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Dietary niche overlap of free-roaming dingoes and domestic dogs: the role of human-provided food

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As both companion animals and opportunistic predators, dogs (*Canis lupus* spp.) have had a long and complex relationship with humans. In Australia, the dingo (*C. l. dingo*) was introduced 4,000 years ago and, other than humans, is now the continent's top mammalian predator. Domestic dogs (*C. l. familiaris*) were introduced by Europeans more recently and they interbreed with dingoes. This hybridization has caused growing concern about the roles that domestic dogs and dingoes play in shaping ecosystem processes. There is also considerable debate about whether anthropogenic environmental changes can alter the ecological roles of dingoes. We used scat analysis to test whether the dingo, as the longer-established predator, occupies a different dietary niche from that of free-roaming domestic dogs, irrespective of human influence. Our results demonstrate considerable dietary overlap between dingoes and domestic dogs in areas where humans provide supplementary food, providing evidence against our hypothesis. However, the consumption by dingoes of a greater diversity of prey, in association with historical differences in the interactions between dingoes and humans, suggests a partial separation of their dietary niche from that of domestic dogs. We conclude that anthropogenic changes in resource availability could prevent dingoes from fulfilling their trophic regulatory or pre-European roles. Effective management of human-provided food is therefore required urgently to minimize the potential for subsidized populations of dingoes and domestic dogs to negatively affect co-occurring prey.

Key words: diet, dietary breadth, human subsidies, top-order predator

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Dogs (*Canis lupus* spp.) are the world's most common domesticated carnivores (Wandeler et al. 1993). They can be split into 2 broad categories, dogs that are both owned and confined to areas of human habitation, and those that are free roaming. Under some circumstances, free-roaming dogs can play an important role in maintaining and structuring ecological communities (Vanak and Gompper 2009b; Ritchie et al., 2014). However, they also interact with humans and with the water and food resources that people either purposely or inadvertently provide for them. Consequently, free-roaming dogs constitute a regular source of conflict with humans because of their negative effects on people and their enterprises. For example, free-roaming dogs depredate live-stock, damage infrastructure, and spread disease (Young et al. 2011). These conflicts have led to various levels of anthropogenic control throughout the ranges of some canid

subspecies (Sillero-Zubiri and Switzer 2004; Baker et al. 2008). Yet, the impacts of dogs on natural environments in some countries have not been well documented and we know little about the nature of interactions between free-roaming dogs and sympatric wildlife (Hughes and Macdonald 2013).

A detailed knowledge of dietary preferences is required to determine the nature of relationships between free-roaming dogs and co-occurring prey. An understanding of the factors that could influence prey selection or, more broadly, food webs is also required. For example, as the largest predators in many systems, dogs can potentially exert strong top-down effects on prey (Caughley et al. 1980; Vanak and Gompper 2009b) and



indirect effects on vegetation where their main prey is herbivorous (Wallach et al. 2010). However, these trophic interactions can be altered in ecosystems where there are external influences such as those resulting from anthropogenic change (Gompper and Vanak 2008). Additionally, dogs have been introduced wherever humans have settled (Wandeler et al. 1993; Butler 2004). These colonizing dogs are often invasive aliens that could potentially disrupt and modify indigenous ecosystems through impacts on prey. Consequently, it is critical to assess the ecological impacts of both native and introduced dogs in areas where they co-occur.

On the mainland of Australia, 2 dog subspecies, the dingo (*C. l. dingo*) and the domestic dog (*C. l. familiaris*) have been introduced by humans (Fleming et al. 2001). The dingo originated from domesticated dogs in east Asia and was introduced at least 4,000 years ago (Oskarsson et al. 2011; Sacks et al. 2013). It now occupies every terrestrial habitat on the Australian mainland (Allen and West 2013). Domestic dogs were introduced more recently, arriving since 1788. Dispersal of domestic dogs into the wild (by deliberate introduction and accidental releases) has been continuing since then (Fleming et al. 2001). Dingoes and domestic dogs now interbreed and hybrids are common (Stephens 2011; Newsome et al. 2013c). This has created a dilemma for land managers and policy makers because hybrids are extremely difficult to distinguish in the field (Elledge et al. 2008; Newsome et al. 2013c).

There is also considerable debate about whether free-roaming domestic dogs and dingo–dog hybrids can occupy the same ecological niches as dingoes (Claridge and Hunt 2008; Purcell 2010), and whether anthropogenic environmental changes have altered the roles of dingoes from their pre-European functions (Fleming et al. 2012). This debate is important to resolve because, other than humans, the dingo is the top mammalian predator in Australia and is considered by many to be a potential trophic regulator (Ritchie and Johnson 2009; Letnic et al. 2012). For example, trophic regulation by dingoes could provide positive benefits to some native species (Dickman et al. 2009), particularly if dingoes suppress smaller introduced predators such as the European red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) that depress populations of many small native prey species (Letnic et al. 2012; Ritchie et al. 2012). To determine the potential for dingoes and dingo–domestic dog hybrids to provide positive ecosystem benefits (see Claridge and Hunt 2008; Allen and Fleming 2012; Fleming et al. 2012), it is therefore critical to assess the factors that could influence their behaviors and functions. Specifically, with respect to anthropogenic environmental change, there is very little known about the diets of free-roaming domestic dogs and dingoes in areas where they co-occur with humans.

In this study, we collected fecal samples to compare the diets of free-roaming dingoes and domestic dogs in the Tanami Desert of central Australia. In this remote arid region, dingo populations containing very few hybrids occur around a pastoral station and mine sites, whereas free-roaming domestic dogs occur around the few human settlements and contain few dingo genes (Newsome et al. 2013b, 2013c). In both areas,

humans provide supplementary water and food ad libitum in the form of refuse, thus allowing a comparison of diets of these canids under similar environmental conditions. There are also extensive regions where dingoes occur away from human-provided sources of food, providing baseline dietary data under more natural circumstances. Therefore, we compared the diets of dingoes, at and away from areas of human influence, with the diets of domestic dogs at areas of human influence. We tested the hypothesis that the dingo, as the longer-established predator, occupies a different dietary niche from that of free-roaming domestic dogs, irrespective of human influence. That is, with access to anthropogenic food sources, the diet of free-roaming dingoes has less anthropogenic food and more wild prey than free-roaming domestic dogs. We use the results to assess whether humans influence food-web interactions in remote regions and to discuss what potential impacts, if any, dingoes and free-roaming domestic dogs might have on co-occurring prey.

