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REVIEW

Diet of the introduced red fox *Vulpes vulpes* in Australia: analysis of temporal and spatial patterns

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ABSTRACT

1. The red fox *Vulpes vulpes* is one of the world's most widespread carnivores. A key to its success has been its broad, opportunistic diet. The fox was introduced to Australia about 150 years ago, and within 30 years of its introduction was already recognised as a threat to livestock and native wildlife.

2. We reviewed 85 fox diet studies (totalling 31693 samples) from throughout the species' geographic range within Australia. Mammals were a major component of fox diet, being present in 70 ± 19% of samples across $n = 160$ locations. Invertebrates (38 ± 26% $n = 130$) and plant material (26 ± 25% $n = 123$) were also both staple foods and often the dominant food category recorded. Birds (13 ± 11% $n = 137$) and reptiles (10 ± 15% $n = 132$) were also commonly reported, while frogs were scarcely represented (1.6 ± 3.6% $n = 111$) in fox diet studies.

3. Biogeographical differences reveal factors that likely determine prey availability. Diet composition varied with ecosystem, level of vegetation clearing and condition, and climate zone.

4. Sample type (i.e. stomach versus scat samples) also significantly influenced reporting of diet composition. Livestock and frogs were underrepresented in records based on analysis of scats, whereas small mammals (native rodents, dasyurid marsupials, and bats) were more likely to be recorded in studies of scats than in studies of stomach contents.

5. Diet varied seasonally, reflecting activity patterns of prey species and food availability. This synthesis also captures temporal shifts in fox diet over 70 years (1951–2020), as foxes have switched to consuming more native species in the wake of successful broadscale biological control of the invasive European rabbit *Oryctolagus cuniculus*.

6. Diet analyses, such as those summarised in this review, capture the evidence required to motivate for greater control of foxes in Australia. This synthesis also highlights the importance of integrated pest species management to meet biodiversity conservation outcomes.

INTRODUCTION

The red fox *Vulpes vulpes* is one of the world's most widely distributed and adaptable carnivores, occupying habitats as varied as arctic tundra, arid deserts, and metropolitan centres (Macdonald 1987, Voigt 1987). Since its introduction to Australia 150 years ago, the fox has become one of the greatest threats to the country's native wildlife (Abbott et al. 2014). Within 30 years of their deliberate release, foxes were already proclaimed to be pests, initially due to their predation of livestock, particularly newborn lambs. Impacts on native wildlife have also been devastating. The fox has contributed to the extinction of an estimated 14 native mammal species and one bird species (Woinarski et al. 2019), and to the ongoing suppression or decline of many others (Stobo-Wilson et al. 2021, Woinarski et al. 2021).

Fox populations have established throughout the southern two thirds of the Australian mainland, i.e. excluding the island of Tasmania and the far northern monsoonal tropics (Centre for Invasive Species Solutions 2011; Fig. 1a). They occur at high densities in several cities (Bateman & Fleming 2012) and are considered urban pests due their potential role in transmission of zoonotic disease (Marks & Bloomfield 1999a,b). In response to the threat posed by foxes to livestock production and native wildlife, they have been the subject of high intensity and broadscale control operations in many Australian habitats (Saunders et al. 1995, Saunders & McLeod 2007).

Further resolving the impacts and improving management of this invasive predator requires that we know more about its biology, including its diet. Foxes are exceptionally successful opportunistic carnivores (Dell'Arte et al. 2007, Henry 2013, Soe et al. 2017), consuming a broad range of food items, including carrion, live vertebrate prey of a range of sizes, invertebrates, vegetation, fruit, and human refuse (e.g. Stepkovitch 2017). Understanding biogeographical patterns in diet can also be informative in

