to test whether the BCI for each cat (dependent variable) was correlated with location as a categorical factor and predictor variables of season (0 = winter, 0.5 = spring/autumn, 1 = summer); age (log-months); gastrointestinal helminth parasite mass (grams, g); measures of diet (the GI mass of rodents, all mammals, birds, reptiles, invertebrates and refuse as separate factors); and supplemental feeding history (0 = unfed, 1 = deliberately fed). This analysis was separately carried out for the $n = 79$ males and $n = 77$ females for which we had complete age and diet data. We used an Akaike Information Criterion (AIC) adjusted for small sample sizes (AICc) for model selection (Grueber et al. 2011). The AICc model weight (ωi) was calculated for each model with ΔAICc <2 (Burnham and Anderson 2002) and we used this to weight standardised β values (i.e. the values that would have been obtained if all variables had first been standardised to a mean of 0 and an SD of 1, calculated for each of the variables included in the top models (Burnham and Anderson 2002; Grueber et al. 2011). The model averaged values were calculated as the sum of the model-weighted β values for each variable ($\Sigma\beta\cdot\omega i$).

Gastrointestinal (GI) helminth parasite biomass, ectoparasites and coat condition of stray cats

We used similar GLM and calculation of model-weighted standardised β values to determine whether the biomass of helminth parasites (dependent variable) was correlated with animal sex, age, location and history of supplemental feeding as predictor variables (Statistica 7.1; StatSoft Inc. 2007). Presence of ectoparasites and coat condition were described only.

Diet analyses of stray cats

Non-parametric Kruskal–Wallis ANOVA was carried out to compare the number of prey by sex, season of capture, location or by feeding history as separate analyses (Statistica 7.1; StatSoft Inc. 2007). After removing 'bait food' from GI contents, we visualised the diets of cats by location and supplemental feeding history using non-metric multidimensional scaling (nMDS) (PAST version 3.15 programme; Hammer, Harper, and Ryan 2001) with Euclidian similarity index for the mass of 11 food categories (domestic sheep carrion *Ovis aries*, European rabbit *Oryctolagus cuniculus*, black rat *Rattus rattus*, house mouse *Mus musculus*, native mammals, birds, reptiles, fish, invertebrates, green grass, refuse; all fauna species listed in Supplementary Table S1). We tested for differences in diet composition due to sex, age category (adults or juveniles), season, location and supplemental feeding history using a one-way permutational multivariate analysis of variance (PERMANOVA) with the mass of the different food types as the dependent variables, followed by a similarity percentage (SIMPER) analysis where there were significant differences.

Values are presented as means ±1 SD throughout.

Results

General health, sex and age of stray cats

Stray cats were brought to the attention of local government authorities, private animal controllers or an animal shelter by private citizens that were concerned about cat welfare and abandonment ($n = 151$, 80.3%), nuisance behaviours ($n = 12$, 6.4%), predation ($n = 17$, 9.0%), illegal Trap-Neuter-Return programmes ($n = 5$, 2.7%) or because cats were found dead ($n = 3$, 1.6%; Supplementary Table S2). All necropsied cats were of common domestic breed and their demographic and detailed health information is presented in Supplementary Table S2. Stray cats appeared healthy with only a few notable health issues ($n = 13$, 6.9% of 188). These included life-threatening injuries in seven cats (four strays were struck by motor vehicles, one was euthanised because of severe facial burns, one cat had a badly damaged forelimb, and another had a 100-mm-length axilla abscess probably due to fighting), GI blockages were detected in six cats (four cats with abnormally distended, ischaemic GI tracts, two cats with extremely large furballs of 92 and 171 g), and one cat had a liver tumour which threatened long-term survival.

The body condition of cats was generally excellent with 81% of cats scoring 3-out-of-3 based on costal and mesenteric fat deposits (BC1 $n = 0$ cats; BC2 $n = 36$; BC3 $n = 152$). The lack of variation detected in these subjective scores meant statistical analyses could not be carried out. All cats had lustrous coats with no apparent fur loss, dermatitis, ringworm or seborrhoea scales. Cat coat condition was generally excellent with 83% of cats scoring 3-out-of-3 (BC1 $n = 0$ cats; BC2 $n = 32$; BC3 $n = 156$). Although 100% of cats hosted fleas (*Ctenocephalides felis*; Beveridge and Emery 2015) or flea dust, there was no significant difference in coat condition scores for cats from different locations ($\chi^2_3 = 2.87$, $P = 0.412$), or for fed/unfed/tip cats ($\chi^2_2 = 2.40$, $P = 0.302$).

Just over half of the 188 cats analysed were male ($n = 97$, 51.6%; Supplementary Table S3), with 47 classified as juveniles (48.5%, age range <4–10 months) and 50 males classified as adult and reproductive (51.5%, age range 1.5–9.5 years). Only one male was desexed (3.5 years). Twenty-five of the 91 female cats showed no evidence of prior breeding (27.5%; age range <4–10 months). Three adult females were desexed (3%; age range 1.5–6.5 years) and the remaining 63 females all exhibited signs of previous or current reproduction (69.2%, age range <4 months–10.5 years). The youngest reproductive female was 5 months old and the oldest pregnant cat was 7.5 years (total of 6 pregnancies with 25 pre-term kittens); these data showed no seasonal difference in reproductive status for females ($\chi^2_3 = 5.60$, $P = 0.133$).

For the 161 cats aged, male cats averaged 2.2 ± 2.0 years and females averaged 2.7 ± 2.4 years. There was no significant age difference for sex ($t_{153} = 1.11$, $P = 0.268$) or feeding history ($t_{153} = 0.44$, $P = 0.662$), but there were differences in age of cats by location ($t_{153} = 4.22$, $P < 0.001$): cats from urban and rural refuse tip locations were older than those from commercial and peri-urban locations. Comparison with the age structure of pet cats from Sydney, Australia (Toribio et al. 2009) revealed a significant age × study interaction term ($G^2_2 = 106.12$, $P < 0.001$), with fewer

Table 2: Summary of multiple regression analyses for stray cat body condition index (BCI, response variable) for: a) male and b) female cats collected from across Perth, Western Australia

(a) Males

	df	L. ratio χ^2	P	AICc	ΔAICc	ωi	Values are $\beta.\omega$i
1	2	36.70	<0.001	568.48	0.00	0.33	Season (−0.02)+age (0.19)
2	2	36.45	<0.001	568.73	0.25	0.29	Age (0.15)+parasite mass (0.05)
3	1	33.09	<0.001	569.25	0.77	0.22	Age (0.12)
4	3	38.65	<0.001	569.99	1.51	0.15	Season (<0.01)+age (0.08)+parasite mass (0.02)
						$\Sigma\beta\cdot\omega$i	Season (−0.028)+age (0.540)+parasite mass (0.070)

(b) Females

	df	L. ratio χ^2	P	AICc	ΔAICc	ωi	
1	1	3.68	0.055	548.71	0.00	0.10	Rodents (0.01)
2	2	6.08	0.048	549.15	0.44	0.08	Rodents (0.01)+reptiles (<0.01)
3	2	6.06	0.048	549.17	0.46	0.08	Feeding[b] (0.02)+location[a] (0.01)
4	2	5.65	0.059	549.57	0.86	0.06	Feeding[b] (0.01)+rodents (0.01)
5	1	2.77	0.096	549.62	0.91	0.06	Mammals (0.01)
6	3	9.04	0.029	549.65	0.94	0.06	Feeding[b] (0.01)+location[a] (0.01)+mammals (0.01)
7	1	2.71	0.100	549.68	0.97	0.06	Feeding[b] (0.01)
8	2	5.40	0.067	549.83	1.12	0.05	Feeding[b] (0.01)+mammals (0.01)
9	2	5.20	0.074	550.02	1.31	0.05	Mammals (0.01)+reptiles (<0.01)
10	3	8.65	0.034	550.04	1.33	0.05	Feeding[b] (0.01)+location[a] (0.01)+rodents (0.01)
11	1	2.35	0.126	550.04	1.33	0.05	Parasite mass (−0.01)
12	2	5.15	0.076	550.08	1.37	0.05	Rodents (0.01)+birds (<0.01)
13	2	5.10	0.078	550.13	1.42	0.05	Mammals (0.01)+parasite mass (−0.01)
14	2	5.10	0.078	550.13	1.42	0.05	Feeding[b] (0.01)+parasite mass (−0.01)
15	1	2.20	0.138	550.19	1.48	0.05	Reptiles (<0.01)
16	2	4.86	0.088	550.37	1.66	0.04	Rodents (0.01)+invertebrates (<0.01)
17	2	4.82	0.090	550.41	1.70	0.04	Rodents (<0.01)+parasite mass (−0.01)
18	2	4.58	0.101	550.65	1.94	0.04	Location[a] (<0.01)+rodents (0.01)
						$\Sigma\beta\cdot\omega$i	Feeding[b] (0.073)+location[a] (0.039)+rodents (0.066)+mammals (0.050)+reptiles (−0.002)+birds (−0.002)+invertebrates (0.002)+parasite mass (−0.027)

[a]Source location: 0 = urban/commercial sites; 0.5 = peri-urban sites, 1 = human refuse tips.
[b]Feeding status: 0 = unfed; 1 = deliberately fed by people.

stray cats older than 5 years of age (12.9% of our sample) in comparison with the pet cat population (64.2%).

Factors determining BCI in stray cats

The numerical BCI values for male stray cats were described by four top models with ΔAICc <2. The strongest factor was the animal's age (model-weighted beta, $\beta\cdot\omega i = 0.540$; Table 2; Fig. 1). Although they did not show strong relationships on their own, the inclusion of season of capture ($\beta\cdot\omega i = -0.028$), and parasite biomass ($\beta\cdot\omega i = 0.070$) improved model fit to the data. There was no effect of location, diet (GI contents, including mass of refuse) or supplementary feeding history for BCI values in males.

The BCI of female strays was described by 18 models with ΔAICc <2, representing a combination of location, parasite biomass, prey mass (rodents, all-mammals, reptiles, birds and invertebrates) and supplemental feeding history (Table 2). No factor in these models strongly predicted female BCI on its own (Fig. 1). There was a positive correlation with supplementary feeding ($\beta\cdot\omega i = 0.073$), and females from rural tips were in better condition than peri-urban, urban or commercial animals ($\beta\cdot\omega i = 0.039$). There was a positive correlation with the mass of mammals ingested ($\beta\cdot\omega i = 0.050$) or rodents alone ($\beta\cdot\omega i = 0.066$; these two predictor variables were autocorrelated and were never included in the same models). There were weak correlations with the mass of reptiles ($\beta\cdot\omega i = -0.002$), birds ($\beta\cdot\omega i = -0.002$) and invertebrates ($\beta\cdot\omega i = 0.002$) present. There was no effect of season or total mass of refuse on body condition for females.

