

Human-resource subsidies alter the dietary preferences of a mammalian top predator

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Abstract Resource subsidies to opportunistic predators may alter natural predator–prey relationships and, in turn, have implications for how these predators affect co-occurring prey. To explore this idea, we compared the prey available to and eaten by a top canid predator, the Australian dingo (*Canis lupus dingo*), in areas with and without human-provided food. Overall, small mammals formed the majority of dingo prey, followed by reptiles and then invertebrates. Where human-provided food resources were available, dingoes ate them; 17 % of their diet comprised kitchen waste from a refuse facility. There was evidence of dietary preference for small mammals in areas where

human-provided food was available. In more distant areas, by contrast, reptiles were the primary prey. The level of seasonal switching between small mammals and reptiles was also more pronounced in areas away from human-provided food. This reaffirmed concepts of prey switching but within a short, seasonal time frame. It also confirmed that the diet of dingoes is altered where human-provided food is available. We suggest that the availability of anthropogenic food to this species and other apex predators therefore has the potential to alter trophic cascades.

Keywords Canidae · *Canis lupus dingo* · Diet · Dingo · Desert

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Introduction

Optimal foraging theories generally predict that animals should promote their fitness by foraging in ways that maximise their net rate of energy gain (Emlen 1966; MacArthur and Pianka 1966) or minimise the risk of starvation (Stephens and Krebs 1986). In its simplest form, maximising the rate of energy gain may be achieved by adopting efficient hunting behaviour or search strategies, exploiting food sources when they become available, and selecting 'optimal' prey (Stephens and Krebs 1986). By evaluating available prey, and selecting only the most profitable, predators' diets should vary according to the quality and availability of alternative foods (Hughes 1993). However, selection can be influenced by prey preferences (Murdoch 1969), hunger, risk of injury (Hayward 2006) and natural fluctuations in prey availability (Dale et al. 1992). In human-modified environments, the dietary preferences of synanthropic animals may also be influenced by the availability of supplementary food (Fedriani et al. 2001).

Understanding this dynamic is important, particularly when considering predators that are highly adaptable and whose foraging preferences and prey-switching behaviours might impact on the distributions, abundances and behaviour of co-occurring species.

One group of predators that frequently takes advantage of anthropogenic resources is free-roaming canids (Atwood et al. 2004; Gompfer and Vanak 2008; Bino et al. 2010). From a management and conservation perspective, canids can have many detrimental effects where they occur at high densities, and can exert additional pressure on human industries and/or ecological communities (Sillero-Zubiri and Switzer 2004). For example, canids depredate livestock, damage infrastructure and spread disease (Baker et al. 2008). Ecologically, invasive or introduced canids can pose serious threats to native species if left uncontrolled, with many examples of extinctions occurring due to hyper-predation (Dickman 1996; Courchamp et al. 2000). Consequently, developing sound management and control programs for canids in human-dominated landscapes is a major priority (Fleming et al. 2001; Sillero-Zubiri and Switzer 2004).

The need to actively manage the impacts of canids has led to various levels of anthropogenic control throughout the ranges of some species. It has also led to the hypothesis that, where top-order or apex canids are removed, trophic cascades will be disrupted (Ripple et al. 2013). This is important to highlight because studies and reviews on trophic cascades have largely overlooked the role of human-resource subsidies (e.g. Estes et al. 2011), despite the obvious influence such resources could have on the abundance and distribution of top predators, including canids. Therefore, studies that provide insight into how human resources influence the ecology and behaviour of canids are critical to develop both practical management strategies and theoretical understanding about the roles of these predators in ecosystem functioning.

On the mainland of Australia, the dingo (*Canis lupus dingo*) has had a long association with humans since its introduction approximately 4,000 years ago (Smith and Litchfield 2009). The dingo is also often considered a top predator and potential trophic regulator (Johnson et al. 2007; Letnic and Koch 2010). Trophic regulation would occur if dingoes suppress the abundance or activity of the European red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) sufficiently to enhance mammalian prey populations that are subject to suppression by them. As an opportunistic, generalist predator (Newsome et al. 1983; Corbett and Newsome 1987; Allen et al. 2012; Allen and Leung 2012), the dingo is an ideal candidate to investigate the effects of human-provided resources on prey populations because it is reasonable to assume that, where humans provide food, dingoes will exploit it. Therefore, given the dingo's ecological flexibility, we investigated the dietary preferences

of dingoes in the presence of anthropogenic resource subsidies. We considered that insights would be best achieved in a region of low productivity and where human-provided resources (food and water) were available in association with strongly localised human activity.

The Tanami Desert in central Australia provides such a site. There, commercial kitchen waste from two refuse facilities associated with mining operations potentially provides a substantial food supplement for local dingo populations. No other such refuse sites occur in the vast areas of the surrounding Tanami bioregion (~26,000 km²). We used this opportunity to quantify the use of human-provided resources by dingoes and the impacts that these resources might have on dingo diet selectivity.