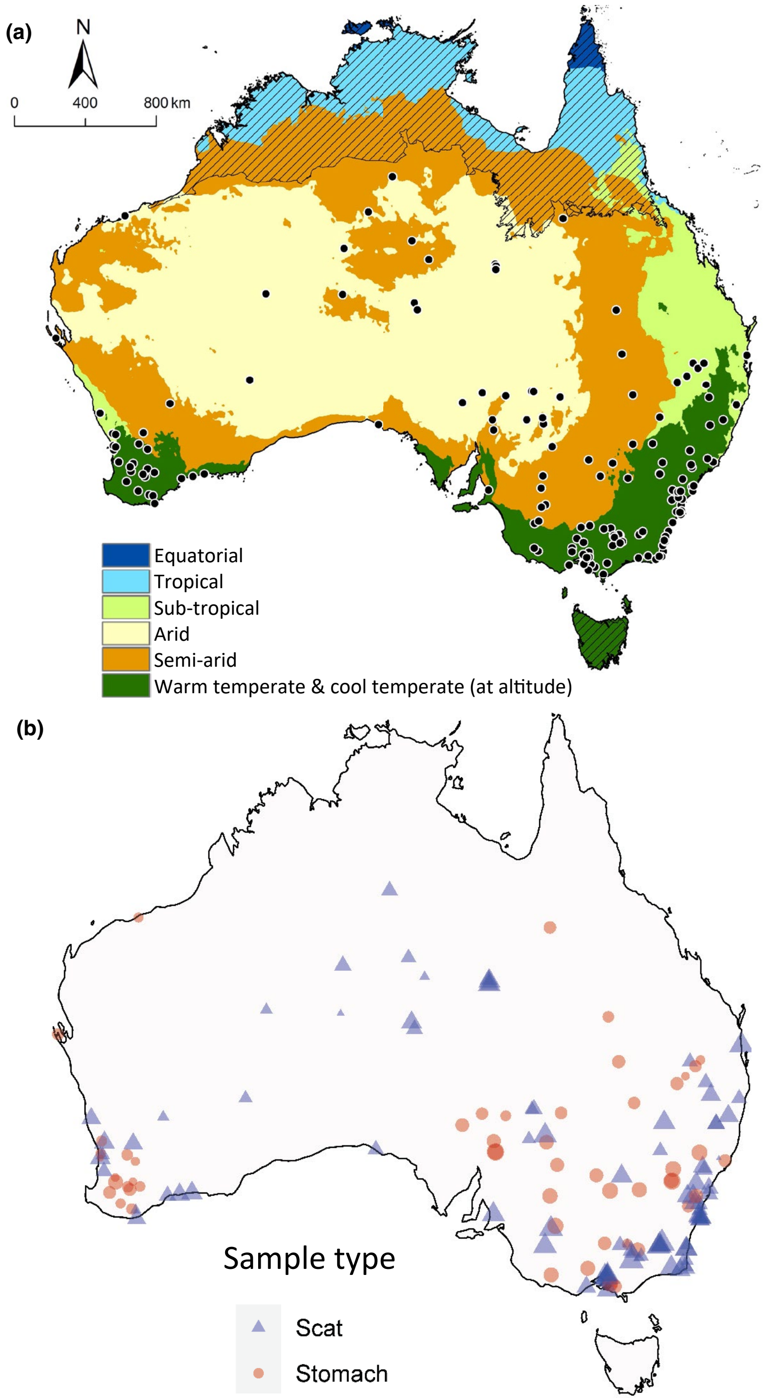

Fig. 1. Locations of Australian studies of diet of red foxes *Vulpes vulpes* analysed in this study. (a) Locations (black circles) shown by bioclimatic zone (biogeographical regions of Australia). The geographic range of the red fox in Australia does not extend north of ~18°S into the equatorial or tropical bioclimatic zone, and introductions to Tasmania have not become established: the hatched overlay shows areas where foxes are not recorded in the Atlas of Living Australia. (b) Showing sample size (relative size of the dots) and sample types (blue triangles = scats analysis, red circles = stomach contents analysis). [Colour figure can be viewed at wileyonlinelibrary.com]

describing and identifying potential avenues for conservation management. Díaz-Ruiz et al. (2013) reviewed 55 studies of red fox diet from the Iberian Peninsula and found shifts in diet composition with latitude and elevation. More broadly, Soe et al. (2017) reviewed 66 studies from 17 European countries and found similar influences of latitude and temperature gradients, as well as the level of anthropogenic modification. Both reviews identified the importance of lagomorphs (principally European rabbits *Oryctolagus cuniculus*) in the diet of the red fox in Europe.

Like foxes, European rabbits were introduced into Australia: the first feral population was established by 1859. They rapidly spread across the southern two thirds of the continent, reaching plague proportions by the 1920s (Brown et al. 2020). Where rabbits are available, they are a significant diet component for foxes in Australia (Catling 1988, Saunders et al. 1995). The spread of rabbits across the continent is likely to have facilitated the dispersal of the fox in their wake (Abbott et al. 2014), and bolsters fox populations where the species coincide. Furthermore, it is likely that the availability of rabbits supplements predator populations, which in turn prey on native species (Courchamp et al. 2000, Abbott et al. 2014, Pintor & Byers 2015, Pedler et al. 2016, Allen et al. 2018). In response to the economic threat posed by rabbits, the myxoma virus was released in Australia in the 1950s, and within months, it had reduced some rabbit populations by 90%. The virus became less effective over time, however, warranting the subsequent introduction of rabbit haemorrhagic disease virus (herein termed 'RHDV-1') in 1996 and more lethal strains of the virus ('RHDV-1 K5') introduced since 2010 (Mutze et al. 1998, Read & Bowen 2001, Mutze et al. 2014, Centre for Invasive Species Solutions 2015). There are concerns that increased control of rabbits will increase the threat posed by foxes to native species. Analyses of changes in red fox diet over space and time can therefore provide insight into whether rabbit biocontrol influences fox diet.