MATERIALS AND METHODS

Distribution of study animals.—Our study was conducted in the northwestern portion of the Tanami Desert (130°18'E, 20°30'S; Fig. 1). This region contains human settlements at Yuendumu (the “community” site) and Mt. Theo (the “outstation” site). Domestic dogs are kept as pets in these 2 sites, although most are free roaming (Newsome et al. 2013c). Located 240 km to the northwest of the community and outstation are gold-mining (The Granites and Dead Bullock Soak [DBS]) and cattle-ranching (Tanami Downs) operations (the “mine” and “pastoral” sites, respectively). Free-roaming dingoes and relatively rare dingo–dog hybrids occur there (Newsome et al. 2013c). In addition to these sites, dingoes occur far from any human settlement or activity in vast areas of the Tanami away from the mines; these landscapes comprise our “desert” sites. The study populations of dingoes and domestic dogs in the Tanami region are likely independent because geographic separation greatly exceeds known home-range sizes (Newsome et al. 2013b).

Distribution of food sources.—At the time of this study, the main sources of human-provided food for domestic dogs around the community and outstation were food scraps, either those in waste facilities or carcasses of animals (mainly *Macropus* spp.) that were hunted and eaten by members of the mostly Aboriginal communities. Also available at the community and outstation, as live prey or carrion, were feral cattle (*Bos* spp.), horses (*Equus caballus*), and camels (*Camelus dromedarius*). In the mine site, the main source of human-provided food was scraps from a commercial kitchen at one site, The Granites. To a lesser extent, food scraps from packed meals also were available at a smaller waste facility at DBS. Cattle, horses, camels, and small quantities of food scraps from a domestic kitchen were available as food for dingoes at Tanami Downs, 50 km farther west of DBS. In addition to the human-provided food, multiple studies over the past 25 years in the Tanami region have identified a variety of

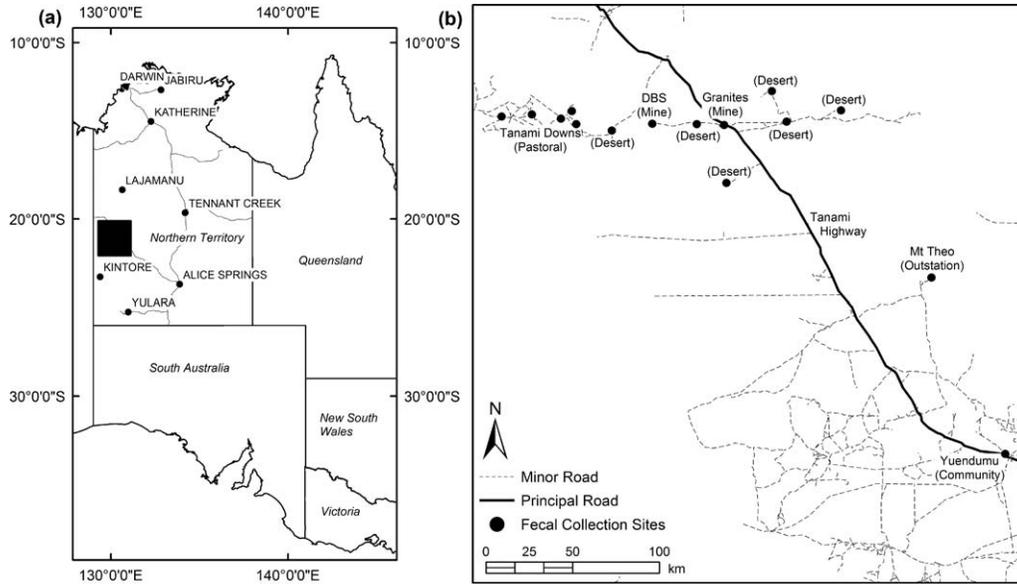


FIG. 1.—Map of Australia showing a) the Tanami Desert (black box) and b) locations where sampling of dingoes (*Canis lupus dingo*; desert, mine, pastoral) and domestic dogs (*C. l. familiaris*; community and outstation) was undertaken in November 2009.

natural prey items that are potentially available to free-roaming dingoes and other dogs (Gibson 1986; Paltridge 2002; Newsome 2011).

Feces collection protocol.—To determine the diets of free-roaming domestic dogs in sites where human-provided food existed, we collected dog feces at the community and outstation from roadsides and waste facilities. To determine the diets of dingoes in sites with human-provided food, we collected feces around the 2 waste facilities in the mine areas (DBS and The Granites) and from roadsides and waterpoints within the bounds of the adjacent pastoral station (Tanami Downs). To determine the diet of dingoes away from sources of human-provided food, we collected feces from roadsides and waterpoints at 7 other remote sites in the desert area. That dingoes in these areas were unlikely to access the refuse tips was confirmed by concurrent global positioning system collar studies (Newsome et al. 2013b).

All feces were collected at one time, in November 2009, to ensure that seasonal differences in natural prey availability did not bias the results (Allen 2012a). Due to the generally high rate of fecal deposition over small areas, it was possible to completely clear the collection sites to exclude feces of uncertain age and still obtain good sample sizes. This clearing was completed in August 2009, thus allowing 4 months for new feces to be deposited. This process was not undertaken at the community or outstation, so samples collected from these sites that were decomposed or not intact were judged to be old and were discarded.

The collection of domestic dog feces in sites surrounding the community and outstation would have been optimal because free-roaming domestic dogs can move relatively long distances from home (8–30 km—Meek 1999). However, as we saw free-roaming dingo-like animals approximately 3–5 km from the community and outstation, it would have been impossible to

distinguish whether the feces we collected had been deposited by domestic dogs, dingoes, or hybrids owing to similarities in the shape and size of domestic dog and dingo feces. Therefore, for surety, data for free-roaming domestic dogs were restricted to the human settlements where these dogs occur exclusively and where their activity is predominantly focused.

