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REVIEW

Continental patterns in the diet of a top predator: Australia's dingo

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ABSTRACT

1. Conserving large carnivores is controversial because they can threaten wildlife, human safety, and livestock production. Since large carnivores often have large ranges, effective management requires knowledge of how their ecology and functional roles vary biogeographically.
2. We examine continental-scale patterns in the diet of the dingo – Australia's largest terrestrial mammalian predator. We describe and quantify how dingo dietary composition and diversity vary with environmental productivity and across five bioclimatic zones: arid, semi-arid, tropical, sub-tropical, and temperate.
3. Based on 73 published and unpublished data sets from throughout the continent, we used multivariate linear modelling to assess regional trends in the occurrence of nine food groups (arthropods, birds, reptiles, European rabbits *Oryctolagus cuniculus*, medium-sized [25–125 kg] and large [169–825 kg] exotic ungulates [including livestock], and other small [<0.5 kg], medium-sized [0.5–6.9 kg] and large [≥7 kg] mammals) in dingo diets. We also assessed regional patterns in the dietary occurrence of livestock and the relationship between dietary occurrence of rabbits and small, medium-sized and large mammals.
4. Dingoes eat at least 229 vertebrate species (66% mammals, 22% birds, 11% reptiles, and 1% other taxa). Dietary composition varied across bioclimatic zones, with dingo diets in the arid and semi-arid zones (low-productivity sites) having the highest occurrence of arthropods, reptiles, birds, and rabbits. Medium-sized mammals occurred most frequently in temperate and sub-tropical zone diets (high-productivity sites), large mammals least in the arid and sub-tropical zones, and livestock most in the arid and tropical zones. The frequency of rabbits in diets was negatively correlated with that of medium-sized, but not small or large mammals.
5. Dingoes have a flexible and generalist diet that differs among bioclimatic zones and with environmental productivity in Australia. Future research should focus on examining how dingo diets are affected by local prey availability and human-induced changes to prey communities.

INTRODUCTION

Large carnivores are threatened with extinction in many parts of the world due to habitat loss, depletion of prey, disease, and persecution by humans (Ripple et al. 2014). The loss of large carnivores can trigger trophic cascades affecting entire ecosystems (Estes et al. 2011). Restoration of large carnivore populations has thus gained momentum as a conservation initiative in Europe (Chapron et al. 2014), Africa (Hayward et al. 2007), North America (Bruskotter & Wilson 2013), and Australia (Dickman et al. 2009). Such restoration plans are controversial, because large carnivores can kill livestock (Bradley & Pletscher 2005), humans (Packer et al. 2011, Dhanwatey et al. 2013), and threatened species (Hervieux et al. 2014, Cremona et al. 2017). Successful management of large carnivores and their prey therefore requires a sound understanding of large carnivore ecology, particularly geographic variations in diet, in order to assess associated ecological, social and economic costs and benefits (Newsome et al. 2016).

Australia's largest terrestrial carnivore – the dingo *Canis dingo* (Crowther et al. 2014, Smith et al. 2018) or *Canis familiaris* (Jackson et al. 2017, the nomenclature is debated; ~15 kg) – illustrates the controversies surrounding large carnivores globally. Dingoes inhabit the majority of mainland Australia and some nearshore islands, but are subject to lethal control (shooting, trapping, and poisoning) in much of their range (Fleming et al. 2001). Due to their roles in regulating populations of native and introduced herbivores (e.g. kangaroos Macropodidae and feral goats *Capra hircus*; Allen et al. 1996, Pople et al. 2000, Letnic & Crowther 2012, Forsyth et al. 2018b) and influencing the behaviour and possibly density of introduced mesopredators (feral cats *Felis catus* and red foxes *Vulpes vulpes*;

Brawata & Neeman 2011, Letnic et al. 2011, Brook et al. 2012, Moseby et al. 2012, Wang & Fisher 2013, Newsome et al. 2017), it has been proposed that lethal control of dingoes should cease in some areas (Letnic et al. 2012), and that dingo populations should be restored where they are absent or rare (Dickman et al. 2009, Ritchie et al. 2012, Newsome et al. 2015). However, proposals to protect and restore dingo populations have been met with concerns regarding predation of livestock and threatened species (Fleming et al. 2012). Developing an in-depth understanding of how the dingo's diet varies throughout Australia could assist evaluation of such proposals, especially if it helps to predict the impacts dingoes could exert on prey species and ecological processes (Lindenmayer et al. 2010, Mech 2012, Wallach et al. 2016).