First, we determined the overall dietary preferences of dingoes in the Tanami Desert. Due to above-average rainfall in the years preceding the study and the stimulatory effects of rain on numbers of native rodents (Dickman et al. 1999; Pavey et al. 2008), we hypothesised that small mammals would occur frequently in the diet of dingoes. Given also that reptiles were identified previously as major prey in the Tanami region (Paltridge 2002), and that seasonal changes in the availability of reptiles are dependent on temperature and thus highly predictable (Green and King 1978; Greer 1981; Paltridge 2002), we predicted further that they too would be consumed during the seasons in which they were most available.

Second, we determined the extent to which dingoes use anthropogenically derived foods by reviewing dietary preferences at and away from sites with human-provided food. We predicted that in areas with human-provided food, the dietary preferences of dingoes would be altered to include such food.

Third, we explored the relationship between the occurrence of prey in dingo diet and prey abundance in the wild. We predicted that dingoes would select prey according to availability and that preferences for natural prey would be independent of anthropogenic food availability.

Finally, we use the results to discuss the functional role of dingoes and opportunistic predators more generally where anthropogenic food subsidies are available.

Materials and methods

Study region and experimental design

The Tanami Desert (130°18'E, 20°30'S) is semi-arid and monsoonal with about 90 % of yearly rain received between November and April. Summers are very hot (mean maximum daily temperature up to 39 °C) and winters cold (mean minimum daily temperature down to 6.6 °C), with frosts occurring rarely. Rainfall is highly variable and was

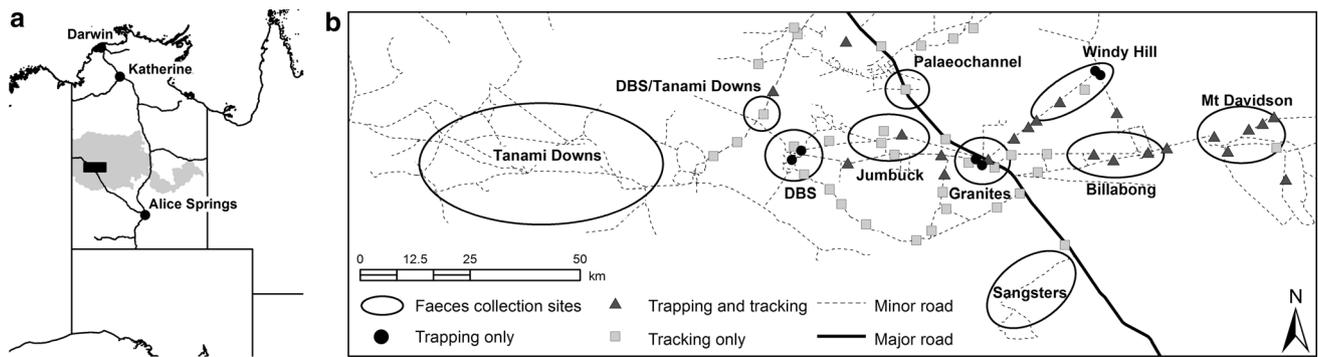


Fig. 1 Study site (box) and the Tanami Desert (grey) in the Northern Territory of Australia (a) and study site and sampling details (b)

below average during this study at 219 and 263 mm in 2008 and 2009, respectively (Bureau of Meteorology 2010). In the preceding years, between August 2005 and July 2007, approximately 1,400 mm of rain fell. Our study was therefore conducted after a period of high rainfall during the low phase of a boom-bust cycle (Letnic and Dickman 2010).

At the time of the study, large quantities of food scraps from a commercial kitchen at the Granites mine were available daily to dingoes at a nearby waste facility (Newsome 2011). Food scraps were available also at a smaller waste facility at a second mine, DBS. In addition, calves and cattle (*Bos* spp.), carrion and small quantities of food from a domestic kitchen were available as food for dingoes at Tanami Downs cattle station. The Granites, DBS and Tanami Downs were therefore considered to be sites where human-resource subsidies were available, and seven other sites, with no human-resource subsidies, were stratified at increasing distances away (Fig. 1).

Overall dietary preferences

Dingo faeces were collected in April, August and November of 2008 and 2009 (i.e. from six trips). Due to the generally high rate of faecal deposition over small areas, it was possible to totally clear collection sites and then re-sample, allowing valid comparisons of diet to be made between trips. Because faeces were not cleared before the first trip, samples collected then that were decomposed and not intact were judged to be very old, and discarded. On following trips very old faeces were rarely found, which affirmed the categorisation used in the first trip.

Prior to identifying contents, faeces were oven dried at 100 °C, then washed in nylon bags to leave hard fragments of bones, hairs and human-derived rubbish. Dried remnants were placed on a sorting tray with quarter divisions, with one quarter split into 5 % divisions to allow for visual sorting. Collections of bones, hairs and other publicly available materials (Brunner and Coman 1974) were used for reference in the identification process. When material could not

be identified to species level, it was grouped broadly or categorised as ‘unknown’. To separate feeding from grooming, faeces containing dingo bones were taken to indicate cannibalism and faeces with no dingo bones and fewer than ten dingo hairs to indicate grooming. Although arbitrary, this was likely a reasonable threshold: faeces usually contained fewer than ten hairs or far more than ten hairs plus dingo bone fragments. Because food from the refuse facility was mostly processed and lacked diagnostic bones or hairs, identification of items from this source in dingo faeces was rarely possible. However, the presence of plastic wrapping, foil, glass and/or paper in faeces confirmed the consumption of anthropogenic food.