Identification of ingesta.—Before processing, all feces were oven dried at 100°C for at least 6 h in paper bags to kill parasites. Feces were then washed in nylon fabric bags, retaining the hard fragments of bones, hairs, and rubbish. They were then dried in the sun. Dried remnants were placed on a sorting tray with quarter divisions, with 1 quarter split into 5% divisions to allow for visual sorting.

Collections of bones and hairs and other publicly available materials were used for reference in the identification process (e.g., Brunner and Coman 1974). When material could not be identified to species level, it was classified and grouped more broadly or placed into the category “unknown.”

Because the human-provided food was mostly processed and typically lacked diagnostic bones or hairs, individual identification of anthropogenic food items in feces was rarely possible. However, when items of plastic wrapping, foil, glass, and/or paper (and other rubbish) were present consistently in feces, we took this to be a reliable indication that human-derived food had been consumed.

Data analyses.—Several analytical methods have been used to assess data on the diet of dingoes on the basis of feces, with the most widely adopted being frequency of occurrence (Newsome et al. 1983; Corbett and Newsome 1987; Corbett 1989, 1995; Thomson 1992; Paltridge 2002). To facilitate comparison between studies, we therefore calculated frequency of occurrence, defined as the proportion of feces in which a particular food group category occurred, for individual prey species. Because frequency of occurrence can overemphasize

the importance of small prey types (Corbett 1989; Klare et al. 2011), we also calculated the percentage of relative occurrence, defined as the proportion of each food-group category in all samples.

To test our hypothesis, dietary data first were assembled into the 5 different sites of the Tanami (mine, pastoral, community, outstation, and desert) and then analyzed and compared using several different methods. To estimate the diversity of prey consumed in each site, we calculated Brillouin's index (Brillouin 1956) using the following equation:

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

where H is dietary diversity, N is the number of individual prey recorded, and n_i is the number of individual prey items in the i th category. After randomizing the order of samples, we plotted dietary diversity against sample size to determine whether the curves reached an asymptote, indicating that sample size was adequate to describe the diet in each site. We then calculated an index of dietary overlap for all pair-wise combinations of sites using Pianka's index (Pianka 1973):

$$O = \frac{\sum P_{ij}P_{ik}}{\sqrt{\sum P_{ij}^2 \sum P_{ik}^2}},$$

where O is dietary overlap, j and k are the subspecies (dingo and domestic dog) being compared, and P_i is the frequency of occurrence of the i th food type. Dietary overlap values range from 0 (no overlap) to 1 (complete overlap).

For more detailed analyses, we grouped prey items into broad prey categories on the basis of taxonomic association. The prey categories used were mammals, birds, reptiles, amphibians, invertebrates, vegetation, and rubbish (Appendix I). Then, to compare the overall composition of the diet of dingoes and domestic dogs between sites we used PRIMER v 5 (Clarke and Gorley 2001). First, we compared presence-absence data for the prey categories using nonmetric multidimensional scaling based on a Bray-Curtis dissimilarity matrix. Second, we used analysis of similarities to determine if the diets of dingoes and domestic dogs differed significantly between sites ($P < 0.05$). Third, we used SIMPER to determine which prey categories contributed to significant differences observed between site combinations (Clarke 1993). To explore the trends further, and to graphically display them, we used redundancy analysis (RDA). This technique is useful for analyzing directional relationships within multivariate data (Lambert et al. 1988; Takane and Hwang 2005) and for determining which species groups contribute to observed dietary patterns.

RESULTS

General diet trends.—Sixty-four different food categories were identified from 780 fecal samples collected from the 5 study site categories: community, outstation, mines, pastoral,

and desert (Appendix I). Dietary diversity estimates for all sites reached asymptotes (Fig. 2), indicating that our sample sizes were adequate to describe the diet of canids in each site. Only 9 (14%) individual food categories were common to all 5 sites, but 41 (64%) were common to the diets of dingoes and domestic dogs (Appendix I). On the basis of the frequency of occurrence data, mammals, vegetation, and rubbish were identified most commonly in domestic dog feces at the outstation and community. Wild prey, mostly large mammals (> 1 kg) and birds, were also identified in feces from these 2 sites. Similar results were obtained for dingo feces collected at the mine site, where mammals and rubbish were frequently identified. In contrast, reptiles (followed by invertebrates and mammals) were most commonly identified in dingo feces in the desert site. In the pastoral site, mammals (primarily cattle) formed the majority of prey items identified in dingo feces.

Dietary overlap.—Dietary overlap between dingoes and domestic dogs was evident in the results of the nonmetric multidimensional scaling analysis, with samples from all sites overlapping in ordination space (Fig. 3). However, there were significant differences in canid dietary composition between all sites (global $R = 0.14$, $P = 0.001$), although there were no significant differences between combinations of the outstation/community sites, compared with mine sites, where anthropogenic food availability was greatest (Table 1). Hence, the diet of dingoes at the mine was similar to that of domestic dogs at the community and outstation, but not similar to dingoes in the pastoral or desert sites. The high degree of dietary overlap between domestic dogs and dingoes was also reflected in Pianka's index (Table 2), with high values (> 0.5) recorded for the outstation, mine, and community site combinations. However, dietary overlap between domestic dogs at the community and dingoes at the pastoral station was also relatively high (Table 2).

Contribution of prey groups to trends.—The relatively high occurrence of rubbish in dingo feces in the mine site was the primary cause of dissimilarity in diet between that site and the other dingo sites (pastoral and desert; Table 3). Similarly, the relatively high occurrence of rubbish in domestic dog feces in the community site was the primary driver of dietary dissimilarity between animals there and at the outstation. More important, though, it was the occurrence of mammals in the diets of dingoes and domestic dogs that contributed equally to dietary dissimilarities between other site combinations. For example, there was a higher occurrence of mammals (primarily cattle) in the diet of dingoes at the pastoral station in comparison with all other sites. The RDA confirms these associations (Fig. 4), and also highlights the importance of reptiles and invertebrates in the diet of dingoes in areas away from human-provided sources of food.