Optimal foraging theory predicts that animals maximise net energy intake by eating the most profitable food source, which encompasses both the energy expended in obtaining food and the energy derived from it (Stephens & Krebs 1986). Along with temporal variation in prey availability within a region, spatial variation in prey communities often results in biogeographical patterns in the diets of carnivores (Clavero et al. 2003, Lozano et al. 2006, Zhou et al. 2011). For example, in the Iberian Peninsula, red fox diets contain invertebrates and lagomorphs most frequently at southern latitudes, and small mammals and fruits/seeds most frequently at northern latitudes (Díaz-Ruiz et al. 2011). Brown bear *Ursus arctos* diets contain more vertebrates and fewer invertebrates and mast at locations with deeper snow, lower temperatures, and lower productivity (Bojarska & Selva 2011). In southern latitudes, the wild cat *Felis silvestris* has a broader diet that is heavily influenced by the availability of preferred prey such as rabbits (Lozano et al. 2006). In Australia, the occurrence of rabbits in the diet of feral cats is highest at mid-latitudes, and dietary occurrence of small mammals (<0.5 kg) is negatively correlated with that of rabbits (Doherty et al. 2015). Due to its larger body size and greater energetic needs, the dingo may exhibit different biogeographical trends in dietary composition to feral cats, but such comparisons to date have been limited to studies at the local scale (Paltridge 2002, Pavey et al. 2008, Spencer et al. 2014, Doherty 2015, Woinarski et al. 2018). Physiological theory predicts that dingoes are expected to feed commonly on prey that is ≤45% of their own mass, and it is plausible that they can survive on invertebrates (Carbone et al. 1999). However, energetic studies have also revealed a 14.5–21 kg carnivore body mass threshold within which species such as dingoes, lynx (*Lynx* spp.) and jackals (*Canis* spp.) can readily switch between hunting small and large prey (Carbone et al. 2007).

We collated an extensive data set on the diet of dingoes, feral domestic dogs *Canis familiaris* and their hybrids, to test hypotheses about biogeographical trends in their dietary composition. Some authors presented data for 'wild dogs', which is another term for dingoes, but also extends to include hybrids between dingoes and feral domestic dogs (Letnic et al. 2012). We pool and present data herein for all three taxa and refer to them collectively as 'dingoes'. This approach was considered appropriate because, although a large proportion of free-ranging dogs in Australia are hybrids (e.g. 99% of dogs in south-eastern Australia; Stephens et al. 2015), they have similar morphology (Parr et al. 2016) and biology (e.g. Cursino et al. 2017) to dingoes. Thus, these animals are likely to have similar diets and perform similar ecological functions to dingoes.

We examined how dingo diet varies between five bioclimatic zones (arid, semi-arid, tropical, sub-tropical, temperate; Fig. 1) and with environmental productivity. These zones broadly correspond with the major climate classifications for Australia (equatorial, tropical,

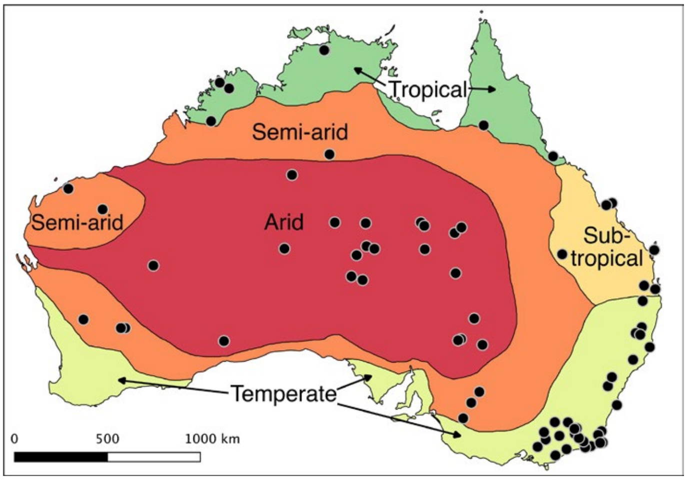

Fig. 1. Map of Australia, showing the locations of dingo dietary studies used in the analyses (black dots) and the five bioclimatic zones.

sub-tropical, desert, grassland, temperate; Stern et al. 2000), although we simplified them in order to represent potential prey distributions, following similar logic to that outlined by Doherty et al. (2015). Specifically, the small equatorial areas in far northern Australia were reclassified as tropical, the small sub-tropical area in the south-west was reclassified as temperate, grassland areas nested within the central desert region were reclassified as arid, and the borders of all zones were smoothed. These zones are characterised by distinct climatic conditions and prey species distributions, but we do not assume that conditions are homogenous within each zone. Rather, our approach assesses whether the bioclimatic zones explain variance in dingo diets. Rabbits are absent from the far northern tropical zone (West 2008) and many medium-sized mammals have become extinct in the arid and semi-arid zones (McKenzie et al. 2007, Woinarski et al. 2014). Medium-sized mammal faunas are most intact in the temperate, tropical and sub-tropical zones (McKenzie et al. 2007), although many of these species have declined in the tropical zone since the 1980s (Woinarski et al. 2011, Ziembicki et al. 2015). Exotic medium-sized and large ungulates, as well as populations of arthropods, birds, reptiles and small mammals, occur throughout all the zones. The arid and semi-arid zones are characterised by variable rainfall that causes fluctuations in animal population densities (van Etten 2009, Letnic & Dickman 2010, Greenville et al. 2016). Local prey availability is likely to be an important determinant of dingo diets, but detailed availability data for such a broad range of possible prey species (invertebrates, birds, reptiles, small mammals, various larger mammals) do not exist for each of the bioclimatic zones and the majority of study sites. Nonetheless, it is still possible to test hypotheses concerning biogeographical patterns in dingo diets by comparing and contrasting the occurrences of prey in dingo scats or stomachs.