GI helminth parasite biomass

Stray cats carried substantial GI helminth parasite biomass—weighing an average of 15.3 ± 8.9 g (range 0.3–42.8 g), or an average of 17.0% of the mass of GI contents (90.2 ± 57.8 g). Most cats carried feline tapeworm (94.7%, *T. taeniaeformis*) and six cats also hosted roundworms (3.2%, *T. cati*). Sixty-nine percent of cats hosted ≥10 g helminth biomass ($n = 123/178$, maximum 43 g). Three models explained the variation in parasite mass for $n = 156$ cats with complete data. All three models included the animal's age, with parasite biomass increasing with age ($\beta\cdot\omega i = 0.220$). All three models also included source location ($\beta\cdot\omega i = 0.189$), with greatest parasite mass for cats from urban and commercial areas and least for cats from peri-urban sites; cats from refuse tips had intermediate parasite burdens. Sex ($\beta\cdot\omega i = 0.025$) and deliberate feeding ($\beta\cdot\omega i = 0.017$) were each in one of the three models but showed the least explanatory power.

Diet analyses of stray cats

Over 60% of stray cats analysed had bait food present in their GI tracts from trapping ($n = 119/188$; Supplementary Table S4); the contribution of other food categories is therefore likely to have been underestimated. The GI tracts of 20 cats were effectively empty of deliberately ingested food stuffs (contained various combinations of bait, incidentally ingested vegetation, soil/rocks, cat fur and GI parasites).

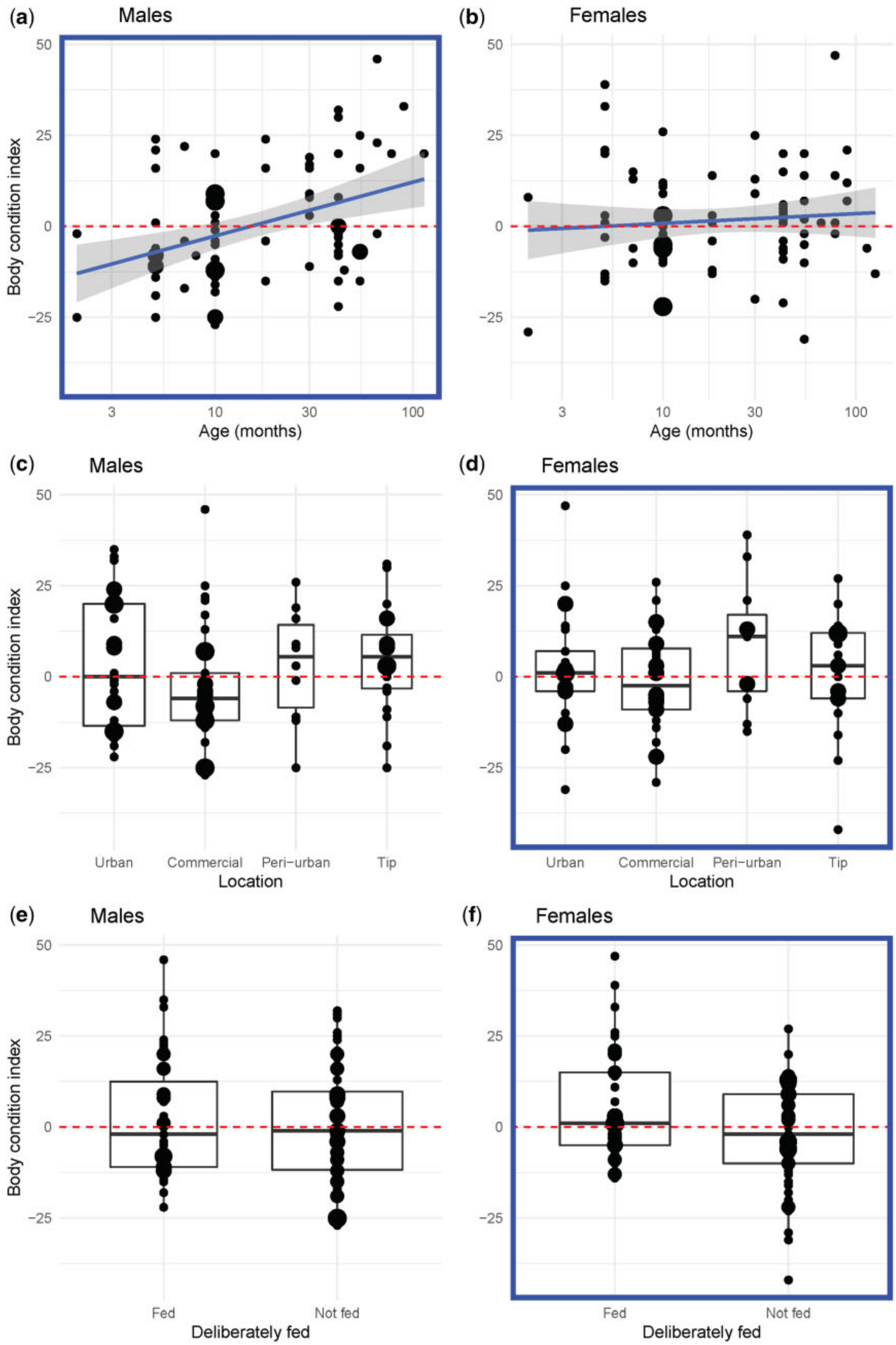

Figure 1: Variables tested for their association with body condition index of 79 male and 77 female stray cats collected across Perth, Western Australia, that had complete age and diet datasets. Male cats in left column and females in right column; blue boxes around graphs indicates a significant association. For boxplots, the width of the boxes or the size of the dots represents relative sample sizes. (**a, b**) BCI versus cat age in months; (**c, d**) BCI versus location; (**e, f**) BCI versus supplemental feeding; (**g, h**) BCI versus season; (**i, j**) BCI versus helminth parasite mass in grams; (**k, l**) BCI versus total mass of fauna consumed; and (**m, n**) BCI versus total mass of refuse consumed