To allow comparison with other studies, we calculated the ‘frequency of occurrence’ for individual prey species. For more detailed analysis, we modelled the odds ratio for the occurrence of species groups (Type) in each faecal sample. Types were based on taxonomic association; the primary categories we used were: birds, invertebrates, mammals, reptiles, rubbish and vegetation. To model the probability of occurrence of each type in faeces, we used a mixed effects logistic regression analysis. Denoting the probabilities of presence by p , the following model was fitted to the data:

$$\begin{aligned} \text{logit}(p) = & \text{Constant} + \text{Trip} + \text{Type} + \text{Trip} : \text{Type} + \text{Site} \\ & + \text{Site} : \text{Trip} + \text{Site} : \text{Type} \\ & + \text{Site} : \text{Trip} : \text{Type} + \text{faeces} \end{aligned}$$

Here $\text{logit}(p) = \log[p/(1 - p)]$ and the terms in bold were fitted as random effects. The model was fitted in *R* (R development Core Team 2009) using ASReml residual maximum likelihood for linear mixed models (Gilmour et al. 2002) in the package asreml (Butler 2009), with adjusted Wald statistics (Kenward and Roger 1997).

Use of anthropogenic food resources

To assess the significance of any trends, all Site \times Trip combinations were subject to ordination using non-metric

multi-dimensional scaling (nMDS), via function isoMDS in the library MASS (Venables and Ripley 2002) within R.

Faecal samples from the two mine sites were then grouped into one area category (Mine). The average probability of occurrence of each species group was then compared with those from Tanami Downs and with the remaining away sites.

To compare diet breadth between the three areas (above), the probabilities of occurrence of natural food items were estimated for each Area \times Trip combination, and Brillouin's index was calculated via repeated bootstrapping (Magurran 1988). To do this, we excluded rubbish and cattle from samples as these were the main forms of human-provided food. We plotted the slope of the average Brillouin index against sample size and assumed sample size sufficiency when plots plateaued. Differences between areas were assessed using two-way ANOVA.

Estimates of prey relative abundance

Prey abundance was sampled between October and November in 2008 and 2009 when both reptiles and small mammals were active. This timing allowed us to assess the abundance of these groups and compare their occurrence in faeces collected at the same times. For small prey species, we used data collected from 28 sites in 2008 and 27 sites in 2009, stratified within a sub-set of the study region (Fig. 1). The number of sites was proportional to the available land units (Domahidy 1990; Wilford and Butrovski 1999). At each site, 25 type-A Elliott traps (Elliott Scientific, Upwey, VIC) were placed 10 m apart in a straight line and baited with oats and peanut butter (Beer 1964). Four buried 20-L buckets (pitfall traps) with 10-m drift fences were also placed adjacent to the Elliott trap line, 50 m apart. All traps were opened for three consecutive nights, checked early each morning, and closed during the day (total 4,125 Elliott and 660 pitfall trap-nights over the 2 years). All trapped animals were identified to species, sexed and weighed.

The relative abundances of prey too large for our traps were estimated from footprints on tracking plots adjacent to roads, following Southgate et al. (2005). We set 300 \times 200-m tracking plots at 22 of the trapping sites (above) and at an additional 35 locations (57 sites in total) (Fig. 1). To standardise effort, we searched each plot for 1 h and recorded the species and number of sets of footprints for each species detected.

Diet selectivity

To compare the availability of prey categories with their occurrence in dingo faeces, we examined the occurrence of all mammals (as well as the most common mammal species group: Muridae) and all reptiles (as well the most common

reptile species groups: large skink, small skink and Varanidae) in traps and/or tracks across four sub-regions of the study region. The sub-regions were based on the minimum distance from the two main sites with human-provided food (DBS and the Granites), and were set with boundaries at 0–10, 10–25, 25–40 and >40 km from the nearest food subsidy. Because prey sampling did not extend to Tanami Downs or the Sangster's site (Fig. 1), faecal samples from these two areas were excluded for all comparisons.

Logistic regression analysis, allowing for possible over-dispersion, was used to determine the incidence of each prey type in faeces within each sub-region. The model for the probability of finding the selected prey type in a faecal sample within a sub-region on a given trip, on the logit scale, is the sum of a baseline effect, an effect associated with the particular sub-region, and an effect associated with the particular trip of interest. That is,

$$\text{logit}(\text{probability}) = \text{Baseline} + \text{Sub-region effect} \\ + \text{Trip effect}$$

Abundance data for the track plots and for the traps, corresponding to the number of observed tracks and observed trapped prey, respectively, were determined using log-linear Poisson modelling, allowing for possible over-dispersion and including an offset corresponding to the number (N) of track plots or the number of traps in the sub-region in a given year. For example, the expected number of tracks or traps within a sub-region on a particular trip was modelled as:

$$\log(\text{mean number}) = \text{Baseline} + \text{Sub-region effect} \\ + \text{Trip effect} + \text{offset}(\log(N))$$