Based on previous work suggesting that dingoes prefer medium-sized (0.5–6.9 kg) and large (≥7 kg) mammals (Corbett 2001, Davis et al. 2015), we tested the following hypotheses:

1. Dietary occurrence of medium-sized mammals (excluding rabbits) will be highest in the temperate, tropical and sub-tropical zones (high environmental productivity), because these zones retain the greatest proportion of their original medium-sized mammal fauna (McKenzie et al. 2007, Fisher et al. 2014, Murphy & Davies 2014).
2. Dietary occurrence of arthropods, reptiles, rabbits, and small mammals will be highest in the arid zone (low environmental productivity), due to lower and fluctuating availability of alternative large prey (e.g. medium-sized mammals and kangaroos; Corbett & Newsome 1987, Doherty et al. 2015).
3. Dietary diversity will be highest in the arid and semi-arid zones, due to the fluctuating nature of prey availability and the predicted importance of arthropods, reptiles, rabbits, and small mammals in these zones.
4. In contrast to the diet of feral cats, dietary occurrence of medium-sized and large, but not small, mammals (excluding ungulates) will be negatively correlated with that of rabbits (Corbett & Newsome 1987, Corbett 2001, Doherty et al. 2015), because medium-sized and large mammals are likely to be the preferred prey of dingoes (Corbett 2001, Davis et al. 2015) unless an abundant alternative food source is available (i.e. rabbits).

We use the results to comment on the range of taxa that dingoes eat and discuss dingo dietary patterns and potential ecological roles at the continental scale.

METHODS

Data collation

We searched the Web of Science and Scopus databases for studies on the diet of dingoes in Australia using the following search string: (dingo OR dog OR wild dog OR "*Canis dingo*" OR "*Canis lupus dingo*" OR "*Canis familiaris dingo*") AND (diet OR predation OR ecology) AND (Australia). We sourced additional studies from reference lists, book chapters, theses, reports, and unpublished data sets. Data collation occurred between January 2015 and March 2017, inclusive. We assumed that authors took reasonable steps to avoid autocorrelation in scat sampling, including collecting appropriate numbers of scats over multiple seasons and over a large enough area, so as to characterise broadly the dietary ecology of each population. We applied the following criteria for including data sets: 1) data were recorded as the percentage frequency of occurrence (%*FO*) or could be converted to this metric (i.e. the percentage of sample units in a study [stomachs or scats] that contain a type of food); 2) sample size was ≥20 scats or stomachs; 3) samples were collected over more than one season; 4) samples were collected within a single bioclimatic zone; 5) the diet did not include a high occurrence (>30%*FO*) of human-provided food (e.g. rubbish); and 6) data were available for each of the nine food groups described below. We excluded studies for which sufficient information could not be obtained to assess eligibility. After screening all studies through our inclusion criteria, we included 73 data sets in our analyses (Appendices S1 and S2).