Although there have been reviews on the impacts of foxes that draw heavily on diet studies (e.g. Saunders et al. 2010), there has been no review of diet studies in Australia. We reviewed data from 85 studies that have quantified the diet of the fox throughout its geographic range in Australia. To account for methodological differences among studies, we examined firstly whether sample type (stomach or scat samples) influenced fox diet. Secondly, temporal patterns in diet were examined, including season as a measure of differences in activity patterns for prey types, and year of collection to capture changing use of rabbit prey in the wake of their biocontrol. Thirdly, we tested for spatial patterns in diet, since ecosystem, climate zone, mean rainfall and temperature, as well as human population density and habitat modification, can influence the availability of food plants and fauna.

METHODS

We collated published information on fox diet in Australia by systematically searching through Web of Science, Google Scholar and Scopus databases, with relevant search terms (for details, see Appendix S1). We sourced additional studies from reference lists: book chapters, theses, reports, and unpublished datasets. We contacted authors where their published data did not provide sufficient details for subsequent analyses. We included data from 85 studies (Appendix S1), with collections commencing in 1951 (Frith 1962) and continuing to 2020, tallying 31693 samples. For each study with a minimum of $n = 10$ samples, we extracted data on diet composition (using frequency of occurrence, FOO, the proportion of all samples for which each of 20 food categories was recorded; Appendix S2). FOO values were separately calculated for mammals by broad taxonomic grouping or origin following Murphy et al. (2019):

1. Introduced mammals included introduced rodents; lagomorphs (Lagomorpha; principally European rabbits but also a few records of European brown hares *Lepus europaeus occidentalis*); livestock; domestic cats *Felis catus*; dogs/dingoes *Canis familiaris*. We also recorded the incidence of fox remains in fox diet, and noted where this was likely to be eaten as part of their diet (in contrast with auto-grooming hairs).
2. Native mammals included monotremes (principally short-beaked echidna *Tachyglossus aculeatus*; few records of platypus *Ornithorhynchus anatinus*); dasyurids (Dasyuridae); marsupial moles (Notoryctidae *Notoryctes* spp.); possums and gliders (Phalangeriformes; commonly Phalangeridae and Pseudocheirinae); bandicoots (Peramelemorphia); koala (Phascolarctidae *Phascolarctos cinereus*); wombats (Vombatidae); macropods (Macropodidae) and potoroids (Potoroidae); native rodents (subfamily Murinae); and bats (principally fruit bats Pteropodidae *Pteropus* spp.).

Diet composition analyses (all food categories analysed together)

To test for differences in the overall composition of the diet of foxes explained by various predictor variables, non-metric multidimensional scaling analysis (nMDS) followed by non-parametric permutational ANOVA (PERMANOVA) was carried out using the 'adonis' function in the *vegan* package (version 2.5-6; Oksanen et al. 2013) in R (version 3.5.2; R Core Team 2013). Diet composition analyses were carried out for 20 food categories (Appendix S2) and only included the subset of those studies that did not have missing data, because nMDS and PERMANOVA require a complete dataset. The predictor variables were as follows:

1. Sample type – scats or stomach contents.
2. Temporal variables: season (separated by seasons or a fifth category that included all data pooled) and year

of collection (midpoint between the start and finish of sample collection).

3. Nine site variables capturing spatial variation derived for a 5 km radius around the study site coordinates (details in Appendix S3): ecosystem category (forest, woodland, grasslands, agricultural, and urban/peri-urban), climate zone (arid, semi-arid, subtropical, warm temperate, and cool temperate), mean annual precipitation, mean annual temperature, distance to the coastline (in kilometres, km), mean terrain ruggedness, vegetation condition/modification [using the Vegetation Assets, States and Transitions (VAST) classification scaled 0–6 from least to most intact], vegetation cover, and human population density.

Human population density and terrain ruggedness were log-transformed, and vegetation cover was square-root-transformed to deal with heteroscedasticity in these variables. Continuous variables were mean-standardised. Because the analysis preferentially weights factors in the order that they are introduced into the analysis, each predictor variable was first analysed individually and then subsequently introduced to the nMDS analysis from strongest to weakest influence on diet composition.