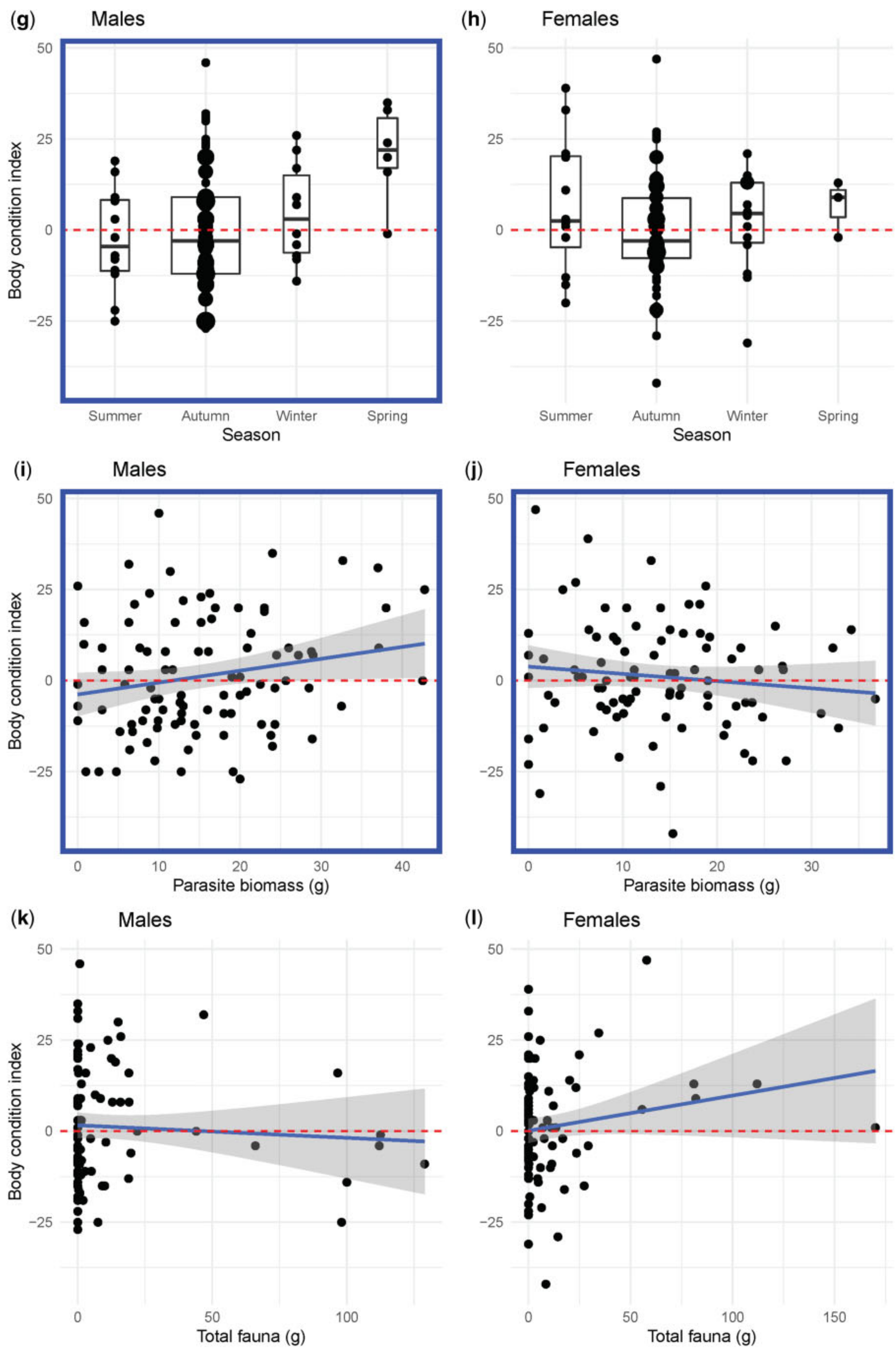

Figure 1: Continued

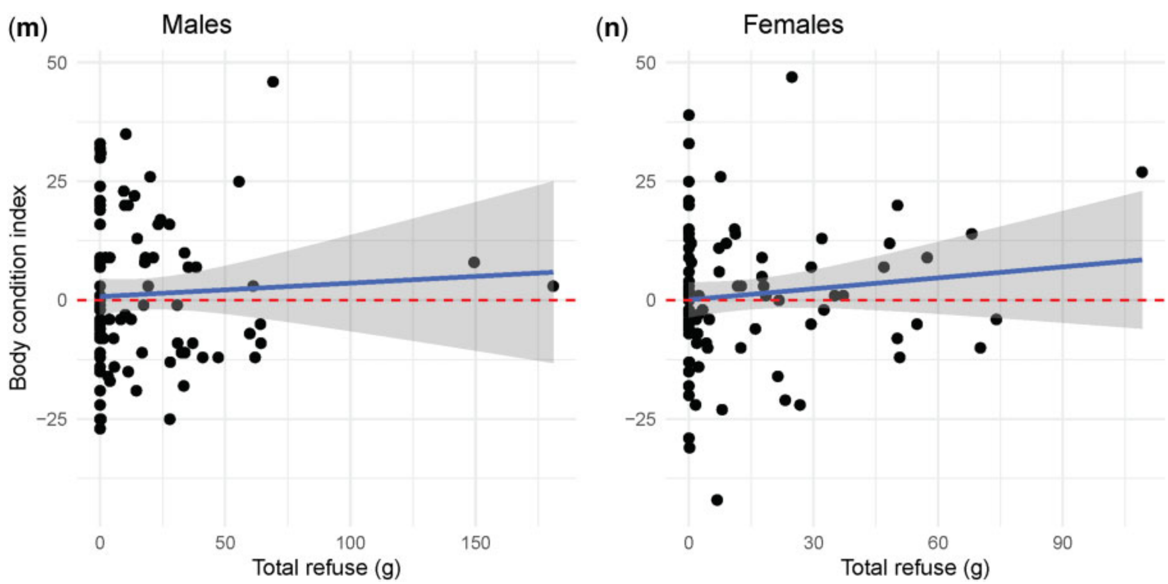

Figure 1: Continued

A total of 2.3 kg of refuse was consumed by 57.5% of the 188 stray cats analysed ($n = 108/188$; Supplementary Table S5). Forty cats (21.3%) had consumed ≥20 g of refuse and the GI tracts of four cats appeared ischaemic (Fig. 2). Refuse made up 44% of the overall total mass of GI tract contents, with an average of 26.1 ± 28.7 g consumed (range 0.1–181.0 g; Fig. 3). Meat scraps were present in 51 cats (27.1% of 188) and made up 38.7% of refuse by mass (Fig. 4). Vegetable and fruit scraps were present in 32 cats (17.0%) and made up 15.2% of refuse mass. Paper was present in 51 cats (27.1%) and made up 38.0% of refuse mass. Plastic items were present in 45 cats (23.9%) and made up 14.1% of refuse mass. Foil was eaten by nine cats making up 0.7% of refuse mass. Miscellaneous refuse items made up 4.7% of refuse mass (Fig. 4) and included packing styrofoam, glass shards, wound bandages, synthetic fibres etc. in 23 cats (12.2%; Fig. 5; Supplementary Table S5). Many cats eating refuse ($n = 23/108$, 21.3%) also ate ≥5 g of fresh green grass (maximum 25 g) which may suggest intestinal discomfort.

More than half of all stray cats had consumed fauna ($n = 96/188$; Supplementary Table S4; excluding the single peri-urban cat that had consumed carrion in the form of rancid sheep meat and wool), across all locations and supplemental feeding histories. Vertebrate prey was consumed by 73 cats, invertebrate prey by 49 cats and both vertebrates and invertebrates by 26 cats (38.8%, 26.1% and 13.8% of 188, respectively). A total of 111 individual vertebrate prey were consumed by cats (Supplementary Table S6), with 83 introduced and 14 native animals identified to species level (belonging to at least 7 and 6 spp., respectively) and an additional 13 prey were identified to higher taxa only.

Mammals made up the majority of identified prey ($n = 77$, 69.4% of 111 prey), especially introduced rodents ($n = 61$, 55.0%). Seven native marsupials (brushtail possums, *Trichosurus vulpecula*, and quenda, *Isoodon fusciventer*) were eaten by cats from urban, commercial and peri-urban but not rural tip locations. Birds represented one quarter of prey consumed ($n = 28$, 25.2% of 111), however, nearly half were domestic chickens, *Gallus domesticus*, taken by peri-urban and rural tip cats ($n = 13$) and may have been hunted or freshly scavenged from refuse. The

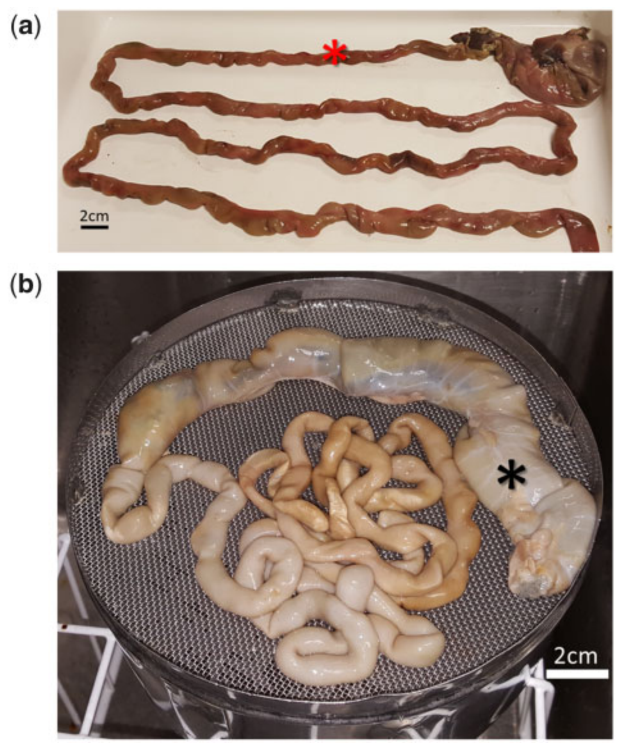

Figure 2: (a) Stomach and small intestine of a healthy adult male stray cat; and (b) the small intestine of an adult female stray cat with 49 g plastic and 20 g newspaper blocking its duodenum (*). The duodenum is markedly distended and the whole small intestine is ischaemic in contrast with (a)

remaining fauna consumed by stray cats included five reptiles (4.5% of 111 prey), a single unidentified fish (0.9%) and numerous invertebrates (individuals not counted).

There was no significant effect of cat sex (Kruskal–Wallis test: $H_{1,n=188} = 0.36$, $P = 0.546$) or season ($H_{3,n=188} = 6.47$, $P = 0.091$) on the number of individual vertebrate prey taken. There was, however, a significant effect of location ($H_{3,n=188} = 8.81$,

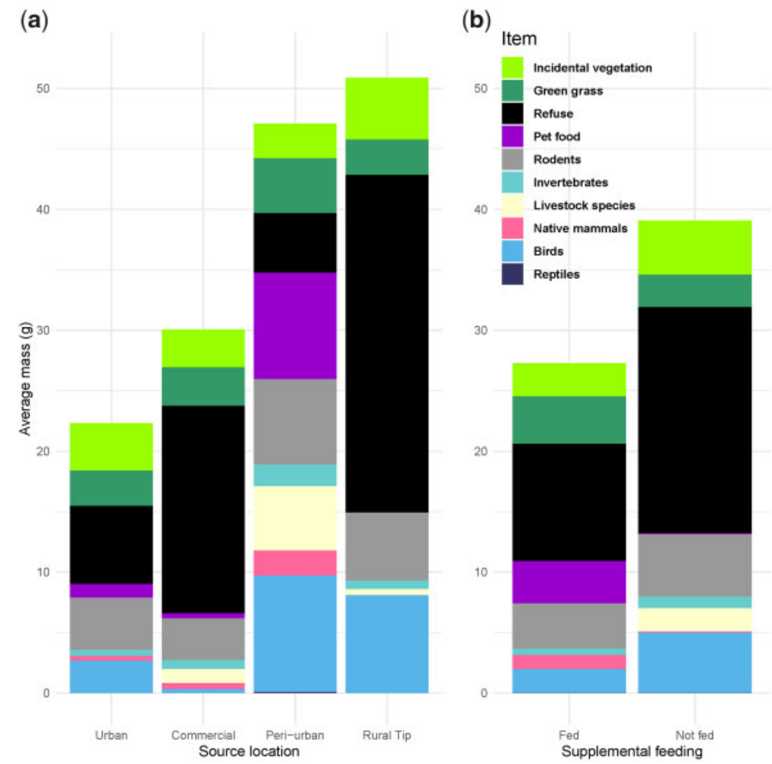

Figure 3: Average mass (g) of different food categories consumed by 188 stray cats from across Perth, Western Australia pooled by: (**a**) location and (**b**) feeding history (unfed urban cats and rural refuse tip cats were pooled as 'not fed' cats for analyses). Excludes bait food, miscellaneous contents and GI parasites

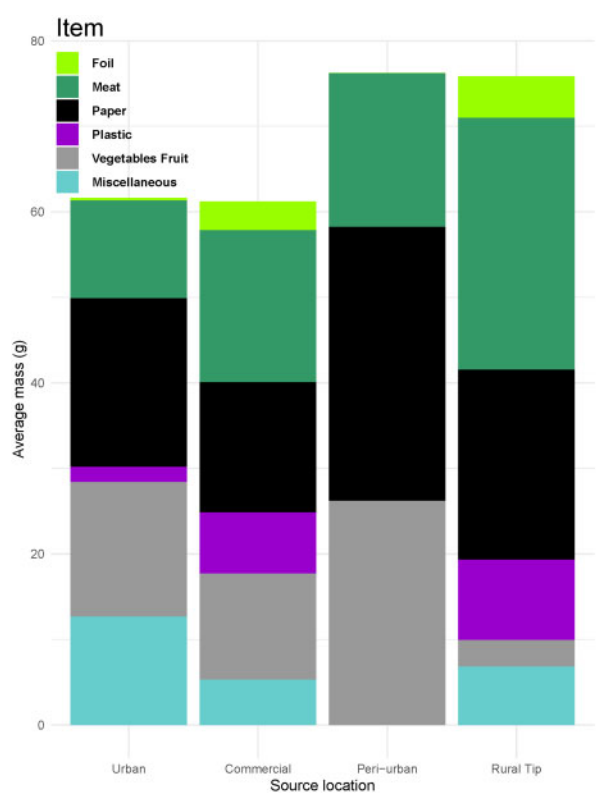

Figure 4: Average mass (g) of each refuse category eaten by 108 of 188 stray cats from locations across Perth, Western Australia. Miscellaneous items included cotton and nylon threads, wound bandages, denim material, shoelaces, nylon stockings, rubber bands, a teabag, metal staples, steel wool, styrofoam and glass

$P = 0.032$), with the greatest number of prey taken by cats from peri-urban locations. Unfed cats took a greater number of prey than fed cats ($H_{1,n=188} = 5.01$, $P = 0.025$).