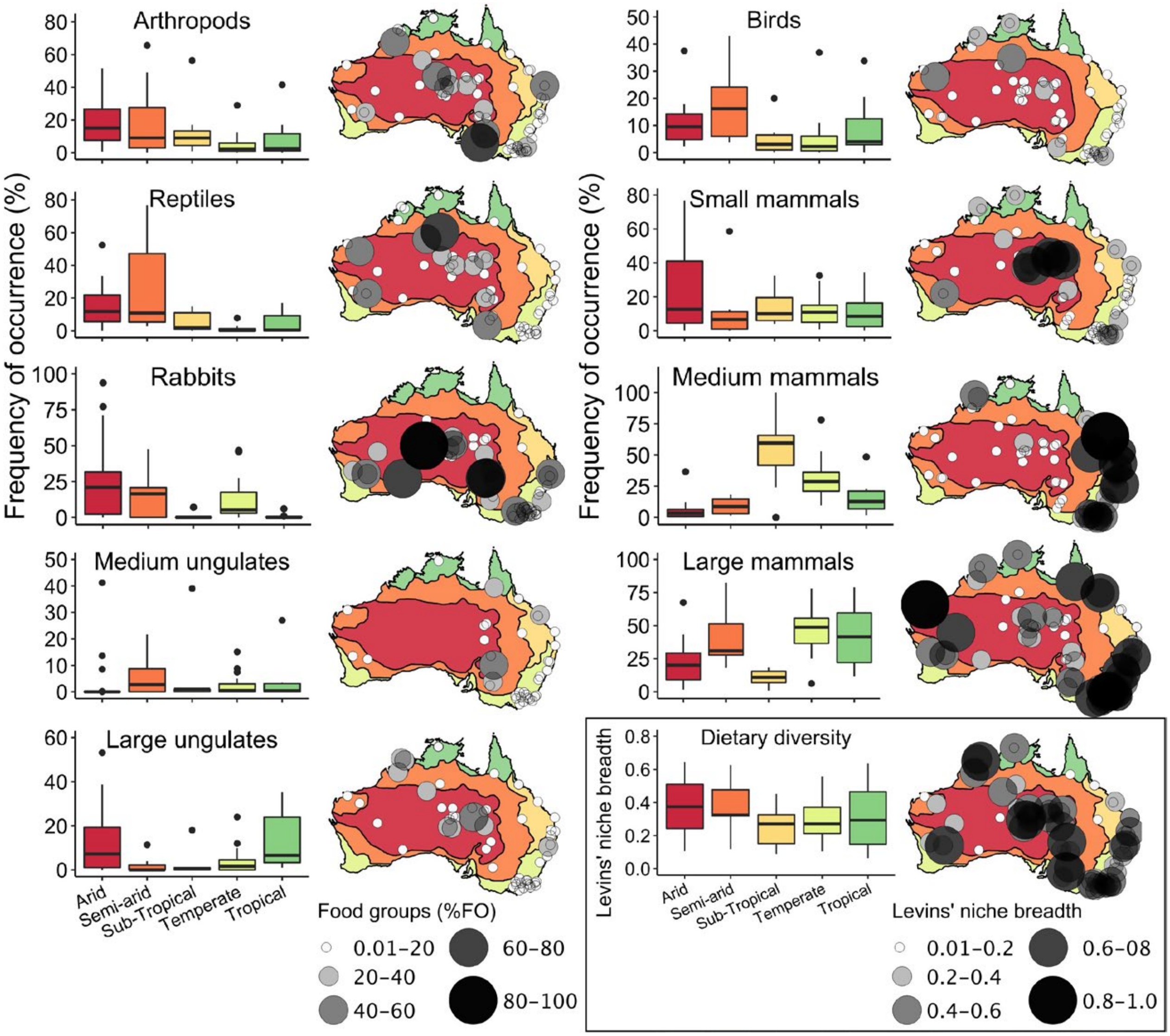

Fig. 2. Regional box plots and study site maps of nine food groups (frequency of occurrence) and dietary diversity (Levins' *B*; inset bottom right) in the diets of dingoes in Australia. Horizontal lines are medians, boxes show interquartile ranges, vertical lines are ranges, and black dots are outliers. The size and shading of the circles on the maps correspond with frequency of occurrence values (percentage of scats/stomachs containing each food group).

Table 1. Pairwise regional differences in dingo dietary composition in Australia based on multivariate linear models

		Arid	Semi-arid	Sub-tropical	Temperate
Semi-arid	*F*	37.24	–	–	–
	P	**0.002**			
Sub-tropical	*F*	78.61	70.66	–	–
	P	**<0.001**	**<0.001**		
Temperate	*F*	119.42	77.84	44.69	–
	P	**<0.001**	**<0.001**	**0.002**	
Tropical	*F*	33.79	32.29	40.52	17.69
	P	**<0.001**	**0.003**	**0.002**	0.082

Significant effects are indicated with bold text (Bonferroni-corrected significance level of 0.005).

Data on food volume or biomass are considered the most suitable metrics for inter-population studies (Klare et al. 2011). However, like other authors (Díaz-Ruiz et al. 2011, Doherty et al. 2015), we found that few studies used either of those metrics. Percentage frequency of occurrence (%*FO*) was the most consistently used measure and is considered a valid metric for comparison of individual food types between different studies (Klare et al. 2011). We therefore gathered data on the %*FO* of nine food groups: 1) arthropods; 2) reptiles; 3) birds; 4) European rabbits; 5) medium-sized (25–125 kg) and 6) large (169–825 kg) exotic ungulates (including livestock); and other

7) small (<0.5 kg), 8) medium-sized (0.5–6.9 kg), and 9) large (≥7 kg) mammals (Appendix S3). The latter three categories consist almost entirely of native mammal species, except for the introduced house mouse *Mus musculus*, black rat *Rattus rattus*, red fox, and domestic cat and dog. To avoid confusion between categories 5, 6, and 9, we refer to category 9 as 'large native mammals' throughout because the only introduced species it contains is the domestic dog. The weight ranges for categories 7–9 were chosen to allow comparison with previous studies (e.g. Glen et al. 2011, Davis et al. 2015, Doherty et al. 2015), although we acknowledge that other classifications have been used (e.g. Corbett 2001, Allen & Leung 2012). Small numbers of records of introduced European hares *Lepus europaeus* in dingo diets were pooled with rabbits, and they are referred to collectively as rabbits. In order to examine regional variation in occurrence of livestock in dingo diets, we also created a separate livestock category for the occurrence of sheep *Ovis aries* and cattle *Bos taurus* in dingo diets. For any values reported as '<1%', we recorded a value of 0.5%. If a study did not provide an overall value for the medium-sized or large mammal categories (categories 5–6 and 8–9 above), we calculated group %*FO* values by summing values across all species within a category. This approach assumes that the remains of only one medium-sized or large mammal are found in each scat/stomach, and is supported by the equivalence of group values and summed individual values reported in several data sets. We used a different approach for the small mammal category because multiple small mammal species are more likely to be found in a single scat/stomach (G. Story, personal observation). In that case, we used the value of the most frequently occurring species as the group value, which is a conservative estimate of the group value. If a study contained separate seasonal values but not overall values, we averaged data across all seasons.