Associations for each individual food category

We analysed variables that influenced the FOO of each of the 20 food categories by fitting separate generalised linear models (GLMs). As candidate models, we examined all combinations of:

1. Sample type.
2. Temporal variables: season [included as a dummy variable (= 1) in one of four season columns ascribing the season when the samples were collected; for studies where no details on time of year of sampling were available, all season columns were marked as nil (= 0) for that study] and year of sample collection.
3. Nine site variables capturing spatial variation (Appendix S3).

We tested for model fit using the quartile–quartile plot fit function in the DHARMa package (Hartig & Lohse 2020) in R. This analysis indicated overdispersion of residuals in 13 food categories, where there was a high proportion of zeros. A negative binomial fit was inappropriate because the data were non-integers and therefore a tweedie GLM was fitted to these food categories (Appendix S2) with the alpha value set in each model to maximise normality of residuals as indicated using the 'tweedie' package (Dunn 2017) in R. Candidate models for each food category were weighted according to the Akaike Information Criterion corrected for small sample size (AICc; Burnham & Anderson 2002) or tweedie-AIC value (t-AIC; Dunn 2017), as appropriate, and we averaged beta estimates across those models that were within <2 units of the best model using *dredge* in the MuMIn package (Barton & Barton 2020) in R. For categorical variables (climate zone and ecosystem), we identified where they were influential by calculating their relative variable importance, defined as the sum of Akaike weights for the top models (ΔAICc or t-AIC < 2) containing the factor. For continuous variables, we calculated the sum of model-weighted beta estimates and 95% confidence interval (with *P*-values) for each of the variables retained within the top model set to visualise their effects.

To identify relationships with lagomorphs, we repeated the GLM for native prey species including lagomorph FOO as an additional predictor variable. For food categories where lagomorphs were retained in the top models, we used *ggeffect* in the 'car' package in R to illustrate the relationships with year of sample collection and relationship with lagomorph FOO (keeping other predictor variables retained in the top models for that food category constant).

Newsome and Corbett (1975) and Sinclair et al. (1990) proposed that predators can suppress the build-up ('plagues') of introduced house mouse *Mus musculus* populations. To determine whether there was a greater incidence of introduced rodents in fox diet during house mouse plagues, for study sites that lie within the extent of the mouse plague-prone region of eastern Australia (fig. 2 of Singleton et al. 2005), we identified those fox diet studies that overlapped with years when a plague was recorded within the same state (Peter Brown, CSIRO, unpublished data, Mutze 1989, Singleton et al. 2005). We compared introduced rodent FOO by plague year (yes/no) using Student's *t*-test.

All values are presented as arithmetic means ± 1 standard deviation (followed by range: [minimum–maximum]). Differences in sample size are due to ability to distinguish food categories between studies; for example, a study may record 'mammals' consumed but may not have sufficient data to distinguish whether these were introduced or native species.

RESULTS

The 85 fox diet studies were distributed throughout the fox's geographic range in Australia (Fig. 1b) and spanned collections over 70 years (1951–2020). Mean sample sizes were 118 ± 146 (range: 12–879) for n = 52 data points for stomach analyses (total 6113 stomachs) and 263 ± 381 (range: 10–1888) for n = 91 data points for scat analyses (total 23897 scats).