To enable graphical representation of dietary differences among sub-regions, using the logistic and log linear regression results (above), we calculated indices of prey selectivity. Ivlev's electivity index (Ivlev 1961) has problems of non-linearity as it approaches the limiting values of +1 and -1, and is affected by small sample sizes (Strauss 1979; Lechowicz 1982). Therefore, we used Strauss's linear index, L :

$$L = r_i - p_i$$

where r_i is the relative occurrence of prey item i in a faeces sample and p_i is the relative abundance of prey item i in the sub-region, both expressed as proportions (Strauss 1979). This index is linear across all values between +1 and -1. We used a randomisation procedure without replacement in the PopTools add-on for Microsoft Excel [i.e. the RESAMPLE procedure (Hood 2003)] followed by Monte-Carlo routines (10,000 iterations) to estimate 95 % confidence limits of the differences to make visual comparisons (Cumming 2009) of selectivity values (between -1 and +1) and also between sub-regions. Hence, negative values of L with confidence intervals not overlapping zero were taken to

Fig. 2 Probability (0–1) of species groups occurring in the diet of dingoes in the Tanami Desert. Means are shown $\pm 95\%$ confidence intervals. *Apr* April, *Aug* August, *Nov* November, *Invert* invertebrate, *Veg* vegetation

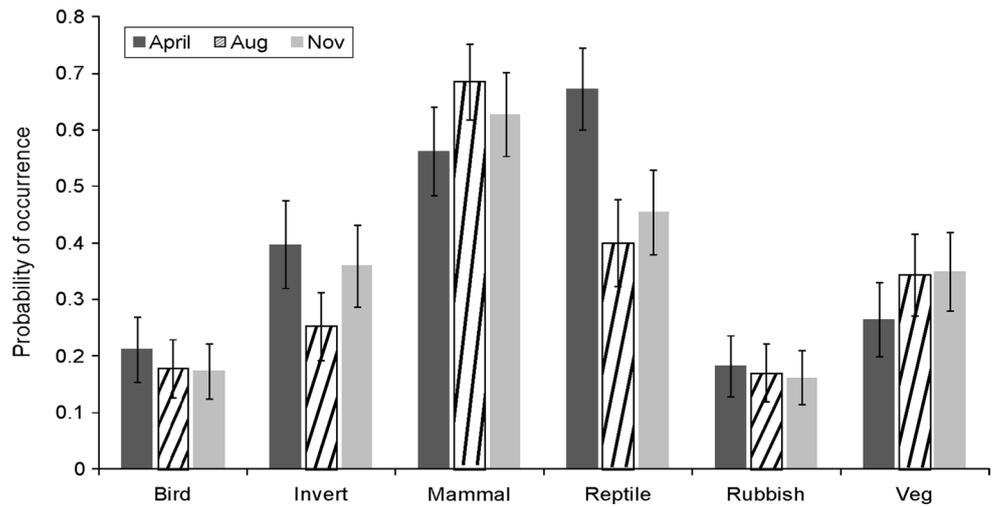
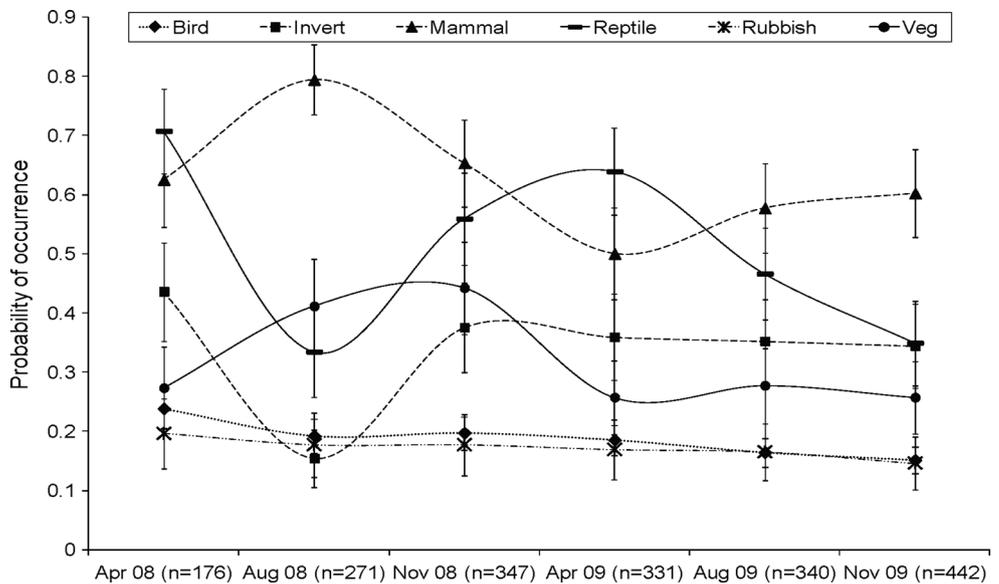


Fig. 3 Probability (0–1) of primary species groups occurring in the diet of dingoes in the Tanami Desert averaged over six trips. Means are shown $\pm 95\%$ confidence intervals. *n* Number of faeces analysed per trip; for other abbreviations, see Fig. 2



represent avoidance or inaccessibility of a particular prey item, zero indices to indicate no selectivity, and positive values with confidence intervals not overlapping zero to indicate prey preference.