We calculated study duration by counting the number of months between the start and end of collection periods and recorded seasons of data collection (summer, autumn, winter, spring). Study duration could not be obtained for one data set (Brisbane Valley, Appendix S2). We classified data sets according to the five bioclimatic zones (arid, semi-arid, tropical, sub-tropical, temperate; Fig. 1). We estimated site-level environmental productivity by averaging

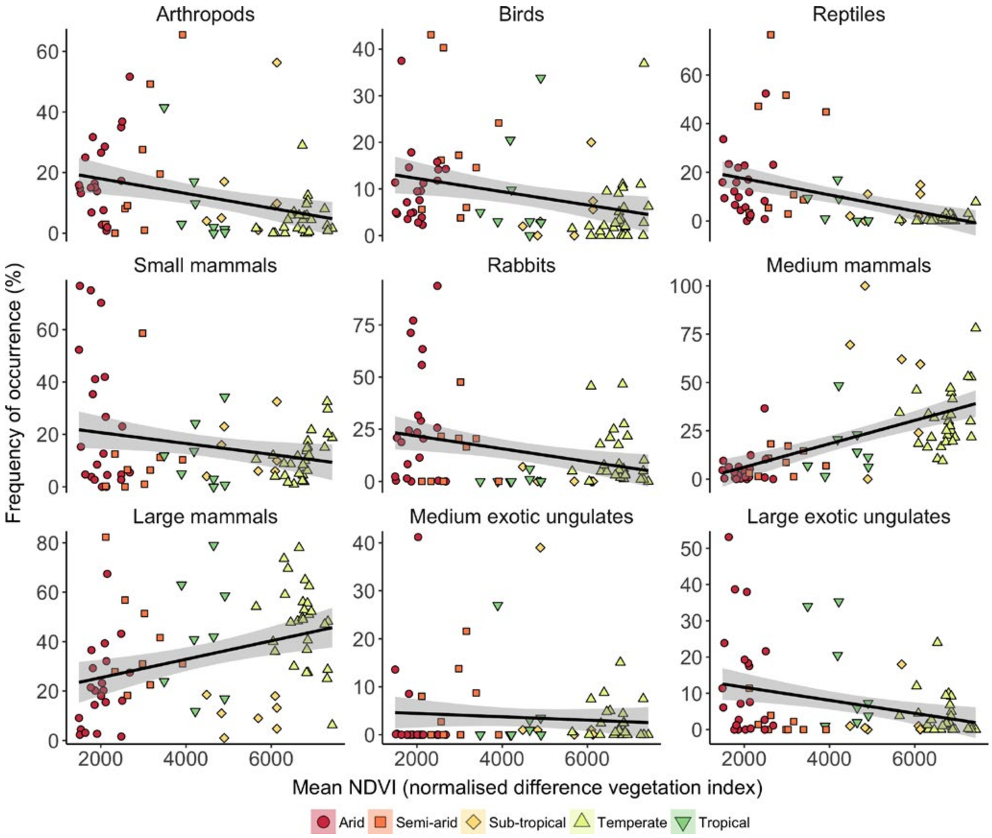

Fig. 3. Relationships between site environmental productivity (NDVI) and occurrence of nine food groups in the diets of dingoes in Australia. Black lines and grey shading are modelled linear relationships with 95% confidence bands. Each symbol represents one study.

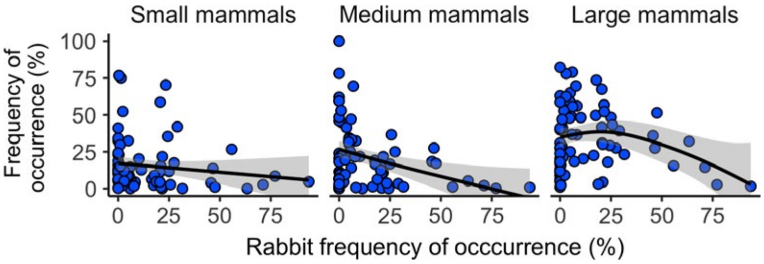

Fig. 4. The frequency of occurrence (%*FO*) of small, medium-sized and large mammals (excluding exotic ungulates) modelled as a function of rabbit frequency of occurrence in dingo diets in Australia. The solid black line is the fitted model mean and the shaded area represents the 95% confidence intervals of the predicted mean. Each symbol represents one study. The exclusion of the tropical zone studies where rabbits do not occur did not influence the nature of these relationships.

mean monthly long-term (1980–2010) normalised difference vegetation index (NDVI) grids (0.05°) from the Vegetation Index and Phenology Lab, University of Arizona (https://vip.arizona.edu/). We calculated mean NDVI in a 100-km radius around each study location centroid, except for coastal and island sites, which we restricted to coastal boundaries.

Statistical analyses

We compiled an inventory of vertebrate species and invertebrate groups recorded as eaten or killed by dingoes in Australia based on information in the dietary studies, as well as other published accounts of dingo predation (e.g. Banks et al. 2003). We use the term "Red Listed" to refer to those species classified as Critically Endangered, Endangered, Vulnerable, Near Threatened, or Data Deficient on the IUCN Red List of Threatened Species (IUCN 2017).

To test for bias caused by variation in sample size, study duration, sampling seasons, or sample material (scat or stomach), we constructed multivariate linear models using the *R* package mvabund (Wang et al. 2012, R Core Team 2016). We included all main terms and used a matrix of the nine food groups as the response variables. Alpha was set at 0.05, and multivariate *P*-values were calculated using 1000 residual resamples.