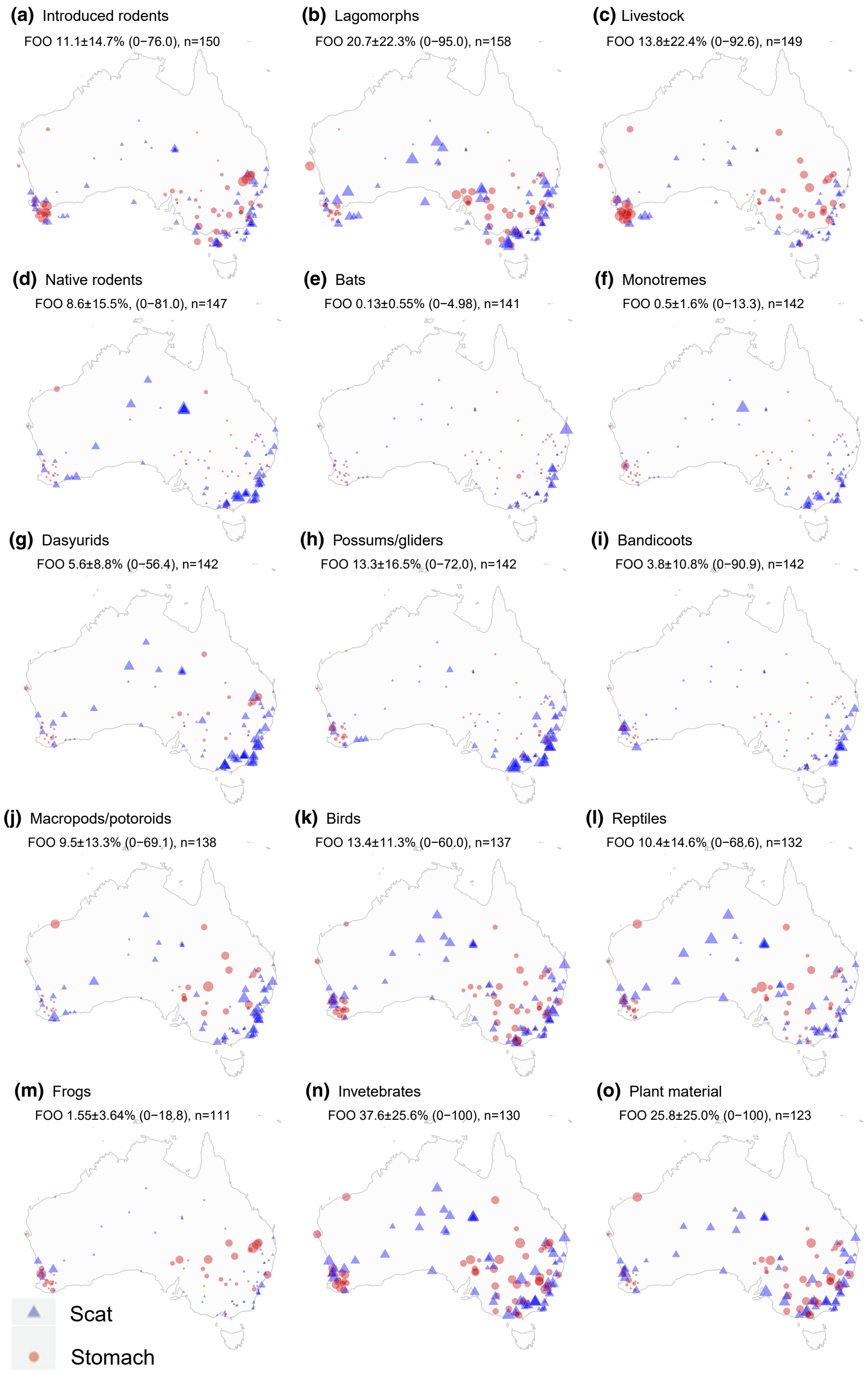

Fig. 2. Frequency of occurrence (FOO) of 15 of the 20 food categories consumed by red foxes *Vulpes vulpes* in Australia. Five mammal taxa were not common diet items (cat, dingo/dog) or do not have wide geographic ranges (marsupial mole, koala, wombat), and are therefore not shown. The size of the dots reflects frequency of occurrence, and the shape reflects sample types (blue triangles = scats analysis, red circles = stomach contents analysis). [Colour figure can be viewed at wileyonlinelibrary.com]

Description of fox diet

Mammals were a major component of fox diet (Fig. 2). Across all 85 studies, mean FOO for mammal prey was 70 ± 19% (n = 160 separate location data points), made up of marginally more introduced than native mammal species (39 ± 28%, n = 148 vs. 35 ± 27%, n = 148; Fig. 2a-j). Feral cat (0.4 ± 1.8% [0–19], n = 140) and dog/dingo (0.3 ± 1.5% [0–14], n = 141) were scarcely recorded. There was low incidence of fox (1.5 ± 3.3% [0–21], n = 140).

Birds (13 ± 11% [0–60.0], n = 137; Fig. 2k) and reptiles (10 ± 15% [0-68.6], n = 132; Fig. 2l) were also reported by most Australian fox diet studies, in contrast with frogs, which were scarcely represented (1.6 ± 3.6% [0–18.8], n = 111; Fig. 2m). Invertebrates occurred frequently in fox diet and were often the dominant food group (38 ± 26% [0–100], n = 130; Fig. 2n). Plant material was recorded in a mean of one in four fox diet samples (26 ± 25% [0–100], n = 123; Fig. 2o) and comprised mostly fruit, grain, or grass.

Factors influencing diet composition

Complete data (i.e. no missing values) were available for 26 studies representing 62 unique location/season combinations. Two thirds of the variation in diet composition could be accounted for by the predictor variables included in this analysis (sum of R^2 values in PERMANOVA; Table 1).