There were no significant differences in diet composition between males and females (PERMANOVA: pseudo-$F_{1,188} = 0.58$, $P = 0.677$). There were, however, significant differences between adults and juveniles (pseudo-$F_{1,188} = 2.49$, $P = 0.049$), with adults having consumed more refuse (SIMPER 47.4% of the difference in diet data between these two age categories), birds (SIMPER 17.4%) and black rats (SIMPER 8.9%) than juveniles, but comparable volumes of house mice (SIMPER 17.2%).

There were significant seasonal differences in diet composition (PERMANOVA: pseudo-$F_{1,188} = 2.44$, $P = 0.020$). Pairwise analyses indicated that diet composition was significantly different between summer and autumn ($P = 0.008$): a greater proportion of refuse was present in GI tracts of cats in autumn (SIMPER 42.9%) while more birds (SIMPER 26.8%) and black rats (SIMPER 19.3%) were present in summer.

There were significant differences in diet composition between locations (PERMANOVA: *pseudo*-$F_{3,188} = 4.67$, $P < 0.001$); pairwise analyses indicated that there were no significant differences between urban and peri-urban cats ($P = 0.156$; pooled for SIMPER analyses), but all other pairs were significant at $P < 0.017$. Refuse, birds and mice were more common in the GI tracts of cats from rural tips compared with cats from commercial locations (SIMPERs refuse: 59.4%, birds: 17.8%, mice: 12.5%) or urban/peri-urban locations (SIMPERs refuse: 54.8%, birds: 23.5%, mice: 11.6%). Refuse was more common (SIMPER 38.4%) but fauna (birds: SIMPER 20.8%, black rats: SIMPER 19.4%) less common for cats from commercial locations compared with urban/peri-urban cats. Refuse represented 55% of total GI tract content mass for cats from rural tips and 57% for cats from

Figure 5: Examples of refuse in stray cat stomachs collected from Perth, Western Australia. **(a)** An adult male consumed: 1. black plastic bag, work-boot shoelaces, 2. Paper, 3. Aluminium foil, 4. a green plastic net, and 5. single shoelace from a work-boot. **(b)** A juvenile consumed: woven plastic bag (for domestic animal-feed pellets), as well as a mouse (seen as grey furballs in picture) and sheep carrion (not shown). **(c)** A juvenile female consumed: glass shards and (not shown) a wound bandage, plastic, paper and tree bark

commercial locations, but 10% for peri-urban cats and 29% for urban cats (Fig. 6a).

There were also significant differences in diet composition with history of supplemental feeding (PERMANOVA: *pseudo*-$F_{1,188} = 3.12$, $P = 0.004$), which was largely due to the greater mass of refuse in unfed cats compared with fed cats (SIMPER 33.4%). Refuse made up an average of 41% of GI tract contents for unfed stray cats, and 35% for fed cats (Fig. 6b). Total fauna consumed was highest for peri-urban locations (Fig. 6c) and cats that had not been deliberately fed (Fig. 6d). Fauna represented 18.0% of the mass of GIs for deliberately fed cats ($n = 34$), 18.1% for cats from rural tips ($n = 30$), but 26.7% for cats that were unfed ($n = 31$; rural tip and unfed data pooled in Fig. 6d). Birds (SIMPER 23.4%) were more common for unfed cats, while the difference for native mammal (fed cats: average 1.2% versus unfed cats: average 0.23% of total volume) only contributed a small degree to this difference in diet composition (SIMPER 1.7%).

Discussion

Based on cat biology and studies of stray cats elsewhere, we made several predictions regarding the Perth stray cat population that, to our surprise, were either not fulfilled or only partially fulfilled. We had predicted that stray cats would be in better physical condition in urban and peri-urban locations; however, while male BCI did not vary significantly between locations, female cats from rural tips and peri-urban locations were in marginally better condition than urban or commercial cats. Body condition of male stray cats was strongly determined by their age, and males collected in winter and spring were in the best condition. For females, there were no strong predictors of body condition, although diet and whether or not they were deliberately fed by people explained some of the variation in body condition. We had also predicted that there would be some cost to body condition of high parasite biomass. Feline tapeworm (*T. taeniaeformis*) was hosted by 95% of cats, with substantial biomass (17% of GI contents mass; 90.2 ± 57.8 g). Contrary to our prediction that high parasite biomass would lead to poor body condition, female stray cats showed only slight negative association between body condition and parasite biomass. As the primary definitive host of both feline tapeworm (*T. taeniaeformis*) and roundworm (*T. cati*), cats can carry substantial parasite burdens without losing obvious body condition (Miller 1932; Beugnet, Halos, and Guillot 2018). In contrast, the body condition of male strays was positively associated with parasite biomass, which would likely reflect the accumulation of parasites with age. We had also predicted better body condition for stray cats that had consumed fauna, and worse condition for those feeding on refuse. The overall diet of stray cats varied with cat age and season, but body condition of cats was not affected by the amount of fauna or refuse consumed.

Factors determining BCI in stray cats

Body condition of male stray cats was strongly determined by their age, and somewhat by season of collection. In contrast, the BCI of females was not associated with age. Campigotto et al. (2019) found that average body mass of domestic breed cats increases from birth, peaks at 8 years of age, and declines thereafter, regardless of sex or reproductive status ($n \geq 12$ million pet cats presenting to veterinary clinics in Canada and the USA). Our male stray population could reflect this relationship with age in domestic cats generally. Male cats sexually mature at later ages than females (puberty at 8–10 months versus >4 months; Root Kustritz 2009) and direct more resources to somatic growth to achieve sexual dimorphism that is driven by male–male competition (Turner and Bateson 2000). In contrast, regular reproductive output from a young age in female strays would require them to consume sufficient food for both their own maintenance requirements as well as to nourish offspring. Nearly 70% of the female strays examined in this study had bred previously or recently or were pregnant at time of euthanasia (the youngest reproductive female was 5 months, the youngest pregnant cat was ≈10 months old, oldest was 7.5 years). Additionally, 29% of reproductive females were under the age of 10 months ($n = 18/63$) confirming early reproduction. Females fed commercially balanced diets gain 40% of their pre-pregnancy weight during gestation, however, nearly all the weight gained is lost during lactation (60%) and weaning (40%) via general physiological changes (Little 2012). Females that hunt and scavenge to survive may therefore experience regular periods of nutritional stress, with little gain in BCI during their reproductive years (≈10 years in a pet cat; Little 2012). A study of wild European lynx (*Lynx lynx*) in Finland similarly found that females across locations had consistently lower body conditions than males because of reproductive stress (Pulliainen, Lindgren, and Tunkkari 1995).

For females, there were no strong predictors of body condition, although location, diet and whether or not they were

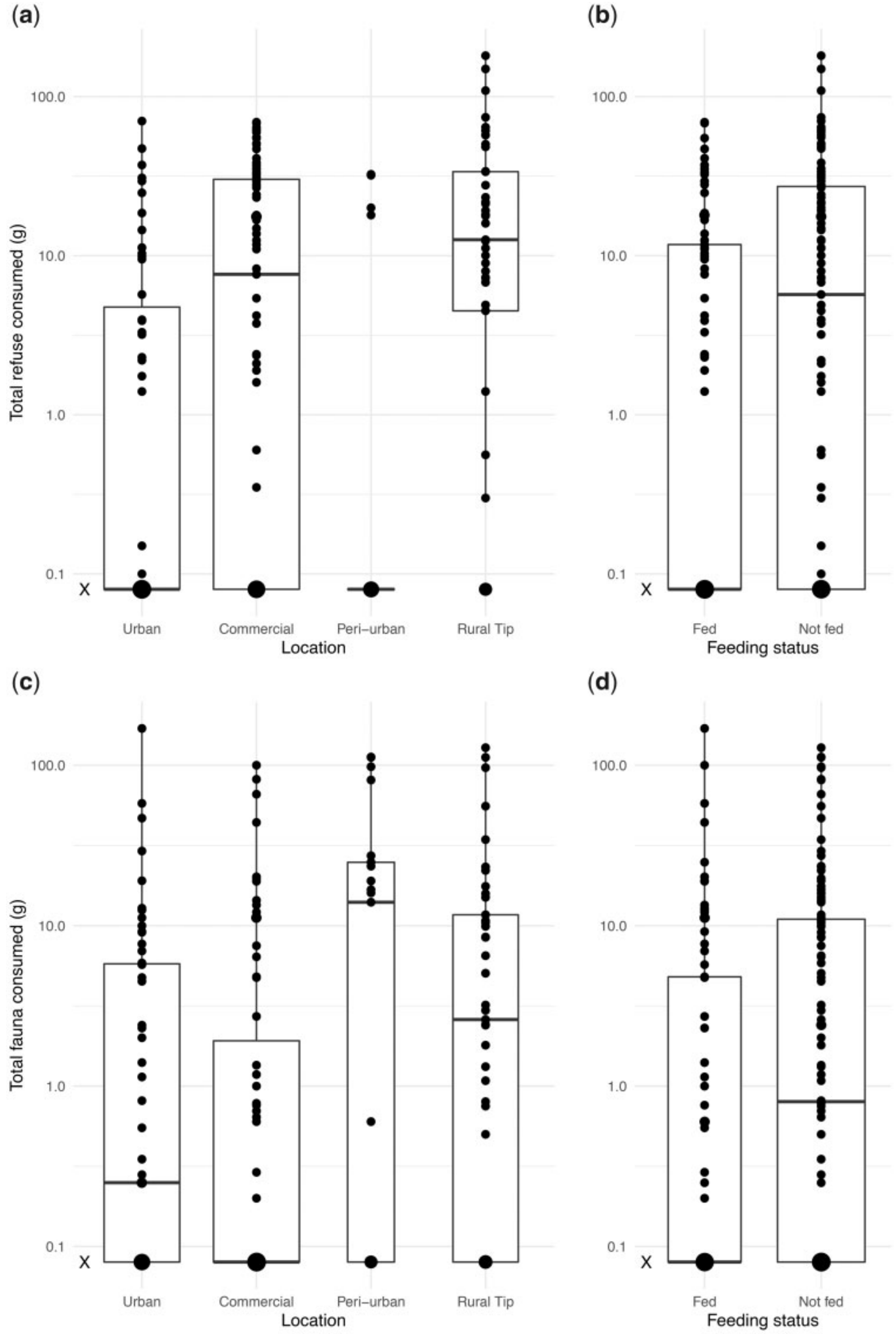

Figure 6: Total mass of refuse and fauna ($\log_{10}$) retrieved from gastrointestinal tracts of 188 stray cats collected from across Perth, Western Australia. Total refuse mass in grams shown for: (**a**) general locations and (**b**) feeding history status (unfed urban cats and rural refuse tip cats were pooled as 'not fed' for analyses). Total fauna mass shown for: (**c**) general locations and (**d**) feeding history status. Data are medians (horizontal lines, quartiles (boxes) and non-outlier range (whiskers); dots represent data for individual cats; 'X' indicates zero values which would not plot on log-transformed axes