Results

Overall diet and dietary preferences

Ingesta were identified from a total of 1,907 dingo faecal samples collected at ten sites in the Tanami region (Fig. 1). Mammals formed the majority of prey items by probability of occurrence, calculated as the unweighted average over sites and trips (63.1 %), followed by reptiles (51 %) and then invertebrates (32.8 %) (Table S1). The centralian blue-tongue lizard (*Tiliqua multifasciata*) occurred most

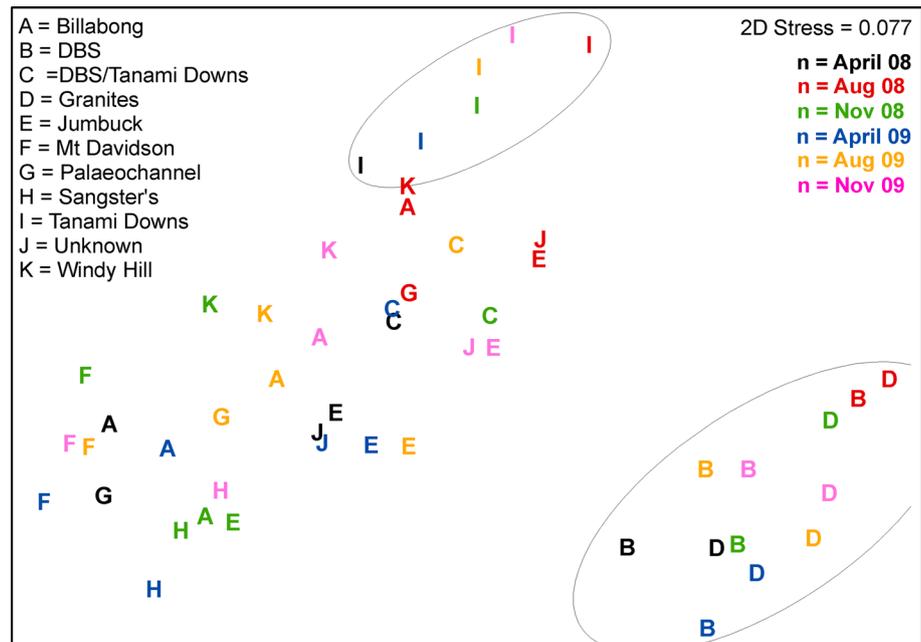
frequently (22.5 % of faecal samples), followed by the desert mouse (*Pseudomys desertor*) (16.7 %). The probability of a faecal sample containing rubbish was relatively high (17.1 %) (Table S1).

When data were pooled and averaged over the 2 study years, mammal occurrence was consistently high (Fig. 2). However, there was evidence of seasonal change in predation on mammals and reptiles between trips. Reptile occurrence was markedly higher in faeces collected in April compared with those collected in cooler periods, particularly August, when reptiles are less active. Conversely, mammals were consumed at higher rates during the cooler months (Fig. 3).

Use of anthropogenic food resources

Analysis of prey group data via linear, mixed model, logistic regressions revealed strong Trip \times Type interactions,

Fig. 4 Two-dimensional multi-dimensional scaling based on average probabilities of primary species groups of prey occurring in dingo faeces for each Site \times Trip combination in the Tanami Desert. *Ellipses* indicate general clusters



averaged over sites. For the primary prey groups, for example, Wald tests showed that food types varied significantly between trips [$F_{(30,205)} = 2.97$, $P < 0.001$]. To explore these trends, we subjected the predicted probabilities of occurrence for prey groups within each Site \times Trip \times Type to ordination via nMDS. The results suggest no clear pattern between dietary results for different trips within sites. However, there was clear separation between DBS and the Granites and all other sites, and secondly between Tanami Downs and all other sites, providing evidence for changes in the diet of dingoes where human activities occur (Fig. 4).

Pooling data into the three categories based on proximity to human-derived food subsidies revealed clear differences in the occurrence of food groups in faeces at mine sites (Fig. 5a) and Tanami Downs (Fig. 5b) as compared with all other areas (Fig. 5c). At the mine sites, mammals were consumed at higher rates than reptiles regardless of season (Fig. 5a). Away from the mine sites, reptiles were consumed at higher rates only at times when they were most active (Fig. 5c). At Tanami Downs, mammals (primarily cattle) dominated the diet of dingoes and there was little difference in consumption of other groups in different seasons (Fig. 5b).

The differences between areas with and without resource subsidies were reflected in dietary diversity, with significant differences occurring [$F_{(2,10)} = 11.44$, $P = 0.003$] across the different areas. Mine site values (Brillouin index average = 2.51 ± 0.029) differed [$F_{(1,5)} = 17.34$, $P = 0.009$] from those away from the mines (Brillouin index average = 2.83 ± 0.004) but not [$F_{(1,5)} = 4.23$, $P = 0.094$] from those at Tanami Downs (Brillouin index average 2.06 ± 0.068).