Table 1. Summary of non-parametric permutational analysis of variance (PERMANOVA) of diet composition for red fox *Vulpes vulpes* diet studies in Australia: 26 studies representing 62 location data points. Diet composition analyses were carried out for 20 food categories (introduced rodents, lagomorphs, livestock, cats, dogs/dingoes, monotremes, dasyurids, marsupial moles, possums/gliders, bandicoots, koalas, wombats, macropods/potoroids, native rodents, bats, birds, reptiles, frogs, invertebrates, and plant material). Predictor variables (three sampling variables in italics, and eight site variables) were introduced into the model in order from strongest to weakest relationship (top to bottom of this table) for each individual predictor variable (each predictor variable was tested first separately). d.f., degrees of freedom, F statistic, R^2, coefficient of determination, and P value: *P < 0.05, **P < 0.01, and ***P < 0.001. VAST: Vegetation Assets, States and Transitions classification scaled 0–6 from least to most intact

Predictor variables	d.f.	F	R^2	P
Ecosystem	4	8.49	0.267	0.001***
Vegetation cover (5 km)	1	10.33	0.081	0.001***
Season	4	2.49	0.078	0.003**
Sample type	1	1.98	0.016	0.063
VAST class	1	1.34	0.010	0.253
Climate zone	3	2.46	0.058	0.002**
Terrain ruggedness (5 km)	1	3.57	0.028	0.007**
Human population density (5 km)	1	3.69	0.029	0.006*
Year of collection	1	7.56	0.059	0.001***
Distance to coast (km)	1	2.39	0.019	0.042*
Mean annual temperature	1	3.20	0.025	0.013*
Residuals	42		0.330	
Total	61		1.000	

Ecosystem category was the strongest factor influencing fox diet composition (PERMANOVA: R^2 = 0.267, P = 0.001; Table 1) and was retained in the top model set for 11 food categories (Fig. 3). Ecosystem was included in all top models describing the incidence in fox diets of introduced rodents (11 ± 15% [0–76], n = 150 site/season data points; more common as prey in agricultural landscapes). Native mammals were most common in fox diet in forest, grassland and urban landscapes. Ecosystem was similarly included in all top models describing the FOO of native rodents (8.6 ± 16% [0–81], n = 147), monotremes (0.5 ± 1.6% [0–13], n = 142), dasyurids (5.6 ± 8.8% [0–56], n = 142), possums/gliders (13 ± 16% [0–72], n = 142), bandicoots (3.8 ± 11% [0–91], n = 142), wombats (0.4 ± 1.1% [0–8], n = 142), kangaroos (9.5 ± 13% [0–69], n = 138), invertebrates and plant material consumption.

Vegetation cover also had a strong influence on fox diet composition (PERMANOVA: R^2 = 0.081, P = 0.001; Table 1, Fig. 4). Summed introduced mammal FOO showed a negative correlation with vegetation cover (P < 0.001): the most common mammal prey taken by foxes was lagomorphs (21 ± 22% [0–95], n = 158; Fig. 2b), while livestock (particularly sheep) were also common in fox diet (14 ± 22% [0–93], n = 149; Fig. 2a). Both these categories were more common in fox diet with low vegetation cover (lagomorphs: P < 0.001, livestock: P = 0.011). By contrast, summed native mammal FOO showed a positive correlation with vegetation cover (P < 0.001). There were strong relationships for three food categories: dasyurids (P = 0.001), possums/gliders (P = 0.001), and macropods/potoroids (P = 0.010) were all more common in fox diet at sites with greater vegetation cover.

Native rodent FOO (P = 0.002) was inversely correlated with vegetation condition (VAST class; Fig. 4); i.e., native rodents were more common as prey around intact vegetation, while possum/glider FOO (P = 0.004), reptile FOO (P = 0.048), frog FOO (P < 0.001), and plant FOO (P = 0.004) were more common as prey around modified or replaced vegetation (positively correlated with VAST class). However, there was no effect of VAST class on overall fox diet composition (PERMANOVA: R^2 = 0.010, P = 0.253; Table 1), which is likely to reflect that collinearity between variables overshadowed the simple relationships shown between vegetation condition and individual food categories.