To address hypotheses 1–2, we assessed how dingo dietary composition varied according to bioclimatic zones and environmental productivity using multivariate linear models. We first specified bioclimatic zone as the predictor variable and a matrix of the nine food groups as the response variables, assuming multivariate normality of errors. We made pairwise comparisons between each level of zone using multivariate *P*-values based on 1000 residual resamples. We then used univariate tests to identify the individual variables that differed between zones. We present boxplots and maps of %*FO* data for each food group to show differences between zones. We then fitted an additional multivariate linear model using mean NDVI as the predictor variable, and we present scatterplots and modelled relationships between dietary occurrence of NDVI and the food groups.

To address hypothesis 3, we calculated dietary diversity using Levins' measure of niche breadth (Levins 1968), standardised on a scale from 0 to 1 (Levins' *B*) using the measure proposed by Hurlbert (1978, for formulas see Newsome et al. 2016). We measured dietary diversity using the nine food groups as the possible resource states. We used analysis of variance to determine if dietary diversity varied between zones. We also used analysis of variance to determine if the frequency of occurrence of livestock in dingo diets varied between zones.

To address hypothesis 4, we used generalised additive models (GAMs) to model the occurrence of small, medium-sized, and large mammals (excluding exotic ungulates) as a function of rabbit occurrence in dingo diets. We used GAMs to account for possible nonlinear relationships. Models were fitted in the R package mgcv (Wood 2011), assuming normality of errors and specifying an identity link function. Relationships were considered significant if *P* was <0.05. To avoid overfitting, we initially set the smooth term basis dimension (*k*) as 5 for all models and then checked model fit using the gam.check function; if the estimated degrees of freedom were close to *k*-1, we refitted the model using a higher *k* value and reassessed the model (Wood 2006).

RESULTS

From 73 data sets and 32225 dingo scats and stomachs, the mean sample size per study was 441 ± 102 (SE, standard error). We identified 229 vertebrate taxa (referred to here as species) that dingoes either prey or feed on in Australia: 62 small mammal species, 50 medium-sized mammals, 29 large native mammals (11 as marine debris), four medium-sized exotic ungulates, six large exotic ungulates, 50 birds, 26 reptiles (four as marine debris), and unidentified fish and frog species (Appendix S3). Of the vertebrate species, 66% were mammals, with smaller numbers of birds (22%), reptiles (11%), and other taxa. Of the mammals, 26% were large species (≥7 kg, including exotic ungulates), 33% medium-sized, and 41% small. Dingoes also ate insects from seven orders, as well as crustaceans and centipedes (Appendix S3). Thirty-nine native terrestrial species that are Red Listed were recorded in dingo diets: two Critically Endangered species, three Endangered, 18 Vulnerable, 15 Near Threatened and one indeterminate rock-wallaby species that is either Endangered or Near Threatened (Appendix S3). This represents approximately 6%, 5%, 19%, and 17% of the total number of species in each category in Australia, respectively (excluding the indeterminate species; IUCN 2017). Dingoes also ate nine Red Listed marine species that were presumably scavenged on beaches (Cheloniidae, Delphinidae, Physeteridae; Appendix S3; Behrendorff et al. 2016). Large native mammals were the most commonly occurring food group across all studies (mean ± SE = 35 ± 2%*FO*), followed by medium-sized mammals (21 ± 2), small mammals (15 ± 2), rabbits (14 ± 2), arthropods (12 ± 2), reptiles (9 ± 2), birds (9 ± 1), and large (7 ± 1) and medium-sized (4 ± 1) exotic ungulates.

The multivariate linear analysis revealed no effect of sample material ($F_{2,69}$ = 6.47, P = 0.715), sample size ($F_{1,68}$ = 6.82, P = 0.546), study duration ($F_{1,67}$ = 7.14, P = 0.584), or season ($F_{8,59}$ = 8.10, P = 0.663) on the %*FO* of food groups in dingoes' diets. We therefore pooled studies with varying sample sizes, durations, sample materials, and seasons for further analysis.

Regional patterns (hypotheses 1–3)

Dietary composition, based on frequency of occurrence, varied across bioclimatic zones ($F_{4,68}$ = 59.99, P = 0.002), and pairwise tests showed that all zones were different to each other, except for the temperate and tropical zones (Table 1). Dietary occurrence of arthropods was highest in the arid and semi-arid zones, and lowest in the temperate and tropical zones (F = 4.19, P = 0.010; Fig. 2). Occurrence of birds (F = 4.68, P = 0.007) and reptiles (F = 10.18, P = 0.002) in diets was highest in the arid and semi-arid zones (Fig. 2). Dietary occurrence of small mammals did not vary according to zone (F = 1.98, P = 0.110), although the highest values and greatest variability occurred within the arid zone (Fig. 2). Rabbit occurrence in diets was highest in the arid and semi-arid zones, and lowest in the tropical and sub-tropical zones (F = 5.09, P = 0.005; Fig. 2). Medium-sized mammals occurred in dingo diets most frequently in the temperate and sub-tropical zones (F = 18.31, P = 0.002; Fig. 2). Large native mammals occurred in dingo diets most frequently in the semi-arid, temperate and tropical zones, and least frequently in the arid and sub-tropical zones (F = 10.89, P = 0.002; Fig. 2). Dietary occurrence of large exotic ungulates was highest in the arid and tropical zones (F = 4.11, P = 0.008), whereas occurrence of medium-sized exotic ungulates did not vary according to zone (F = 0.58, P = 0.708; Fig. 2). Dingo dietary diversity did not vary according to zone ($F_{4,68}$ = 1.88, P = 0.124), although the highest values generally occurred in the arid and semi-arid zones (Fig. 2). Occurrence of livestock (cattle and sheep) in dingo diets varied between zones ($F_{4,68}$ = 3.46, P = 0.013), with the highest values occurring in the arid (mean ± SE = 13 ± 3%*FO*) and tropical (13 ± 5) zones, and much lower values in the semi-arid, sub-tropical, and temperate zones (range of means = 0.3–6%*FO*).