DISCUSSION

Our results demonstrate considerable dietary overlap between dingoes and domestic dogs (Fig. 3; Table 2). They

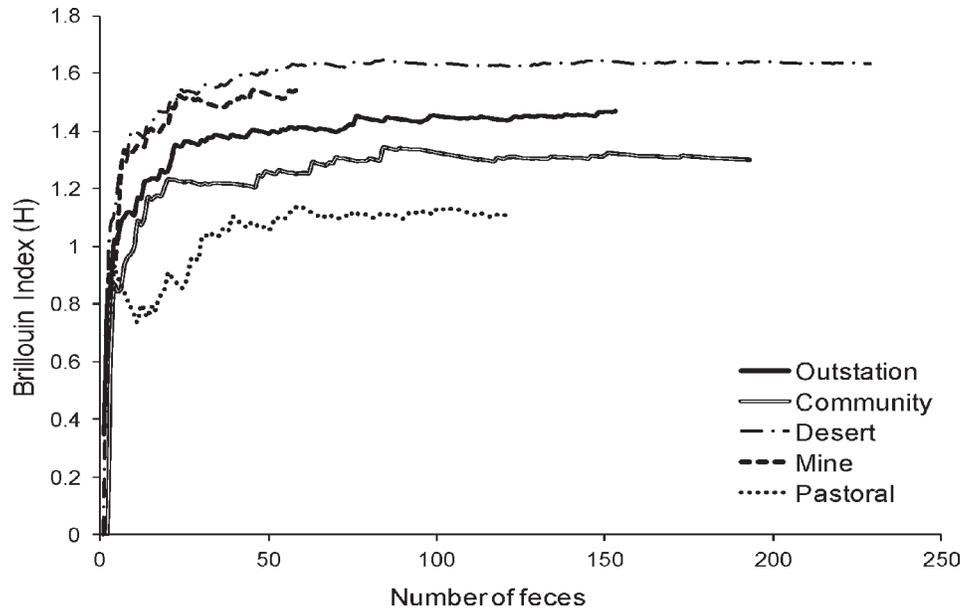


FIG. 2.—Cumulative dietary diversity indicated by the Brillouin index (H) based on analysis of fecal samples of dingoes (*Canis lupus dingo*; desert, mine, pastoral) and domestic dogs (*C. l. familiaris*; outstation and community) in the Tanami Desert, central Australia. In all cases, sufficient sample size was reached (at asymptote) before right censure of feces collection.

also confirm that dingoes and free-roaming domestic dogs are effective scavengers that can readily take advantage of human-provided food, especially waste (Appendix I). As such, our results suggest that there is considerable potential for humans to influence the diets of both taxa. The high overlap in the diet of dingoes at the mine with that of domestic dogs at the community and outstation (Table 1) provides evidence against our null hypothesis, that the dingo occupies a different dietary

niche from free-roaming domestic dogs, irrespective of human influence. However, our data also demonstrate several key distinctions in the diets of dingoes and free-roaming domestic dogs that partially separate their ecological niches (Appendix I). This separation has important implications when considering dingoes as trophic regulators and in determining whether or not anthropogenic changes have altered their roles from pre-European times, as suggested by Fleming et al. (2012).

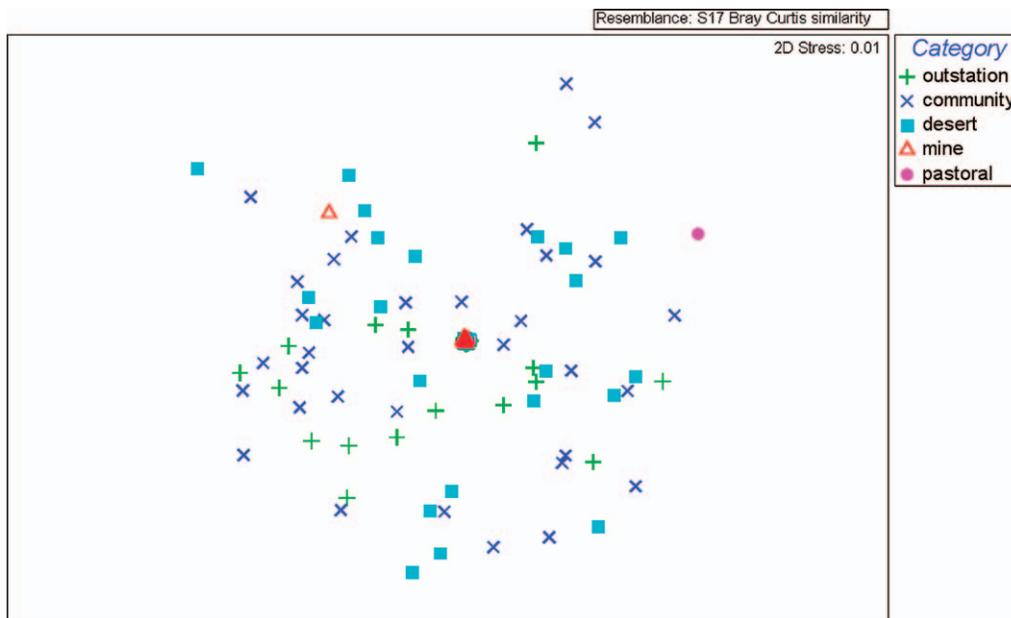


FIG. 3.—Multidimensional scaling plot comparing the diets of dingoes (*Canis lupus dingo*; desert, mine, pastoral) and domestic dogs (*C. l. familiaris*; outstation and community) in the Tanami Desert, central Australia. Each point represents 1 fecal sample. Relative dissimilarity between the prey types identified in the samples is based on the distance between any 2 points.

Table 1.—Analysis of similarities showing the difference in diet (R) between each site combination in the Tanami Desert, central Australia. Dingoes (*Canis lupus dingo*) were present in the desert, mine, and pastoral areas, and domestic dogs (*C. l. familiaris*) at the community and outstation areas.