There was an influence of climate zone categories on fox diet composition (PERMANOVA: R^2 = 0.058,

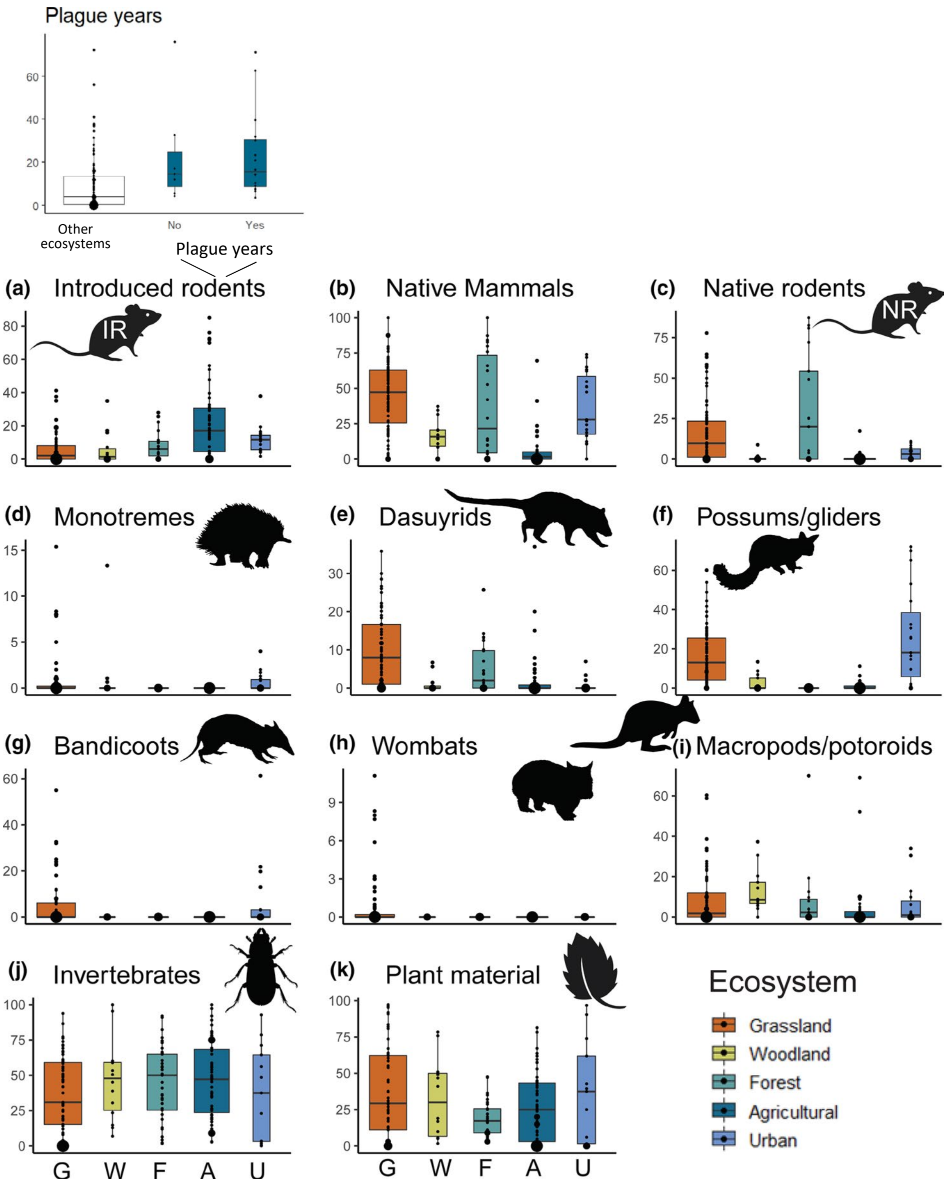

Fig. 3. Frequency of occurrence (FOO) of food categories consumed by red foxes *Vulpes vulpes* in Australia shown by ecosystem for those food categories where ecosystem was retained in the top model set (AICc/t-AIC < 2). Box plots show the median (horizontal line), quartiles (box) and non-outlier range (whiskers), with width of the columns representing relative sample sizes. Dots represent individual data points (multiple data points are represented with larger dots). The graph above (a) shows FOO for introduced rodents, for sites where house mouse plagues are commonly reported (filled columns; for both years of mouse plague and years without mouse plague reported), and for sites where house mouse plagues are not commonly reported (white column). [Colour figure can be viewed at wileyonlinelibrary.com]

P = 0.002; Table 1). Climate zone was included in all top models describing the incidence of mammals in fox diets (all together, summed introduced species, summed native species, and for seven food categories: introduced rodents, lagomorphs, livestock, dasyurids, possums/gliders, bandicoots, and macropods/potoroids), reptiles, invertebrates, and plant material (Fig. 5). Introduced rodents were more common in fox diet at subtropical sites, and lagomorphs in arid and semi-arid zones, while livestock FOO was greater for semi-arid and warm temperate sites. For native mammals, there was greater incidence of dasyurids in cool temperate sites and bandicoots in warm temperate sites, while possums/gliders were the most common in both warm and cool temperate sites. Macropods/potoroids were more often prey of foxes in arid and semi-arid landscapes. Reptile FOO was greatest for arid and semi-arid sites. Invertebrate FOO was highest for subtropical, semi-arid, and cool temperate sites, while plant material