Dietary composition also varied according to environmental productivity ($F_{1,71}$ = 110.1, P = 0.002). The frequency of occurrence of arthropods (F = 9.68, P = 0.004), birds (F = 7.05, P = 0.010), reptiles (F = 20.78, P = 0.002), small mammals (F = 4.74, P = 0.039), rabbits (F = 7.95, P = 0.009), and large exotic ungulates (F = 9.11, P = 0.003) decreased with increasing NDVI (Fig. 3). The dietary occurrence of medium-sized (F = 39.20, P = 0.002) and large (F = 10.97, P = 0.002) mammals increased with NDVI, whereas occurrence of medium-sized exotic ungulates showed no relationship (F = 0.60, P = 0.459; Fig. 3).

The influence of rabbits (hypothesis 4)

Occurrence of rabbit in dingo diets was negatively correlated with that of medium-sized mammals (estimated degrees of freedom, e.d.f. = 1.11, F = 7.35, P = 0.005), but not small mammals (e.d.f. = 1.00, F = 1.41, P = 0.239) or large native mammals (e.d.f. = 2.00, F = 2.78, P = 0.071; Fig. 4).

DISCUSSION

Our study is the most comprehensive analysis of the diet of dingoes in Australia to date. We reveal that this top predator has a flexible and generalist diet that differs among bioclimatic zones and includes more than 200 vertebrate species. In partial support of our first and second hypotheses, medium-sized mammals occurred in dingo diets in high frequencies in the temperate and sub-tropical zones, whereas rabbits, reptiles, and arthropods occurred most frequently in the arid and semi-arid zones. The analysis based on environmental productivity (NDVI) provided further support for these results. These results are consistent with Davis et al. (2015), who found that mammals occurred most frequently in wild dog diets in the wetter, montane parts of the State of Victoria (south-eastern Australia), whereas reptiles, insects, and plant material were more common in diets in the semi-arid parts of the State. Similarly, Corbett (2001) found that reptile occurrence in dingo diets was highest in arid central Australia. This may be because lizard species richness is highest in the central deserts and lowest in the south-east (Powney et al. 2010). Reptile occurrence in the diets of feral cats (Bonnaud et al. 2011, Doherty et al. 2015) and European wildcats (Lozano et al. 2006) has also been linked to biogeographical patterns in reptile species richness. The high dietary occurrence of arthropods in arid areas illustrates the adaptability of dingo diets (Letnic & Dickman 2010). It is not clear from our analysis whether dingoes feed heavily on invertebrates when they are abundant and potentially most profitable (due to their high protein content and ease of handling), or if dietary occurrence increases only when other prey is less available – similar to coyotes *Canis latrans* increasing their consumption of soft-mast when deer abundance is low (Swingen et al. 2015).

The high occurrence of medium-sized mammals in dingo diets in the high-productivity temperate and sub-tropical zones – but not in the tropical zone – is similar to the pattern recorded for feral cats in Australia (Doherty et al. 2015, but see Stokeld et al. 2018). This pattern probably occurs because a larger proportion of medium-sized mammals persist in mesic eastern Australia compared to in arid regions of the continent, where many species of medium-sized mammals are now rare or extinct (McKenzie et al. 2007, Woinarski et al. 2015). Populations of medium-sized mammals have also declined in the tropical zone since the 1980s (Woinarski et al. 2011, Ziembicki et al. 2015), which could limit their availability as a food source for dingoes. Further, extant medium-sized mammals may persist at lower densities in the arid zone than in mesic, coastal regions, due to lower environmental productivity, although this requires further investigation.

Despite regional variation in the occurrence of individual food types in dingo diets, we found less evidence that the diversity of diets differed between bioclimatic zones (hypothesis 3). If dingoes were to be characterised as prey specialists, as suggested by Corbett (2001), we would have expected much lower average dietary diversity values in some zones. There were, however, some outliers. The lowest dietary diversity score was from a study in Kakadu National Park, Northern Territory, where large native mammals (agile wallaby *Notamacropus agilis* and other macropods) dominated the dingo's diet (Stokeld et al. 2016). Similarly low dietary diversity scores were recorded from a study in Shoalwater Bay, Queensland (Allen et al. 2012), and in the Blue Mountains, New South Wales (Pascoe et al. 2011), where medium-sized mammals (primarily possums *Trichosurus vulpecula* and unidentified peramelid bandicoots) and large native mammals (swamp wallaby *Wallabia bicolor* and other macropods) dominated dingo diets, respectively. Dingoes may focus on specific prey groups in some instances, especially in circumstances where particular prey are superabundant (e.g. waterbirds; Newsome et al. 1983). In general, however, we conclude that dingoes have a flexible and generalist diet that changes in relation to both spatial (this study; Cupples et al. 2011, Davis et al. 2015) and temporal (Corbett & Newsome 1987, Paltridge 2002, Forsyth et al. 2018a, Stokeld et al. 2018) variation in prey availability.