Diet selectivity

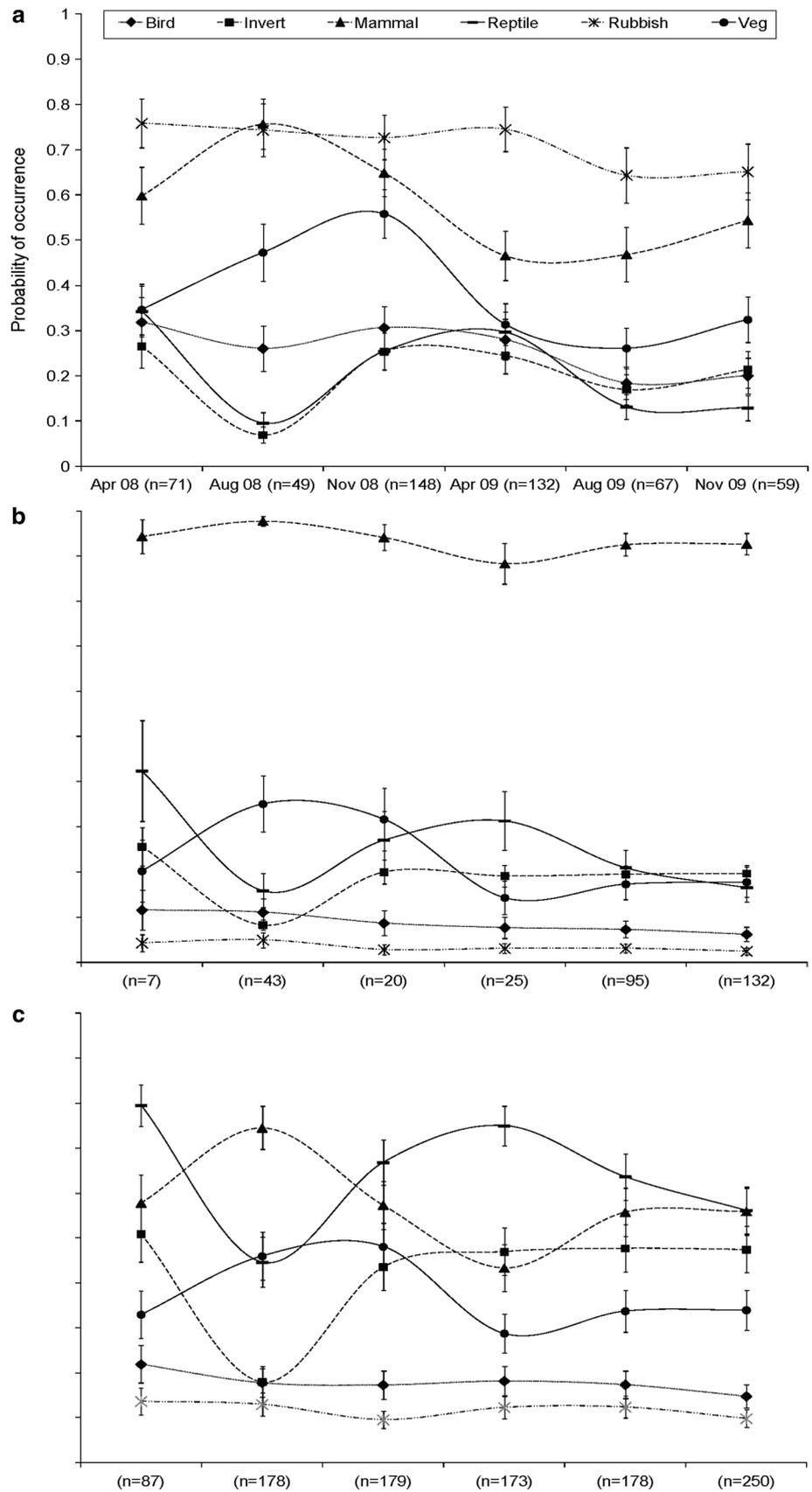
In November 2008 and 2009 small mammals (358 and 1,033 captures, respectively) and reptiles (198 and 461 captures, respectively) formed the majority of trap captures. In 2008 and 2009, across the tracking plots, 94 and 69 tracks, respectively, were recorded for mammals, as were 96 and 89 tracks, respectively, for reptiles.

Based on Strauss's index and corresponding 95 % confidence intervals, dingoes showed increasing selectivity for reptiles (and the large skink and Varanidae species groups) at distances up to 40 km from human-provided food (Fig. 6). In contrast, selectivity by dingoes for mammals (or the murid rodent and small skink species groups) remained unchanged with distance from human-provided food (Fig. 6).