deliberately fed by people explained some of the variation. When climatic conditions are warm and mild, male and female cats can breed all year round (Spotte 2014). Perth has warm summers and mild winters (average 2016 daily winter temperatures 10.6–14.6°C; Bureau of Meteorology 2016) which may explain why we found no evidence for seasonal influence on female BCI. Data from Australian animal shelters also confirm that cats breed year-round (kitten numbers peak between December and May in Melbourne, State of Victoria: Marston and Bennett 2009; and Perth, WA: Crawford, Fontaine, and Calver 2017). The BCI values of male strays in Perth were significantly higher in winter and spring seasons (June to November) and this may reflect their attainment of optimum condition for these peak mating months (Spotte 2014), whereas female condition did not notably vary with season.

Contrary to our predictions, the BCI of male cats was not influenced by location, however, female strays from rural tips and peri-urban locations were actually in better condition than urban or commercial cats. This may suggest that peri-urban and rural tip locations offer more hunting/refuse resources than urban and commercial areas. We also found that female BCI was positively influenced by supplemental feeding by people, but male condition was not, so it appears that female cats with access to food from caretakers are able to improve their physical condition compared with cats that are not deliberately fed.

We predicted that there would be some cost to body condition of high parasite biomass. Despite their high parasite biomass, female stray cats showed only slight negative association between body condition and parasite biomass. As the primary definitive host of both feline tapeworm (*T. taeniaeformis*) and roundworm (*T. cati*), cats can carry substantial parasite burdens without losing obvious body condition (Miller 1932; Beugnet, Halos, and Guillot 2018). In contrast, the body condition of male strays was positively associated with parasite biomass. This may reflect the accumulation of parasites with age rather than a causal relationship (Nichol, Ball, and Snow 1981). Older animals can support higher parasite numbers/biomass because larger body sizes offer parasites larger niches than younger, smaller animals (e.g. Rohde 1994). The immune system of younger animals is also more likely to be overwhelmed by parasitic burdens, resulting in death (Lopate 2012), but young cats that survive into adulthood may have greater resistance and accumulate more parasites as they continue to age.

GI helminth parasite biomass

Feline tapeworm was hosted by 95% of cats with substantial biomass (17% of GI contents mass; 90.2 ± 57.8 g); a greater proportion than has been reported for other studies of stray cats internationally (e.g. up to 74% of necropsied cats in Qatar; Abu-Madi et al. 2010). The zoonotic feline roundworm was also present in 3% of stray cats in our study.

In the State of Victoria, 78% of 127 cat carcasses from remote locations were infected with feline tapeworm and 78% hosted roundworm (Coman 1972). In contrast, a study of cats from five sources in the city of Perth detected feline roundworm in only 2% of cats from breeders ($n = 95$ faecal samples), but no roundworms were detected in cats from refuges, pet shops, private owners or boarding facilities ($n = 323$); feline tapeworm was also not detected in any of the surveyed cats (McGlade et al. 2003). These differences in prevalence are unlikely to be attributable to different examination techniques (Little et al. 2015); instead, they may reflect differences in prophylactic care given to cats in private facilities versus rural cats (McGlade et al. 2003). Additionally, Coman (1972) attributed the high prevalence of tapeworm in rural cats in Victoria to the importance of mice in their diet. One quarter of our stray cats had consumed rodents prior to trapping. Although similar numbers of cats consumed rodents in each location (15 in urban, 13 in commercial, 7 in peri-urban and 12 in rural tip locations), we did find that parasite biomass varied between locations, being greatest for cats from urban and commercial areas, and lower for cats from peri-urban and rural refuse tip sites. The larger biomass of parasites in urban and commercial locations may therefore reflect greater consumption of rodents; and/or large numbers of helminth eggs surviving in the favourable climes of Perth (e.g. Sommerfelt et al. 2006) and/or greater densities of cats living in these locations (Turner and Bateson 2000). Although stray cats appear unaffected by parasites superficially (blood tests could have detected anaemia, compromised immune function, other parasites), the high prevalence of helminths in analysed stray cats overall is of concern. Given that young cats are particularly vulnerable to parasites (Lopate 2012), roundworm is zoonotic and tapeworm infections are asymptomatic (i.e. not always signified by anal scooting or weight loss; Beugnet, Halos, and Guillot 2018), we consequently recommend that owners of pet cats in Perth routinely administer anti-helminth medication (McNamara et al. 2018; Chalkowski et al. 2019). Further studies on parasites and disease of stray cats in Australia are needed because even though parasites can be well managed in pet cats by owners and veterinarians, stray cats remain 'potential reservoirs for parasites that can pose veterinary and public health concerns' (Salman et al. 2018, p.966).

Refuse threatens stray cat welfare

Refuse was consumed by nearly 60% of stray cat analysed, making up an astounding average of 44% of the total GI volume. These values were much greater than previous studies report, where the general pattern seems to be that refuse is generally a supplementary food that comprises a smaller proportion of overall diet (Spotte 2014). For example, a study of 97 faecal samples from strays on a Brazilian university campus identified 21% vegetable matter and 15% non-food items (i.e. refuse) in winter and 18% vegetable matter and 15% non-food items in summer (Campos et al. 2007). The refuse proportions we recorded is likely to be due to examination of the whole GI tract versus faecal samples only. Refuse could also be readily available at the locations from which strays were removed. A study of lethally controlled and roadkill cats in Israel (Brickner-Braun, Geffen, and Yom-Tov 2007), found that stomach contents varied according to location, with cats from urban areas consuming only cat food, human food and refuse (all referred to as 'trash', p.130), whereas cats from human settlements in rural locations supplemented their trash diet with mammals, and cats from open agricultural/natural landscapes consumed more mammals and less trash. In our study, cats from all locations also consumed refuse, and consumption was similarly greatest at commercial and rural tip locations (57% and 55% of contents, respectively), where refuse may be more available than in urban and peri-urban locations (29% and 10%, respectively). This may also suggest that Perth's stray cats actively choose to scavenge food, possibly to save energy compared with hunting. No studies of the motivation for scavenging or the impact of refuse consumption on cat health could be found. However, pet cats that consume indigestible material are frequently presented to veterinary practices for medical intervention (Papazoglou, Patsikas, and Rallis 2003; Burkitt et al. 2009).

The dominance of refuse over other ingested foods across locations may suggest that stray cats in Perth are hungry despite their good body condition. Cats have a strong aversion to foods containing rancid fats (National Research Council 1986), yet despite this, 47% of strays consumed decomposing meat scraps ($n = 51/108$; e.g. sandwich ham, roast chicken and cooked prawns). Thirty percent of strays eating refuse also consumed vegetables and fruit despite limited digestibility and low nutritional value ($n = 32/108$; National Research Council 1986). Whilst paper, plastic and foil could have been eaten during efforts to remove meat from food-wrappings, 53% of cats consumed non-nutritious materials without meat. It is possible that cats can eat small amounts of refuse and pass this through their system with no impact on their health and could also alleviate immediate hunger without instantly compromising body condition. However, we recorded vast amounts of various non-nutritious, dangerous items that in our opinion, pose a threat to the health and welfare of stray cats (Papazoglou, Patsikas, and Rallis 2003).

Maximum weights for non-nutritious materials eaten by Perth stray cats were: 88 g paper, 42 g plastic, 11 g foil, 14 g Styrofoam and 30 g of miscellaneous items. Items such as glass shards, metal staples, steel wool, a pair of boot shoelaces, and a whole teabag were consumed and would have caused discomfort. Fresh green grass was consumed by 62% of cats that had eaten refuse, possibly to aid movement of refuse through the GI. From examination of GI tracts it was not always clear whether refuse was consumed over one day (GI contents normally reflect ≈24 h of food consumption; Mugford and Thorne 1980; Chandler, Guilford, and Lawoko 1997; Wyse et al. 2003) or whether it had accumulated over time because cats were unable to transition the masses through their GIs. Foreign objects can persist in the cat GI for long periods and can be asymptomatic until local peritonitis or fibrosis occurs (Papazoglou, Patsikas, and Rallis 2003; Burkitt et al. 2009). At least four stray cats from Perth had distended ischaemic GIs, with one containing 131 g of refuse. Cats that experience complete GI blockages exhibit symptoms for up to one week (e.g. vomiting, fever and dehydration), with symptom duration increasing likelihood of death/euthanasia (Levitt and Bauer 1992). This suggests that without veterinary attention, many cats die from GI blockages. In our study, one stray cat ate a half-spread of newspaper and another had an entire pair of full-length ladies' nylon stockings running from oesophagus to bowel, suggesting the cat had difficulty transitioning the stockings along the GI. Had such cats not been trapped by animal controllers, we believe it likely that they would not have survived much longer.

Even if cats are able to pass refuse through their GIs, consumption of refuse long-term may eventually compromise health (and welfare) by depriving cats of essential nutrients (e.g. taurine; Morris, Rogers, and Pacioretty 1990). Animals with macronutrient deficiencies can seek them out in unusual food items (termed 'pica'; e.g. common in livestock; Firyal 2007). Pet cats develop pica when they are not fed *ad libitum*, experience prolonged nutritional or emotional stress (e.g. reproduction, early weaning, rehoming), hormonal changes, GI lymphoma, anaemia and/or Feline Immunodeficiency Virus and other diseases (Bradshaw, Neville, and Sawyer 1997; Beaver 2003). Pet cats with pica preferentially consume shoelaces, threads and fabric, plastic, rubber, paper or cardboard and wood (Demontigny-Bédard et al. 2016). It was common for strays in our study to have consumed one or more of these items. Animals with pica can none-the-less have good body condition and fat stores, and this may explain why stray cats in our study showed no association between body condition and refuse consumption. To our knowledge, the prevalence of pica in stray cats has not been determined and it would have been useful to run blood panels to screen for macronutrient deficiencies and disease (Hellard et al. 2011; Day 2013).