Site category	R	P
Outstation, community	0.01	0.04
Outstation, mine	0.03	0.15
Community, mine	0.04	0.13
Community, pastoral	0.06	0.003
Outstation, pastoral	0.11	0.001
Desert, pastoral	0.11	0.001
Outstation, desert	0.19	0.001
Community, desert	0.22	0.001
Desert, mine	0.24	0.001
Mine, pastoral	0.64	0.001

Around the mine sites, the primary source of food in the diet of dingoes was human-provided rubbish (relative occurrence of 55%). This was higher than for domestic dogs at the community (38%) and outstation (29%; Appendix I). However, there was still a high degree of overlap in diet of dingoes and domestic dogs between the 3 sites (Table 2). There were also no significant differences in the overall diets of domestic dogs at the outstation and community compared with dingoes at the mine (Table 1). This high use of human food waste is consistent with dietary studies on canids elsewhere. For example, Butler and du Toit (2002) and Vanak and Gompper (2009a) found that human-derived foods contributed 88% and 83% of the diet of free-roaming domestic dogs in Zimbabwe and India, respectively. In both cases, this was due to inappropriate forms of waste disposal by humans that made food readily available to dogs.

Inadequate waste disposal methods were also evident in our study. At the community and outstation, surplus food was often accessible to dogs within household perimeters. The remains of animals that were killed for food by humans, including domestic stock and native wildlife, were also left in situ, providing easily accessible food for free-roaming dogs. Similarly, around the mines, large quantities of leftover food from a commercial kitchen were accessible by dingoes (Newsome 2011). It is therefore unsurprising that food waste formed the majority of the food ingested by dingoes and domestic dogs in sites where this resource existed (Appendix I). However, there were some minor differences in the occurrence of wild prey consumed by dingoes and domestic dogs between sites, even when animals had access to human-derived sources of food. This was reflected in the comparison of dietary diversity, which was higher for dingoes around the mines in comparison with dogs in the community and outstation sites (Fig. 2).

Interpretation of our data would be greatly assisted by estimates of prey availability, a longer collection period for fecal samples, and experimental manipulation of the amount of human-derived food that was available to the canids. For example, prey availability and minor changes in habitat quality between sites (which were disparate) could influence the diet of

Table 2.—Pianka's index showing pair-wise comparisons of dietary overlap (O) between each site combination (Table 1) in the Tanami Desert, central Australia. Dingoes (*Canis lupus dingo*) were present in the desert, mine, and pastoral areas, and domestic dogs (*C. l. familiaris*) at the community and outstation areas. Bold values (> 0.5) reflect greater overlap.

Site category	O
Mine, pastoral	0.17
Desert, pastoral	0.23
Community, desert	0.24
Outstation, pastoral	0.26
Outstation, desert	0.39
Desert, mine	0.41
Community, mine	0.55
Community, pastoral	0.58
Outstation, mine	0.60
Outstation, community	0.76

dingoes and domestic dogs. However, according to the data, dingoes in the mine site consumed slightly higher numbers of rodents (6% relative occurrence) and reptiles (4%) than domestic dogs in the community (0.46% and 0.45%, respectively) and outstation (0.3% and 0.6%, respectively; Appendix I). Hence, free-roaming domestic dogs around towns did not consume some wild prey as frequently as free-roaming dingoes around the mine, despite both having access to human-provided food resources. In contrast, wild prey (mainly reptiles, 31% relative occurrence) formed the majority of prey items for desert dingoes away from the mine site where there was no human-provided food (Appendix I). Cattle (46% relative occurrence) dominated the diet of dingoes in the pastoral site, but it is not known if cattle were hunted and killed or consumed as carrion (Allen 2010).

In addition to any potential (unknown) differences in prey availability, there are several possibilities that could account for the observed differences in wild prey consumed by dingoes and domestic dogs. Most important, there are historical and cultural reasons to expect a difference. First, the dingo has been present on the mainland of Australia for at least 4,000 years (Oskarsson et al. 2011; Sacks et al. 2013). Second, the dingo became feral after its arrival in Australia, because indigenous Australians had pseudonadic lifestyles that made full domestication of the dingo difficult (Smith and Litchfield 2009). In contrast, domestic dogs have had a close relationship with humans for over 15,000 years (Hughes and Macdonald 2013), and in our study, although they were free roaming, domestic dogs still lived in close association with humans. These differences would undoubtedly influence the hunting abilities or efficiencies of these 2 canids. Domestic dogs have little need to hunt and are efficient scavengers (Meek 1999; Butler and du Toit 2002; Butler 2004; Hughes and Macdonald 2013). Dingoes, on the other hand, hunt alone and in groups (Newsome et al. 1983). They also change the size of prey they consume in relation to prey availability (Corbett and Newsome 1987), and have managed to adapt and thrive in most habitats in Australia (Fleming et al. 2001).

Table 3.—SIMPÉR results showing the average dissimilarity (Av diss), average abundance (Av ab), percentage contribution to the overall dissimilarity (% cont), and cumulative percentage (Cum %) for each site combination (Table 1) of dietary comparisons of dingoes (*Canis lupus dingo*) and domestic dogs (*C. l. familiaris*) in the Tanami Desert, central Australia. Dingoes were present in the desert, mine, and pastoral areas, and domestic dogs at the community and outstation areas.