Discussion

Dingo faeces contained a wide variety of prey (45 species identified) and also significant amounts of human-derived rubbish that indicated scavenging at the waste facilities. This study is the first to report such a high occurrence of rubbish in the diet of dingoes across multiple years and seasons, although the Tanami Desert is not the only place where it is likely to occur. Despite this, wild prey still occurred in faeces from all collection areas, with mammals and then reptiles consumed most often (Fig. 2). The high proportion of mammals that we found is consistent with the results of other studies in arid Australia (Allen and Leung 2012). However, it was small mammals (<100 g) rather

Fig. 5 Probability (0–1) of primary species groups occurring in the diet of dingoes at waste facilities around mine sites (a), at Tanami Downs (b), and away from mine sites (c) in the Tanami Desert averaged over six trips. Means are shown $\pm 95\%$ confidence intervals. *n* Number of faeces analysed per trip; for abbreviations, see Fig. 2



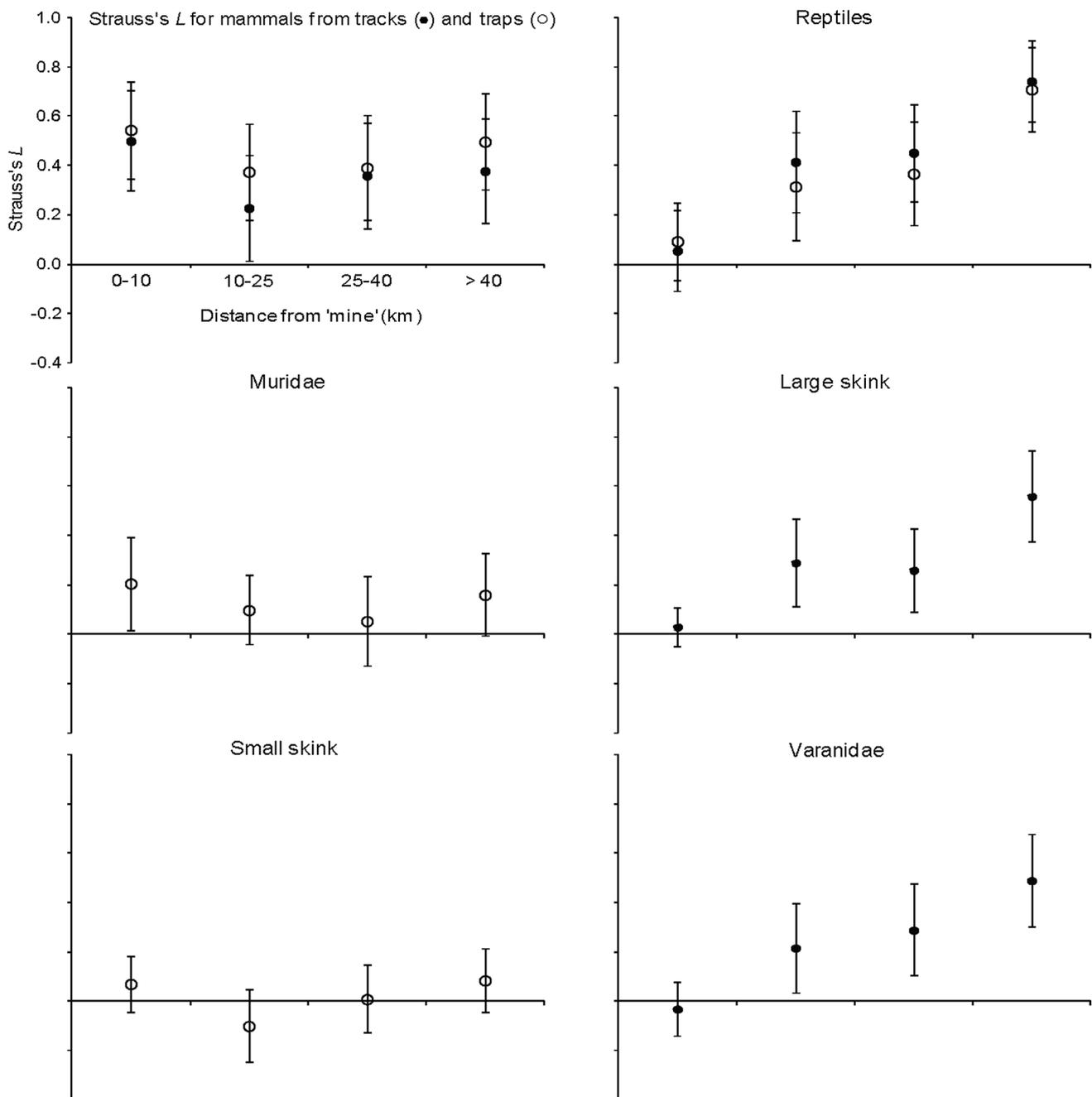


Fig. 6 Electivity index showing a greater preference by dingoes for reptiles (including large skinks and Varanidae) at increasing distances away from human-provided food (mine). There was no apparent dif-

ference in the preference for mammals (or murid rodents or small skinks) at increasing distances away from the mine

than large mammals that contributed to this trend. Further, the high occurrence of reptiles in the diet of dingoes in our study contrasts with general trends in dingo diet based on a review by Allen and Leung (2012) in which reptiles accounted for only 6 % of dingo diet.

In central Australia, Corbett and Newsome (1987) showed that dingo diet is related functionally to the relative abundances of major prey species. The main driver of small

mammal abundance in this region is rainfall (Dickman et al. 1999). Hence, in good seasons with above-average rain, small mammals (e.g. rodents) can be important prey for dingoes (Pavey et al. 2008). This was demonstrated in our study, but the highest occurrence of small mammals was in winter (Fig. 3). Whilst interpretation of this trend would be assisted by estimates of the abundance of prey during winter, it can still be readily explained: reptile

activity is temperature-dependent, with skinks and varanids being most active in summer between October and April (Green and King 1978; Greer 1981; Paltridge 2002).