Whether stray cats consumed refuse because of hunger, nutrient deficiency, environmental availability or a combination of these factors, the ingestion of so much refuse by so many cats should concern people tasked with managing stray populations. We therefore recommend that stray cats living in locations where refuse is readily available should be prioritised for trap-removal.

Fauna predation

Free-roaming cats hunt fauna where it is available, no matter their age, sex, hunger or availability of food from people (Cove et al. 2018; Hernandez et al. 2018). Our study confirmed this, with fauna consumed by cats of mixed ages and sex, across all locations, seasons and supplemental feeding histories. There was no effect of cat sex on diet composition but there was an effect of age, with adult cats consuming more refuse, birds and black rats than juveniles, but comparable volumes of mice. The hunting skills of cats increase with age and repeated exposure to prey-type (Bradshaw, Casey, and Brown 2012). Rats are particularly challenging prey so the effect of age on rat consumption may reflect hunting skills acquired through experience (Bradshaw, Casey, and Brown 2012). Season affected overall diet composition with refuse making up a greater proportion of diet in the autumn whereas more birds and black rats were consumed in summer. A dietary study of stray cats living on a Brazilian university campus (Campos et al. 2007) identified greater proportions of vegetable matter and non-food items (i.e. refuse) in faecal samples collected during winter compared with summer. Perth strays may similarly scavenge more in autumn and switch to consuming more fauna in summer, when many reptiles, birds and marsupials are active and abundant.

We did not examine prey availability so cannot widely extrapolate our findings, but we note that while there was no effect of cat sex on the number of prey consumed there was an effect of location. Peri-urban cats consumed significantly more individual prey than cats from other locations. However, the overall composition of the diet of peri-urban cats did not differ from urban cats (cats from both locations consumed more fauna but less refuse than commercial or rural tip cats) and may reflect greater availability of fauna in both locations (but lower availability of refuse). Commercial locations are generally more homogenised than urban and peri-urban areas so may offer fewer predation opportunities, and in our study, rural tip cats may also have access to less diverse and native fauna, but more refuse (main prey were introduced rodents, European rabbits and domestic chickens).

Diet composition also varied with supplemental feeding status, with unfed cats consuming more refuse, and a greater mass and number of prey, than fed cats. These results may reflect greater hunger and/or opportunism in the foods consumed by unfed strays (Turner and Bateson 2000). However, regardless of feeding status, the number of prey taken per cat can be large. Hernandez et al. (2018) used collar-mounted cameras to quantify hunting behaviour of stray cats in TNR colonies on Jekyll Island, USA, and reported that, despite being regularly fed by people, each cat took an average of 4.37 vertebrates per day (range 0–16.5 for 18 cats across 3.8–60 hours of video footage). In our study, 111 vertebrates were consumed by just 73 cats (≈1.5 prey/cat/day). Our vertebrate predation rate is likely to be an underestimate as cats were trapped for up to 12 h before euthanasia and were unable to hunt during this time. The highest number of prey was consumed by a cat from a commercial location despite being fed by people for several months prior to trapping. Prior to trapping, this single stray consumed three mice, one bird, one reptile and several invertebrates (plus refuse, fresh grass, incidental vegetation and bait food). Native marsupials were also consumed by more fed than unfed cats.

Although only seven marsupials were consumed in total, the native brushtail possum and quenda occur in only a few urban locations in Perth (Woinarski, Burbidge, and Harrison 2014). The quenda has recently been reclassified as new species of bandicoot endemic to Perth and the south-west of Australia (Travouillon and Phillips 2018)—with its conservation status under review. A survey of public sightings of quenda in Perth in 2012 (Howard et al. 2014), found that sightings had declined since the previous survey in 1993 (particularly along the peri-urban fringe) but that quenda survived in locations that had retained large areas of native vegetation, wetland or riparian habitat. Stray cats that had consumed quenda and arboreal brushtail possums were trapped in such areas, suggesting that strays, in addition to roaming pet cats (Howard et al. 2014), may threaten these marsupials where they persist in Perth. Given that stray cats predate ≈149 million mammals per year in Australia (Murphy et al. 2019), more research into the impact of stray cat predation on Australia's endemic fauna is urgently needed.

Conclusions and recommendations

The stray cats that we processed all appeared to be in optimal to excellent health on visual inspection, with most (81%) cats subjectively scoring 3-out-of-3 ('heavy') based on costal and mesenteric fat deposits (no cats were identified as 'poor condition'; BCS = 1). Most cats were sexually intact (98%) and adult (66.5%), and there was a high reproductive rate, with two-thirds of reproductive females (69%) showing evidence of breeding, with the youngest reproductive cat aged 5 months and the oldest pregnant cat aged 7.5 years. Furthermore, only 13 (7%) cats exhibited obvious health issues. Despite these positive measures, our sample of stray cats showed high gastrointestinal parasite biomass and a worryingly large proportion of human refuse in their GIs, much of it indigestible and including sharp and dangerous objects. Although the majority of stray cats sampled were sufficiently mobile prior to being trapped (according to public reports about the strays and excluding cats hit by cars; Supplementary Table 2), there were several individuals with obvious symptoms of infection, cancer, trauma and bowel blockage (e.g. axilla abscess, liver tumour, damaged limb, ischaemic GIs) and we believe that the number of cats exhibiting injuries, gastrointestinal complications or systemic disease would have been higher had organs been examined histologically or had blood had been screened for diseases (e.g. Wilson, Tidemann, and Meischke 1994).

When we compared the age structure of our stray cat sample with published data for pet cats from Sydney, Australia (Toribio et al. 2009) we found that even though our strays appeared to be in good body condition, their survival is markedly truncated. Few stray cats (13%) were older than 5 years of age compared with almost two thirds of pet cats (Toribio et al. 2009). Similarly, Warner (1985) revealed short lives for free ranging cats around farmsteads in rural Illinois, USA, with survival beyond 4 years uncommon and <1% surviving 7 years or more, where reduced longevity of stray cats was attributable to anthropogenic factors (e.g. 48% vehicle collisions, humans, dogs, farm machinery and chemicals), conspecifics (5%), cold weather (4%), disease (17%) or unknown reasons because the cats disappeared (27%). Stray cat survival is therefore threatened by multiple factors. Considering that only visual and gross physical assessment of cat health was carried out during necropsies, the apparent good health of cats may belie undiagnosed conditions that further explain the truncated age structure of stray cats in Perth, or indicate that in the absence of veterinary intervention sick or injured cats die quickly.

The body condition of male cats increased with age and peaked in winter and spring, while female body condition was slightly higher in peri-urban and rural tip locations and when they were deliberately fed by people. Human resources may thus be bolstering the reproductive health of female strays. Even when deliberately fed by people, strays were consuming fauna. While these data captured only modest levels of predation by stray cats on endemic wildlife, these numbers may not represent the real threat with other studies reporting devastating predation levels from even a single cat (Greenwell, Calver, and Loneragan 2019). Stray cat diet also included dangerous items that potentially threaten life and 79% of calls to remove the strays in our samples were related to welfare concerns for strays including sick, injured or dead cats and 21% were complaints of nuisance or predation threat to native fauna. Control of stray cats is advocated to reduce attacks on wildlife, disease spread (to humans, domestic animals and wildlife) and public nuisance, as well as address welfare issues for the cats themselves (Marra and Santella 2016; Read 2019; Woinarski, Legge, and Dickman 2019). Overall, these data indicate that removal of stray cats from the environment will benefit public health, reduce nuisance and respond to welfare concerns for the stray cats themselves, while acknowledging at least the potential for predatory impacts.

Of the control options available, TNR would not address the public health, nuisance or welfare issues because the cats are returned to the environment and, as our data show, even with supplementary feeding, strays will likely host many parasites, consume endemic fauna, scavenge dangerous refuse and be subject to other hazards including vehicle collisions. Trapping followed by adoption of socialised animals and euthanasia of others would better address all issues, with trapping and adoption likely to be more acceptable to the community (Travaglia and Miller 2018). We support approaches such as those proposed by for the Brisbane Local Government Area (Brisbane City Council 2018) and the Australian Capital Territory (ACT 2019) to reduce numbers of stray cats by trapping and rehoming, with euthanasia as a last resort. These measures also incorporate owner education regarding the value of desexing, registering, identifying and containing pet cats to reduce the flow of cats from the owned population to the stray population (see also Crawford, Fontaine, and Calver 2017; Crawford and Calver 2018 for the importance of these measures). We found limited evidence of such transitions (four desexed cats in our sample must have been owned at one time, 2%), but higher levels have been documented in other studies. For example, in the ORCAT TNR programme in Florida, USA, Kreisler et al. (2019) reported that an average of 7% of the cats trapped were desexed but not ear-tipped to indicate TNR involvement, so they represent a minimum value for cats lost or abandoned by owners (the real value would be higher because of entire animals lost or abandoned). The results of the present study of health and diet indicate that greater research on a range of issues concerning cats is needed and that stray cats should be actively removed from urban environments. Inaction is not an option.

Supplementary data

Supplementary data are available at *JUECOL* online.

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References

Abu-Madi, M. A. et al. (2010) 'Intestinal Helminths of Feral Cat Populations from Urban and Suburban Districts of Qatar', *Veterinary Parasitology*, **168**: 284–92.

Arhant, C., Wogritsch, R., and Troxler, J. (2015) 'Assessment of Behavior and Physical Condition of Shelter Cats as Animal-Based Indicators of Welfare', *Journal of Veterinary Behavior*, **10**: 399–406.

Australian Capital Territory Government (2019) *Draft ACT Cat Plan 2019–29*. Australian Capital Territory, Australia.

Beaumont, M. et al. (2001) 'Genetic Diversity and Introgression in the Scottish Wildcat', *Molecular Ecology*, **10**: 319–36.

Beaver, B. V. (2003) *Feline Behavior: A Guide for Veterinarians*, 2nd ed. St Louis, USA: Saunders.

Beugnet, F., Halos, L., and Guillot, J. (2018) *Textbook of Clinical Parasitology in Dogs and Cats*, 2nd ed. Ingelheim, Germany: Boehringer Ingelheim Animal Health.

Beveridge, I. and Emery, D. eds (2015) *Australasian Animal Parasites: Inside and Out*, pp. 241–4. Cairns North, Australia: The Australian Society for Parasitology Inc.