Site category	Av diss	Food category av	Av ab species 1	Av ab species 2	Av diss	% cont	Cum %
Outstation, community (1 and 2 = domestic dog)	71.72	Rubbish	0.61	0.87	26.26	36.61	36.61
		Mammal	0.57	0.64	21.32	29.73	66.34
		Vegetation	0.24	0.22	10.49	14.63	80.97
		Bird	0.22	0.06	7.47	10.41	91.38
Outstation, mine (1 = domestic dog, 2 = dingo)	73.97	Rubbish	0.61	2.15	33.64	45.48	45.48
		Mammal	0.57	0.56	12.92	17.47	62.95
		Vegetation	0.24	0.51	10.42	14.08	77.04
		Bird	0.22	0.29	7.93	10.72	87.76
		Invertebrate	0.18	0.25	6.29	8.5	96.29
Community, mine (1 = domestic dog, 2 = dingo)	73.13	Rubbish	0.87	2.15	34.86	47.67	47.67
		Mammal	0.64	0.56	13.83	18.91	66.59
		Vegetation	0.22	0.51	10.54	14.41	80.99
		Bird	0.06	0.29	6.07	8.29	89.29
		Invertebrate	0.08	0.25	5.09	6.96	96.24
Community, pastoral (1 = domestic dog, 2 = dingo)	62.67	Mammal	0.64	1.11	23.62	37.69	37.69
		Rubbish	0.87	0.02	17.69	28.22	65.91
		Vegetation	0.22	0.16	8.37	13.35	79.27
		Invertebrate	0.08	0.21	6.1	9.73	88.99
		Reptile	0.01	0.19	4.63	7.38	96.38
Outstation, pastoral (1 = domestic dog, 2 = dingo)	63.78	Mammal	0.57	1.11	21.32	33.42	33.42
		Rubbish	0.61	0.02	14.33	22.47	55.89
		Vegetation	0.24	0.16	8.83	13.85	69.74
		Invertebrate	0.18	0.21	7.83	12.28	82.02
		Bird	0.22	0.04	6.87	10.76	92.78
Desert, pastoral (1 and 2 = dingo)	67.44	Mammal	0.61	1.11	18.56	27.52	27.52
		Reptile	1.00	0.19	17.18	25.47	52.99
		Invertebrate	0.88	0.21	14.92	22.13	75.12
		Vegetation	0.42	0.16	8.95	13.26	88.38
		Bird	0.17	0.04	4.47	6.62	95
Outstation, desert (1 = domestic dog, 2 = dingo)	79.70	Reptile	0.01	1.00	16.8	21.08	21.08
		Mammal	0.57	0.61	16.11	20.21	41.29
		Invert	0.18	0.88	15.19	19.06	60.35
		Rubbish	0.61	0.15	13.56	17.02	77.36
		Vegetation	0.24	0.42	10.16	12.75	90.11
Community, desert (1 = domestic dog, 2 = dingo)	81.03	Mammal	0.64	0.61	17.55	21.66	21.66
		Reptile	0.01	1.00	17.24	21.28	42.94
		Rubbish	0.87	0.15	16.56	20.43	63.37
		Invertebrate	0.08	0.88	14.63	18.05	81.42
		Vegetation	0.22	0.42	10.09	12.45	93.87
Desert, mine (1 and 2 = dingo)	80.77	Rubbish	0.15	2.15	28.96	35.85	35.85
		Reptile	1.00	0.15	12.86	15.92	51.77
		Invertebrate	0.88	0.25	11.67	14.44	66.21
		Mammal	0.61	0.56	11.33	14.03	80.24
		Vegetation	0.42	0.51	9.77	12.1	92.34
Mine, pastoral (1 and 2 = dingo)	75.30	Rubbish	2.15	0.02	33.87	44.99	44.99
		Mammal	0.56	1.11	14.27	18.95	63.94
		Vegetation	0.51	0.16	9.82	13.05	76.99
		Invertebrate	0.25	0.21	6.57	8.73	85.71
		Bird	0.29	0.04	5.8	7.7	93.41

Dingoes are also the largest predator on mainland Australia and a potential regulator of fauna at lower trophic levels (Letnic et al. 2012). Thus, when humans directly or indirectly alter the availability of food resources, predator–predator and predator–prey interactions can be altered to the point where prey populations can be negatively affected through hyperpredation (Courchamp et al. 2000; Gompper and Vanak 2008; Allen and Leung 2012), especially when prey numbers are

limited (Vanak and Gompper 2009b). For example, subsidized dog populations were shown to influence kid/female ratios in a declining mountain gazelle (*Gazella gazella gazella*) population (Manor and Saltz 2004), and to shape the landscape-scale distribution of southern puda (*Pudu puda*), a threatened forest ungulate (Silva-Rodríguez and Sieving 2012). In the Tanami Desert, relatively high densities of dingoes occur locally as a result of human-resource subsidies (Newsome et al. 2013c); the

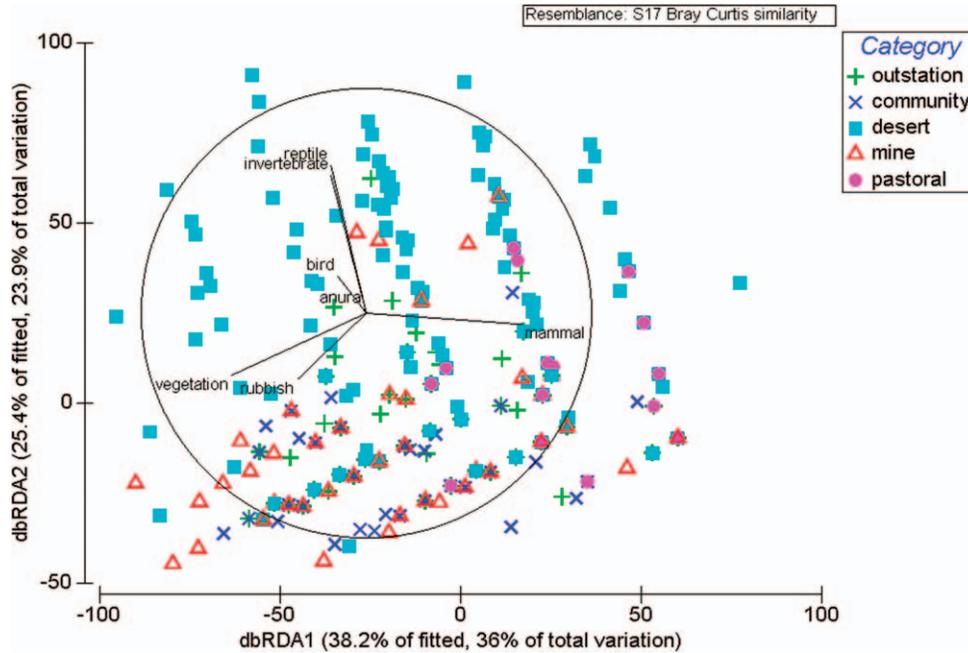


FIG. 4.—Redundancy analysis (RDA) using the weighted averages of occurrence of prey species groups in dingo (*Canis lupus dingo*; desert, mine, pastoral) and domestic dog (*C. l. familiaris*; outstation and community) feces in the Tanami Desert, central Australia.

supplementary food has further effects on resource selection, activity, and social structuring (Newsome et al. 2013a, 2013b). These effects, in combination with dietary shifts in sites with supplementary food resources documented herein, suggest that anthropogenic changes in resource availability at our study site could prevent dingoes from fulfilling their trophic regulatory or pre-European roles (Fleming et al. 2012).