Small mammals, by contrast, are available year round (Geiser 2004). Their high occurrence in dingo faeces during cooler periods, therefore, is not unexpected, especially as larger mammalian prey is relatively scarce and most reptiles are less active in winter (Green and King 1978; Christian et al. 1995). Nonetheless, the overall results suggest a dietary preference for reptiles over small mammals when both are active in summer, and thus reaffirm broad concepts of prey switching (Murdoch 1969, 1977; Oaten and Murdoch 1975). Additionally, our results provide a possible extension of the theory of alternation of predation proposed by Corbett and Newsome (1987) in that prey switching by dingoes may occur within a short, seasonal time frame. It also conforms with the general idea that animals will forage in ways that maximise their net rate of energy gain (Emlen 1966; MacArthur and Pianka 1966). High use of the waste facilities by dingoes was likely energetically optimal because there was a superabundant food supply. There was also no specific territorial defence of the focal resource by resident dingoes, allowing free access for transient individuals (Newsome et al. 2013a).

The occurrence of human-provided food resources at the mine sites was a major factor in our study. To interpret how this affected dingo prey selection, we explored the selection of natural prey in different areas and seasons. This was difficult because the presence of cattle at Tanami Downs could in itself affect prey availability, the prey eaten and the occurrence of prey in faeces. For example, localised water availability and phosphoric grazing pressure by cattle may affect rodents and reptiles by reducing seed production, the availability of insects (Letnic et al. 2004) and herbage and cover (James et al. 1999). However, the impacts of mining operations are restricted to a much smaller area than those of free-ranging cattle, and because there are water sources throughout most of the study region (at bores, pipelines and old water tanks) and no major changes in habitat availability, the main difference at mine sites is the presence of waste food. This made comparisons between these and all other areas appropriate and compelling. From those comparisons, different dietary preferences were clearly evident at the mine sites, with mammals consumed at consistently high rates regardless of trip or season (Fig. 5a). This contrasts with sites away from the mine where dingoes displayed far greater levels of switching from small mammals to reptiles at times when reptiles were plentiful (Fig. 5c).

We explored the preference by dingoes for reptiles over mammals in relation to their availability during a subset of the study period and found that reptiles were selected more often away from human-provided food than close to it (Fig. 6). More sampling at different times would provide

clearer insight; however, as sampling was conducted when both small mammals and reptiles are active (November), it was an ideal time to explore selectivity patterns. As the only difference between areas in the study region is the availability of human-provided food, our results suggest that the dietary preferences of dingoes differ when human-provided food is available. There are a number of ways to interpret this trend, but the most likely explanation is that the daily energetic requirements of dingoes around mine sites were met primarily by waste scavenging, allowing them to hunt small mammals (which may be more easily caught) rather than reptiles that are larger in size and more 'optimal' in that they return more energy per gram (Paltridge 2002). The overall choice within the small-mammal category also reflects preference for species that provide a trade-off between size and relative ease of capture. For example, the most readily eaten species, *Pseudomys desertor*, is relatively large (25 g) compared with the sandy inland mouse, *Pseudomys hermannsburgensis* (12 g) but likely much slower than the similar-sized spinifex hopping mouse, *Notomys alexis* (30 g) which is bipedal when moving fast (Dickman et al. 1999).

The hypothesis that human-provided foods alter the diet of dingoes is strengthened by the finding that dietary breadth was low around the mine sites. There were also clear differences in the occurrence of prey species in faeces collected from areas with human-provided food (mine sites and the pastoral station) compared with those well away from intensive human activity (Figs. 4, 5). For example, at mine sites, rubbish was consistently present in the diet with occurrence >60 % across all trips (Fig. 5a). Even higher occurrences of cattle (>90 %) were observed at Tanami Downs (Fig. 5b). Although the actual amount of human-provided food consumed around mine sites could not be fully quantified, large quantities of food were constantly available (Newsome 2011). Intensive foraging by dingoes living around the mine was corroborated also by frequent visual observations of them at the refuse tip at all times of the day, by mark-recapture data and by extensive radio-tracking of dingoes living around the mine (Newsome et al. 2013a, b, c). On Tanami Downs, cattle were the main prey of dingoes, but it is not known whether this was from direct predation or scavenging on carcasses.

There is global recognition that predators can have important roles in structuring ecosystems to benefit biodiversity (Ritchie and Johnson 2009; Terborgh and Estes 2010; Estes et al. 2011). For example, trophic regulation of ecosystems by dingoes may provide positive benefits to some native species (Johnson et al. 2007; Glen et al. 2007; Johnson and VanDerWal 2009; Letnic et al. 2009a, b, 2011; Letnic and Koch 2010), with benefits accruing from dingoes suppressing smaller introduced predators such as the European red fox and possibly also the feral cat. However,

first trip. Bill Low, Al Glen and Alex Diment provided valuable comments on early drafts.

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