Blancher, P. (2013) 'Estimated Number of Birds Killed by House Cats (*Felis catus*) in Canada', *Avian Conservation and Ecology*, **8**: 3–22.

Bradshaw, J. W. S., Casey, R. A., and Brown, S. L. (2012) *The Behaviour of the Domestic Cat*, **2**nd edn, p. 264. Oxfordshire, UK: CABI Publishers.

——, Neville, P. F., and Sawyer, D. (1997) 'Factors Affecting Pica in the Domestic Cat', *Applied Animal Behaviour Science*, **52**: 373–9.

Brickner-Braun, I., Geffen, E., and Yom-Tov, Y. (2007) 'The Domestic Cat as a Predator of Israeli Wildlife', *Israel Journal of Ecology & Evolution*, **53**: 129–42.

Brisbane City Council (2018) *Biosecurity Plan for the Brisbane Local Government Area*. Brisbane, Australia.

Brunner, H., and Triggs, B. (2002) *Hair ID: An Interactive Tool for Identifying Australian Mammalian Hair*. Ecobyte Pty Ltd. Collingwood, Australia: CSIRO Publishing.

Bureau of Meteorology. (2016) *Perth in Winter 2016: Coldest Winter Days for at Least Two Decades*. *Seasonal Climate Summary for Perth*. Perth, Western Australia: Bureau of Meteorology. <www.bom.gov.au/climate/current/season/wa/archive/201608.perth.shtml>.

Burkitt, J. M. et al. (2009) 'Signalment, History, and Outcome of Cats with Gastrointestinal Tract Intussusception: 20 Cases (1986–2000)', *Journal of the American Veterinary Medical Association*, **234**: 771–6.

Burnham, K. P., and Anderson, D. R. (2002) *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*, 2nd ed. Fort Collins, USA: Springer.

Bush, B. et al. (2007) *Reptiles and Frogs in the Bush: Southwestern Australia*. Crawley, Australia: University of Western Australia Press.

Campigotto, A. J. et al. (2019) 'Investigation of Relationships between Body Weight and Age among Domestic Cats Stratified by Breed and Sex', *Journal of the American Veterinary Medical Association*, **255**: 205–12.

Campos, C. B. et al. (2007) 'Diet of Free-Ranging Cats and Dogs in a Suburban and Rural Environment, South-Eastern Brazil', *Journal of Zoology*, **273**: 14–20.

Carver, S. et al. (2016) 'Pathogen Exposure Varies Widely among Sympatric Populations of Wild and Domestic Felids across the United States', *Ecological Applications*, **26**: 367–81.

Castro-Prieto, J., and Andrade-Nunez, M. J. (2018) 'Health and Ecological Aspects of Stray Cats in Old San Juan, Puerto Rico: Baseline Information to Develop an Effective Control Program', *Puerto Rico Health Sciences Journal*, **37**: 110–4.

Centonze, L. A., and Levy, J. K. (2002) 'Characteristics of Free-Roaming Cats and Their Caretakers', *Journal of the American Veterinary Medical Association*, **220**: 1627–33.

Cat Haven (2017) *Annual Statistics*. Perth, Western Australia: Cat Haven. <www.cathaven.com.au/about/statistics/>.

Chalkowski, K. et al. (2019) 'Who Let the Cats Out? A Global Meta-Analysis on Risk of Parasitic Infection in Indoor versus Outdoor Domestic Cats (*Felis catus*)', *Biology Letters*, **15**: 20180840.

Chandler, M. L., Guilford, G., and Lawoko, C. R. O. (1997) 'Radiopaque Markers to Evaluate Gastric Emptying and Small Intestinal Transit Time in Healthy Cats', *Journal of Veterinary Internal Medicine*, **11**: 361–4.

Childs, J. E., and Ross, L. (1986) 'Urban Cats: Characteristics and Estimation of Mortality Due to Motor Vehicles', *American Journal of Veterinary Research*, **47**: 1643–8.

Coman, B. J. (1972) 'A Survey of the Gastro-Intestinal Parasites of the Feral Cat in Victoria', *Australian Veterinary Journal*, **48**: 133–6.

Cove, M. V. et al. (2018) 'Free-Ranging Domestic Cats (*Felis catus*) on Public Lands: Estimating Density, Activity, and Diet in the Florida Keys', *Biological Invasions*, **20**: 333–44.

Crawford, H. M., and Calver, M. C. (2018) 'Attitudes and Practices of Australian Veterinary Professionals and Students Towards Early Age Desexing of Cats', *Animals*, **9**: 2.

——, ——, and Fleming, P. A. (2019) 'A Case of Letting the Cat Out of the Bag - Why Trap-Neuter-Return is Not an Ethical Solution for Stray Cat (*Felis catus*) Management', *Animals*, **9**: 171.

——, Fontaine, J. B., and Calver, M. C. (2017) 'Using Free Adoptions to Reduce Crowding and Euthanasia at Cat Shelters: An Australian Case Study', *Animals*, **7**: 92.

Day, M. J. (ed.) (2013) *Canine and Feline Gastroenterology*. Saint Louis, USA: W.B. Saunders.

Demontigny-Bédard, I. et al. (2016) 'Characterization of Pica and Chewing Behaviors in Privately Owned Cats: A Case-Control Study', *Journal of Feline Medicine and Surgery*, **18**: 652–7.

El-Seify, M. A. et al. (2017) 'Gastrointestinal Helminths of Stray Cats in Alexandria, Egypt: A Fecal Examination Survey Study', *Veterinary Parasitology: Regional Studies and Reports*, **8**: 104–6.

Faya, M. et al. (2011) 'Domestic Queens Under Natural Temperate Photoperiod Do Not Manifest Seasonal Anestrus', *Animal Reproduction Science*, **129**: 78–81.

Finkler, H., Hatna, E., and Terkel, J. (2011) 'The Influence of Neighbourhood Socio-Demographic Factors on Densities of Free-Roaming Cat Populations in an Urban Ecosystem in Israel', *Wildlife Research*, **38**: 235–43.

Firyal, S. (2007) 'Pica (Depraved Appetite; Allotrophagia) in Domestic Animals and Man', *Pakistan Veterinary Journal*, **27**: 208–10.

Fournier, A. et al. (2017) 'Epidemiological Analysis of Reproductive Performances and Kitten Mortality Rates in 5,303 Purebred Queens of 45 Different Breeds and 28,065 Kittens in France', *Reproduction in Domestic Animals*, **52**: 153–7.

Giuliano Albo, A., and Nebbia, C. (2004) 'Incidence of Poisonings in Domestic Carnivores in Italy', *Veterinary Research Communications*, **28**: 83–8.

Government of Western Australia (2011) Cat Act 2011. Perth, Australia.

Greenwell, C. N., Calver, M. C., and Loneragan, N. R. (2019) 'Cat Gets Its Tern: A Case Study of Predation on a Threatened Coastal Seabird', *Animals*, **9**: 445.

Grue, H., and Jensen, B. (1979) 'Review of the Formation of Incremental Lines in Tooth Cementum of Terrestrial Mammals', *Danish Review of Game Biology*, **11**: 1–48.

Grueber, C. E. et al. (2011) 'Multimodel Inference in Ecology and Evolution: Challenges and Solutions', *Journal of Evolutionary Biology*, **24**: 699–711.

Gunther, I. et al. (2015) 'Nuisances and Welfare of Free-Roaming Cats in Urban Settings and Their Association With Cat Reproduction', *Preventive Veterinary Medicine*, **119**: 203–10.

—— et al. (2016) 'Feeders of Free-Roaming Cats: Personal Characteristics, Feeding Practices and Data on Cat Health and Welfare in an Urban Setting of Israel', *Frontiers in Veterinary Science*, **3**: 10.

Hammer, Ø., Harper, D. A. T., and Ryan, P. D. (2001) 'Past: Paleontological Statistics Software Package for Education and Data Analysis', *Palaeontologia Electronica*, **41**: 1–9.

Hellard, E. et al. (2011) 'When Cats' Ways of Life Interact with Their Viruses: A Study in 15 Natural Populations of Owned and Unowned Cats (*Felis silvestris catus*)', *Preventive Veterinary Medicine*, **101**: 250–64.

Hernandez, S. M. et al. (2018) 'The Use of Point-of-View Cameras (Kittycams) to Quantify Predation by Colony Cats (*Felis catus*) on Wildlife', *Wildlife Research*, **45**: 357–65.

Howard, K. et al. (2014) *Community Quenda Survey 2012*. Perth, Australia: University of Western Australia.

Hwang, J. et al. (2018) 'Disentangling the Link Between Supplemental Feeding, Population Density, and the Prevalence of Pathogens in Urban Stray Cats', *PeerJ*, **6**: e4988.

Izawa, M., Doi, T., and Ono, Y. (1982) 'Grouping Patterns of Feral Cats (*Felis catus*) Living on a Small Island in Japan', *Japan Journal of Ecology*, **32**: 373–82.

Kreisler, R. E., Cornell, H. N., and Levy, J. K. (2019) Decrease in Population and Increase in Welfare of Community Cats in a Twenty-Three Year Trap-Neuter-Return Program in Key Largo, FL: The ORCAT Program', *Frontiers in Veterinary Science*, **6**.

Levitt, L., and Bauer, M. S. (1992) 'Intussusception in Dogs and Cats: A Review of 36 Cases', *The Canadian Veterinary Journal*, **33**: 660–4.

Levy, J. K. (2011) 'Contraceptive Vaccines for the Humane Control of Community Cat Populations', *American Journal of Reproductive Immunology*, **66**: 63–70.

Little, S. et al. (2015) 'High Prevalence of Covert Infection with Gastrointestinal Helminths in Cats', *Journal of the American Animal Hospital Association*, **51**: 359–64.

Little, S. E. (ed.) (2012) *The Cat: Clinical Medicine and Management*. Saint Louis, USA: W.B. Saunders.

Lockwood, R. (2005) 'Cruelty toward Cats: Changing Perspectives', in D. J. Salem and A. N. Rowan (eds) *The State of the Animals III*, pp. 15–26. Washington, DC: Humane Society Press.

Lopate, C. (ed.) (2012) *Management of Pregnant and Neonatal Dogs, Cats, and Exotic Pets*. Iowa, USA: John Wiley & Sons, Inc.

Loss, S. R., Will, T., and Marra, P. P. (2013) 'The Impact of Free-Ranging Domestic Cats on Wildlife of the United States', *Nature Communications*, **4**: 1396–402.