A simple and obvious approach to mitigate any potential changes to dogs' ecological roles is to develop appropriate management strategies to dispose of or restrict access to domestic waste in sites where free-roaming domestic dogs or dingoes and humans co-occur (Denny et al. 2002; Bino et al. 2010). An alternative option is lethal control. However, Gompper and Vanak (2008) argue that several potential difficulties are associated with this approach. First, like many human–wildlife management problems, it would require sustained effort at a large scale. Second, simply restoring the broader carnivore community could mitigate many of the problems that can arise where predator populations are subsidized (Gompper and Vanak 2008). In Australia, however, domestic dogs have successfully dispersed and interbred with dingoes throughout much of the range of the latter species (Newsome and Corbett 1985; Stephens 2011). Therefore, relying on intraguild feedback loops (such as dingoes killing or suppressing the activity of domestic dogs) is unlikely to be successful in mitigating problems associated with domestic dog abundance, dispersal, or genetic introgression in Australia (Daniels and Corbett 2003); nor is it likely to deter opportunistic predators, such as the dingo, from exploiting readily available anthropogenic resources. Therefore, restricting the access of dingoes and domestic dogs to anthropogenic food sources should be seen as a management imperative.

If restricting dingo and domestic dog access to anthropogenic food is possible, it may reduce the likelihood of negative impacts on native prey. However, with respect to our study, domestic dogs were primarily scavengers of human refuse. There was little evidence that they were preying to any great extent upon native or threatened species, or that they might pose a direct threat to native prey. However, free-roaming domestic dogs can make long forays (Meek 1999) and represent source populations of individuals that can interbreed with dingoes (Newsome et al. 2013c), especially those that live close to townships (Allen et al. 2013). In view of the geographical isolation of the region, controlling, by restraining and/or desexing, remote domestic dog populations may be necessary to reduce hybridization and population growth. Limiting the frequency of lethal dingo control in pastoral areas around townships may also slow the hybridization process (Allen 2012b). In summary, the simplest way to minimize problems arising from overabundant dogs is to remove—physically or by effective containment barriers or prevention strategies—the resource subsidy that supports them. Hence, even if targeted control is considered a viable option, it is imperative to concurrently develop appropriate waste management strategies to slow or stop population recovery.

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APPENDIX I

Frequency ($F[O]$) and relative ($R[O]$) percent occurrence of prey categories in dingo (*Canis lupus dingo*) and domestic dog (*C. l. familiaris*) feces collected in November 2009 at 5 site categories in the Tanami Desert, central Australia.