We found partial support for our fourth hypothesis – where rabbits occur in the diet of dingoes less frequently, the frequency of other medium-sized, but not large mammals, increases in the diet of dingoes. Dietary occurrence of rabbits was greatest in the low-productivity arid and semi-arid zones where the largest numbers of medium-sized mammals have become extinct, or have otherwise declined (McKenzie et al. 2007, Woinarski et al. 2014). It is possible that, prior to their decline, native medium-sized mammals constituted the majority of dingoes' diets in arid Australia, but they have since been replaced by rabbits. The decline of many medium-sized mammals could also explain the high occurrence of small mammals, reptiles and arthropods in dingo diets in arid Australia, although records of dingo diet and prey availability estimates from before European colonisation of Australia are needed to confirm this. Occurrence of rabbits and large native mammals in dingo diets showed no relationship when rabbit occurrence was less than ~30%*FO*, but above this the occurrence of large native mammals in dingo diets tended to decrease. This pattern was mostly driven by six studies from arid or semi-arid sites containing the highest occurrence of rabbit in dingo diets (48–94%*FO*). One of those studies (Corbett & Newsome 1987) found that rabbits formed a consistent component of dingo diets irrespective of abundance, whereas large mammals (red kangaroos *Osphranter rufus*) occurred in the diet most frequently during times of drought. This suggests that the dingo's diet is not always functionally related to the abundance of its prey. A fruitful area for future research lies at the intersection of biogeography and optimal foraging theory (Costa et al. 2008, Sandvik et al. 2016), particularly regarding the effects of biogeographical variation in prey availability on foraging behaviour.

CONCLUSIONS

The number of Red Listed species occurring in dingo diets (39 species) was higher than that in the diets of feral cats (28), even though cats ate almost double the number of species that dingoes did (400 and 229 species, respectively; Doherty et al. 2015). The presence of threatened species in dingo diets is consistent with direct observations of dingo predation on remnant (Fisher et al. 2000) and reintroduced (Moseby et al. 2011, Cremona et al. 2017) mammal populations. These species presumably co-existed with dingoes prior to European colonisation, but today, a combination of small population sizes, predator naivety of reintroduced animals and interactions between multiple threatening processes (e.g. altered fire regimes, habitat loss, and high rates of predation by red foxes and/or feral cats) means that some species are particularly vulnerable to even low levels of predation (Cremona et al. 2017). Therefore, predation by dingoes should be a key consideration when populations of threatened species are being established outside of predator-free reserves. It is also important to consider the net effects of dingoes on species and ecosystems (Nimmo et al. 2015), since dingoes can suppress populations of large herbivores (Allen et al. 1996, Morris & Letnic 2017, Forsyth et al. 2018b) and influence the behaviour and possibly density of introduced mesopredators (Letnic et al. 2011, Brook et al. 2012, Newsome et al. 2017).

A key factor influencing how dingoes are managed is the level of predation they inflict on livestock. Our analysis revealed that the occurrence of livestock (i.e. sheep and cattle) in dingo diets was the highest in the arid and tropical zones, where average %*FO* was 13%. However, relatively few studies have been conducted in areas where intensive livestock grazing occurs, so our results are likely to underestimate the occurrence of livestock in dingo diets. Further, Thomson (1992) noted that dingoes can kill sheep in excess without eating them, which means that dietary studies may underestimate the impacts of these predators on livestock. Dietary studies are also unable to discriminate between predation and consumption of carrion, and cannot detect the non-lethal impacts of dingo attacks on livestock. Further studies are therefore needed to quantify the impacts of dingoes on livestock fully. Research should include comparisons of rates of killing and rates of consumption (e.g. scavenging of carrion vs. predation), assessment of whether lethal control of dingoes actually decreases livestock losses attributed to dingoes (Allen 2014, 2015, Campbell et al. 2018), and evaluation of the net effects of dingoes on pastoral production (Prowse et al. 2014).

Overall, our continent-wide analysis of dingo diet supports the idea that dingoes have a flexible and generalist diet that differs among bioclimatic zones and with environmental productivity in Australia. The possible drivers of these differences include high reptile species richness in arid areas, the decline and extinction of many medium-sized mammal species in central and northern Australia, and the absence of introduced rabbits from the far northern tropics. Future shifts in prey communities are likely to result from ongoing declines in populations of native mammal species, more effective control of introduced species, and changing land management practices, particularly under climate change. Further research on the consequences of these changes for the diets of dingoes will advance our understanding of the foraging behaviour of dingoes and their functional roles in ecosystems.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Reference list of published studies that contributed data to the analyses of this study.
Appendix S2. Summary of the data sets used in the analyses.
Appendix S3. List of taxa eaten by dingoes and the IUCN Red List category of the native species.