Marra, P. P., and Santella, C. (2016) '*Cat Wars: The Devastating Consequences of a Cuddly Killer*.' Princeton, USA: Princeton University Press.

Marston, L. C., and Bennett, P. C. (2009) 'Admissions of Cats to Animal Welfare Shelters in Melbourne, Australia', *Journal of Applied Animal Welfare Science*, **12**: 189–213.

McGlade, T. R. et al. (2003) 'Gastrointestinal Parasites of Domestic Cats in Perth, Western Australia', *Veterinary Parasitology*, **117**: 251–62.

McNamara, J. et al. (2018) 'Survey of European Pet Owners Quantifying Endoparasitic Infection Risk and Implications for Deworming Recommendations', *Parasites & Vectors*, **11**: 571.

Milewski, L. M., and Khan, S. A. (2006) 'An Overview of Potentially Life-Threatening Poisonous Plants in Dogs and Cats', *Journal of Veterinary Emergency and Critical Care*, **16**: 25–33.

Miller, H. M., Jr. (1932) 'Superinfection of Cats with *Taenia taeniaeformis*', *Journal of Preventive Medicine*, **6**: 17–29.

Mirmovitch, V. (1995) 'Spatial Organisation of Urban Feral Cats (*Felis catus*) in Jerusalem', *Wildlife Research*, **22**: 299–310.

Morris, J. G., Rogers, Q. R., and Pacioretty, L. M. (1990) 'Taurine: An Essential Nutrient for Cats', *Journal of Small Animal Practice*, **31**: 502–9.

Mugford, R. A., and Thorne, C. J. (1980) 'Comparative Studies of Meal Patterns in Pet and Laboratory Housed Dogs and Cats', in R. S. Anderson (ed.) *Nutrition of the Dog and Cat*, pp. 3–14. Oxford, UK: Pergamon Press.

Murphy, B. P. et al. (2019) 'Introduced Cats (*Felis catus*) Eating a Continental Fauna: The Number of Mammals Killed in Australia', *Biological Conservation*, **237**: 28–40.

National Research Council. (1986) *Nutrient Requirements of Cats in 'Nutrient Requirements of Domestic Animals Revised Edition*. Washington DC, USA: National Academy Press.

Natoli, E. et al. (1999) 'Relationships between Cat Lovers and Feral Cats in Rome', *Anthrozoös*, **12**: 16–23.

—— et al. (2006) 'Management of Feral Domestic Cats in the Urban Environment of Rome (Italy)', *Preventive Veterinary Medicine*, **77**: 180–5.

—— et al. (2005) 'Bold Attitude Makes Male Urban Feral Domestic Cats More Vulnerable to Feline Immunodeficiency Virus', *Neuroscience & Biobehavioral Reviews*, **29**: 151–7.

NHMRC. (2013) *Australian Code for the Care and Use of Animals for Scientific Purposes*. Australian Government, Canberra, Australia: National Health and Medical Research Council.

Nichol, S., Ball, S. J., and Snow, K. R. (1981) 'Prevalence of Intestinal Parasites in Feral Cats in Some Urban Areas of England', *Veterinary Parasitology*, **9**: 107–10.

Nutter, F. B., Levine, J. F., and Stoskopf, M. K. (2004) 'Reproductive Capacity of Free-Roaming Domestic Cats and Kitten Survival Rate', *Journal of the American Veterinary Medical Association*, **225**: 1399–402.

Papazoglou, L. G., Patsikas, M. N., and Rallis, T. (2003) 'Intestinal Foreign Bodies in Dogs and Cats', *Compendium on Continuing Education for the Practising Veterinarian - North American Edition*, **25**: 831–44.

Pedersen, N. C. (1988) *Feline Infectious Diseases*. California, USA: American Veterinary Publications, Inc.

Pulliainen, E., Lindgren, E., and Tunkkari, P. S. (1995) 'Influence of Food Availability and Reproductive Status on the Diet and Body Condition of the European Lynx in Finland', *Acta Theriologica*, **40**: 181–96.

Read, J. L. (2019) *Among the Pigeons: Why Our Cats Belong Indoors*. Mile End, Australia: Wakefield Press.

Robertson, S. A. (2008) 'A Review of Feral Cat Control', *Journal of Feline Medicine and Surgery*, **10**: 366–75.

Rohde, K. (1994) 'Niche Restriction in Parasites: Proximate and Ultimate Causes', *Parasitology*, **109**: S69–S84.

Root Kustritz, M. V. (2009) *Clinical Canine and Feline Reproduction: Evidence-Based Answers*. Iowa, USA: Wiley & Blackwell.

RSPCA. (2017) Australia National Statistics 2016–2017. Australia: Royal Society for the Prevention of Cruelty to Animals.

Salman, D. et al. (2018) 'Prevalence of *Toxoplasma gondii* and Other Intestinal Parasites in Cats in Tokachi Sub-Prefecture, Japan', *Journal of Veterinary Medical Science*, **80**: 960–7.

Scarlett, J., and Johnston, N. (2012) 'Impact of a Subsidized Spay Neuter Clinic on Impoundments and Euthanasia in a Community Shelter and on Service and Complaint Calls to Animal Control', *Journal of Applied Animal Welfare Science*, **15**: 53–69.

Schulte-Hostedde, A. I. et al. (2005) 'Restitution of Mass-Size Residuals: Validating Body Condition Indices', *Ecology*, **86**: 155–63.

Serrano, E., and Millãn, J. (2014) 'What is the Price of Neglecting Parasite Groups When Assessing the Cost of Co-infection?' *Epidemiology and Infection*, **142**: 1533–40.

Simpson, K., and Day, N. (2010) *Field Guide to the Birds of Australia*, 8th ed. Hawthorn, Australia: Penguin Books.

Sommerfelt, I. E. et al. (2006) 'Prevalence of *Toxocara Cati* and Other Parasites in Cats' Faeces Collected from the Open Spaces of Public Institutions: Buenos Aires, Argentina', *Veterinary Parasitology*, **140**: 296–301.

Spotte, S. (2014) *Free-Ranging Cats*. Chichester, UK: John Wiley & Sons, Ltd.

Stanek, J. F. et al. (2003) 'Epidemiology of *Sarcocystis neurona* Infections in Domestic Cats (*Felis domesticus*) and Its Association with Equine Protozoal Myeloencephalitis (EPM) Case Farms and Feral Cats from a Mobile Spay and Neuter Clinic', *Veterinary Parasitology*, **117**: 239–49.

StatSoft Inc. (2007) STATISTICA (data analysis software system), version 8.0. Tulsa, USA. <http://www.statsoft.com/Products/STATISTICA-Features> accessed 5 January 2020.

Swarbrick, H., and Rand, J. (2018) 'Application of a Protocol Based on Trap-Neuter-Return (TNR) to Manage Unowned Urban Cats on an Australian University Campus', *Animals*, **8**: 77.

Szwabe, K., and Błaszkowska, J. (2017) 'Stray Dogs and Cats as Potential Sources of Soil Contamination with Zoonotic Parasites', *Annals of Agricultural and Environmental Medicine*, **24**: 39–43.

Taylor, M. A., Coop, R. L., and Wall, R. L., eds (2015) Parasites of Dogs and Cats, 4th edn., Chapter 12. in *Veterinary Parasitology*, pp. 599–677. Hoboken, USA: Wiley Blackwell.

Toribio, J.-A. L. M. et al. (2009) 'Demographics and Husbandry of Pet Cats Living in Sydney, Australia: Results of Cross-Sectional Survey of Pet Ownership', *Journal of Feline Medicine and Surgery*, **11**: 449–61.

Travaglia, M., and Miller, K. K. (2018) 'Cats in the Australian Environment: What's Your Purr-Spective?' *Australasian Journal of Environmental Management*, **25**: 153–73.

Travouillon, K. J., and Phillips, M. J. (2018) 'Total Evidence Analysis of the Phylogenetic Relationships of Bandicoots and Bilbies (Marsupialia: Peramelemorphia): Reassessment of Two Species and Description of a New Species', *Zootaxa*, **4378**: 224–56.

Turner, D. C., and Bateson, P. (eds) (2000) *The Domestic Cat: The Biology of its Behaviour*, 2nd edn. Cambridge, UK: Cambridge University Press.

Uetake, K. et al. (2014) 'A Survey of Attitudes of Local Citizens of a Residential Area toward Urban Stray Cats in Japan', *Journal of Applied Animal Welfare Science*, **17**: 172–7.

Vitale Shreve, K. R., and Udell, M. A. R. (2017) 'Stress, Security, and Scent: The Influence of Chemical Signals on the Social Lives of Domestic Cats and Implications for Applied Settings', *Applied Animal Behaviour Science*, **187**: 69–76.

Vnuk, D. et al. (2016) 'Metal Projectile Injuries in Cats: Review of 65 Cases (2012–2014)', *Journal of Feline Medicine and Surgery*, **18**: 626–31.

Waap, H., Gomes, J., and Nunes, T. (2014) 'Parasite Communities in Stray Cat Populations from Lisbon, Portugal', *Journal of Helminthology*, **88**: 389–95.

Warner, R. E. (1985) 'Demography and Movements of Free-Ranging Domestic Cats in Rural Illinois', *The Journal of Wildlife Management*, **49**: 340–6.

Weary, D. M., and Robbins, J. A. (2019) 'Understanding the Multiple Conceptions of Animal Welfare', *Animal Welfare*, **28**: 33–40.

Wilson, P. M., Tidemann, C. R., and Meischke, H. R. C. (1994) '*Are Cats on Rubbish Dumps a Problem? Sydney, New South Wales*', in D. W. Paxton (ed.) *Urban Animal Management Conference Proceedings*, pp. 163–74. Sydney, Australia: Australian Veterinary Association.

Woinarski, J. C., Legge, S. M., and Dickman, C. R. (2019) *Cats in Australia: Companion and Killer*. Clayton South, Australia: CSIRO Publishing.

Woinarski, J. C. Z., Burbidge, A. A., and Harrison, P. L. (2014) *The Action Plan for Australian Mammals 2012*. Collingwood, Victoria: CSIRO Publishing.

Wyse, C. A. et al. (2003) 'A Review of Methods for Assessment of the Rate of Gastric Emptying in the Dog and Cat: 1898–2002', *Journal of Veterinary Internal Medicine*, **17**: 609–21.

Yamaguchi, N. et al. (2015) *Felis silvestris,* Wild Cat: The International Union for Conservation of Nature Red List of Threatened Species 2015: e. T60354712A50652361, p. 17.