Category	Taxonomic grouping	Individual species	Mine		Pastoral		Desert		Community		Outstation			
			(Dingo) $n = 59$		(Dingo) $n = 123$		(Dingo) $n = 251$		(Dog) $n = 192$		(Dog) $n = 155$			
			$F[O]$	$R[O]$	$F[O]$	$R[O]$	$F[O]$	$R[O]$	$F[O]$	$R[O]$	$F[O]$	$R[O]$		
Mammal	Muridae	<i>Mus musculus</i>	1.69	0.43	—	—	1.20	0.37	—	—	—	—		
		<i>Notomys alexis</i>	—	—	—	—	—	—	0.52	0.23	—	—		
		<i>Pseudomys desertor</i>	15.25	3.90	1.63	0.94	8.76	2.71	—	—	0.65	0.30		
		<i>Pseudomys hermannsburgensis</i>	—	—	—	—	0.80	0.25	—	—	—	—		
		Unknown	5.08	1.30	0.81	0.47	4.78	1.48	0.52	0.23	—	—		
	Dasyuridae	Unknown	—	—	—	—	1.20	0.37	—	—	—	—		
	Peramelidae	<i>Macrotis lagotis</i>	1.69	0.43	—	—	0.80	0.25	—	—	—	—		
	Lagomorpha	<i>Oryctolagus cuniculus</i>	—	—	—	—	0.40	0.12	1.04	0.45	—	—		
	Macropodidae (small)	<i>Onychogalea unguifera</i>	—	—	1.63	0.94	—	—	—	—	—	—		
	Macropodidae (large)	<i>Macropus rufus</i>	—	—	1.63	0.94	1.99	0.62	1.56	0.68	7.74	3.66		
		<i>Macropus robustus</i>	—	—	1.63	0.94	8.76	2.71	4.17	1.82	11.61	5.49		
	Macropodidae	Unknown (small or large)	1.69	0.43	2.44	1.42	6.77	2.10	4.17	1.82	17.42	8.23		
	Monotrematae	<i>Tachyglossus aculeatus</i>	—	—	0.81	0.47	3.59	1.11	—	—	3.23	1.52		
	Canidae	<i>Canis lupus</i> spp.	18.64	4.76	12.20	7.08	8.37	2.59	16.15	7.05	5.16	2.44		
		<i>Vulpes vulpes</i>	—	—	—	—	0.40	0.12	—	—	—	—		
	Felidae	<i>Felis catus</i>	6.78	1.73	1.63	0.94	1.99	0.62	—	—	—	—		
	Bos	<i>Bos</i> spp.	1.69	0.43	79.67	46.23	3.59	1.11	34.38	15.00	5.81	2.74		
	Equus	<i>Equus caballus</i>	—	—	0.81	0.47	—	—	—	—	—	—		
	Camelidae	<i>Camelus dromedarius</i>	1.69	0.43	4.88	2.83	5.58	1.73	—	—	1.94	0.91		
Mammal	Unknown	1.69	0.43	0.81	0.47	1.99	0.62	1.04	0.45	5.16	2.44			
	Total mammal	55.89	14.29	110.58	64.15	60.97	18.87	63.55	27.73	58.72	27.74			
Bird	Eggshell	Unknown	10.17	2.60	—	—	1.20	0.37	2.60	1.14	9.68	4.57		
	Bird (small)	<i>Melopsittacus</i> spp.	1.69	0.43	—	—	—	—	—	—	—	—		
	Bird	Unknown (small or large)	16.95	4.33	4.07	2.36	15.94	4.93	3.13	1.36	12.26	5.79		
	Total bird	28.81	7.36	4.07	2.36	17.14	5.30	5.73	2.50	21.94	10.37			
Reptile	Elapidae	Unknown	—	—	—	—	2.79	0.86	—	—	—	—		
	Geckonidea	Unknown	—	—	1.63	0.94	6.37	1.97	0.52	0.23	—	—		
	Scincidae (large)	<i>Tiliqua multifasciata</i>	6.78	1.73	4.07	2.36	43.03	13.32	—	—	—	—		
	Scincidae (small)	Unknown	3.39	0.87	12.20	7.08	5.58	1.73	0.52	0.23	0.65	0.30		
	Varanidae	<i>Varanus gouldii</i>	—	—	—	—	1.99	0.62	—	—	—	—		
		<i>Varanus acanthurus</i>	—	—	0.81	0.47	23.51	7.27	—	—	—	—		
	Unknown	5.08	1.30	—	—	16.33	5.06	—	—	0.65	0.30			
	Total reptile	15.25	3.90	18.71	10.85	99.60	30.83	1.04	0.45	1.30	0.61			
Amphibian	Anura	Unknown	—	—	—	—	0.80	0.25	—	—	—	—		
	Total amphibian	—	—	—	—	0.80	0.25	—	—	—	—			
Invertebrate	Invertebrate	Ants; undetermined species	10.17	2.60	6.50	3.77	43.43	13.44	4.69	2.05	5.81	2.74		
		Beetles; undetermined species	8.47	2.16	4.88	2.83	25.10	7.77	1.56	0.68	5.16	2.44		
		Centipede; undetermined species	—	—	—	—	—	—	—	—	1.29	0.61		
		Cockroach; undetermined species	1.69	0.43	—	—	—	—	—	—	—	—		
		Grasshopper; undetermined species	1.69	0.43	5.69	3.30	10.36	3.21	—	—	5.16	2.44		
		Invertebrate; unknown	—	—	—	—	0.80	0.25	—	—	—	—		
		Larvae; undetermined species	1.69	0.43	0.81	0.47	1.20	0.37	1.56	0.68	—	—		
		Maggots; undetermined species	1.69	0.43	3.25	1.89	0.80	0.25	—	—	—	—		
		Scorpion; undetermined species	—	—	—	—	3.19	0.99	—	—	0.65	0.30		
		Spider; undetermined species	—	—	—	—	3.19	0.99	—	—	—	—		
			Total invertebrate	25.40	6.49	21.13	12.26	88.07	27.25	7.81	3.41	18.07	8.54	
		Vegetation	Fruit	Unknown	5.08	1.30	—	—	16.33	5.06	—	—	—	—
			Grass	Grass	33.90	8.66	16.26	9.43	19.12	5.92	19.79	8.64	23.23	10.98
	Seeds	—		—	—	—	1.59	0.49	—	—	—	—		
	Vegetation	Unknown	11.86	3.03	—	—	4.78	1.48	44.27	19.32	27.10	12.80		
		Total vegetation	50.84	12.99	16.26	9.43	41.82	12.95	64.06	27.95	50.33	23.78		
Rubbish	Rubbish	Aluminum foil	23.73	6.06	—	—	2.39	0.74	12.50	5.45	10.97	5.18		
		Charcoal	3.39	0.87	—	—	1.20	0.37	9.38	4.09	7.10	3.35		
		Chicken eggshell	16.95	4.33	—	—	0.40	0.12	10.42	4.55	1.94	0.91		
		Elastic	—	—	—	—	—	—	0.52	0.23	—	—		
		Foam	1.69	0.43	—	—	—	—	1.56	0.68	—	—		

APPENDIX I.—Continued.

Category	Taxonomic grouping	Individual species	Mine		Pastoral		Desert		Community		Outstation	
			(Dingo) <i>n</i> = 59		(Dingo) <i>n</i> = 123		(Dingo) <i>n</i> = 251		(Dog) <i>n</i> = 192		(Dog) <i>n</i> = 155	
			<i>F</i> [O]	<i>R</i> [O]	<i>F</i> [O]	<i>R</i> [O]	<i>F</i> [O]	<i>R</i> [O]	<i>F</i> [O]	<i>R</i> [O]	<i>F</i> [O]	<i>R</i> [O]
		Fruit pips	8.47	2.16	—	—	0.80	0.25	1.04	0.45	0.65	0.30
		Glass	28.81	7.36	—	—	1.20	0.37	4.69	2.05	—	—
		Hard plastic	8.47	2.16	—	—	—	—	8.33	3.64	1.94	0.91
		Leather	20.34	5.19	—	—	0.40	0.12	1.04	0.45	0.65	0.30
		Meat bones	20.34	5.19	—	—	0.80	0.25	4.17	1.82	9.68	4.57
		Nylon padding	1.69	0.43	—	—	—	—	3.65	1.59	5.16	2.44
		Nylon woven	6.78	1.73	—	—	—	—	1.56	0.68	0.65	0.30
		Paper	40.68	10.39	—	—	4.78	1.48	12.50	5.45	7.10	3.35
		Plastic bag	13.56	3.46	—	—	1.59	0.49	9.90	4.32	6.45	3.05
		Plastic wrap	1.69	0.43	0.81	0.47	—	—	1.04	0.45	—	—
		Rocks	5.08	1.30	0.81	0.47	0.40	0.12	1.04	0.45	—	—
		Rubber	1.69	0.43	—	—	—	—	—	—	0.65	0.30
		Sand	—	—	—	—	—	—	3.13	1.36	6.45	3.05
		String	11.86	3.03	—	—	0.80	0.25	0.52	0.23	1.94	0.91
		Total rubbish	215.22	54.98	1.62	0.94	14.76	4.56	86.99	37.95	61.33	28.96