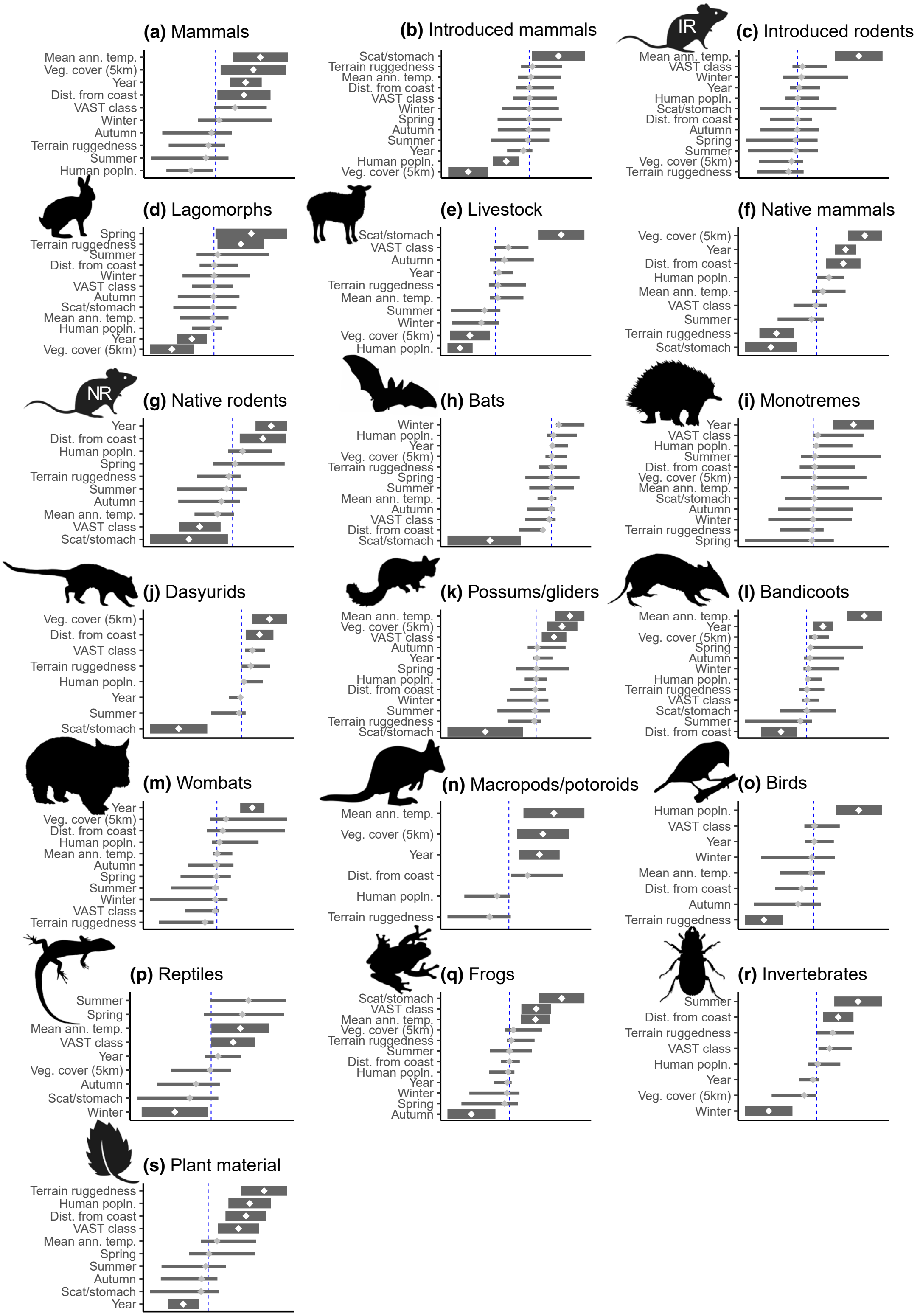

Fig. 4. Beta estimates (diamonds) ±95% confidence intervals (bars) for predictor variables (see Table 1 for details) that were retained in the top model set (AICc or t-AIC < 2) for red fox *Vulpes vulpes* food categories. Food categories with insufficient data (cat, dingo/dog, marsupial mole, koala) could not be modelled. Variables with confidence intervals that do not overlap with zero (vertical dotted line) are considered influential; those with significant *P*-values are indicated with thick confidence interval bars. Positive relationships are to the right of the zero line and negative relationships to the left of this line. [Colour figure can be viewed at wileyonlinelibrary.com]

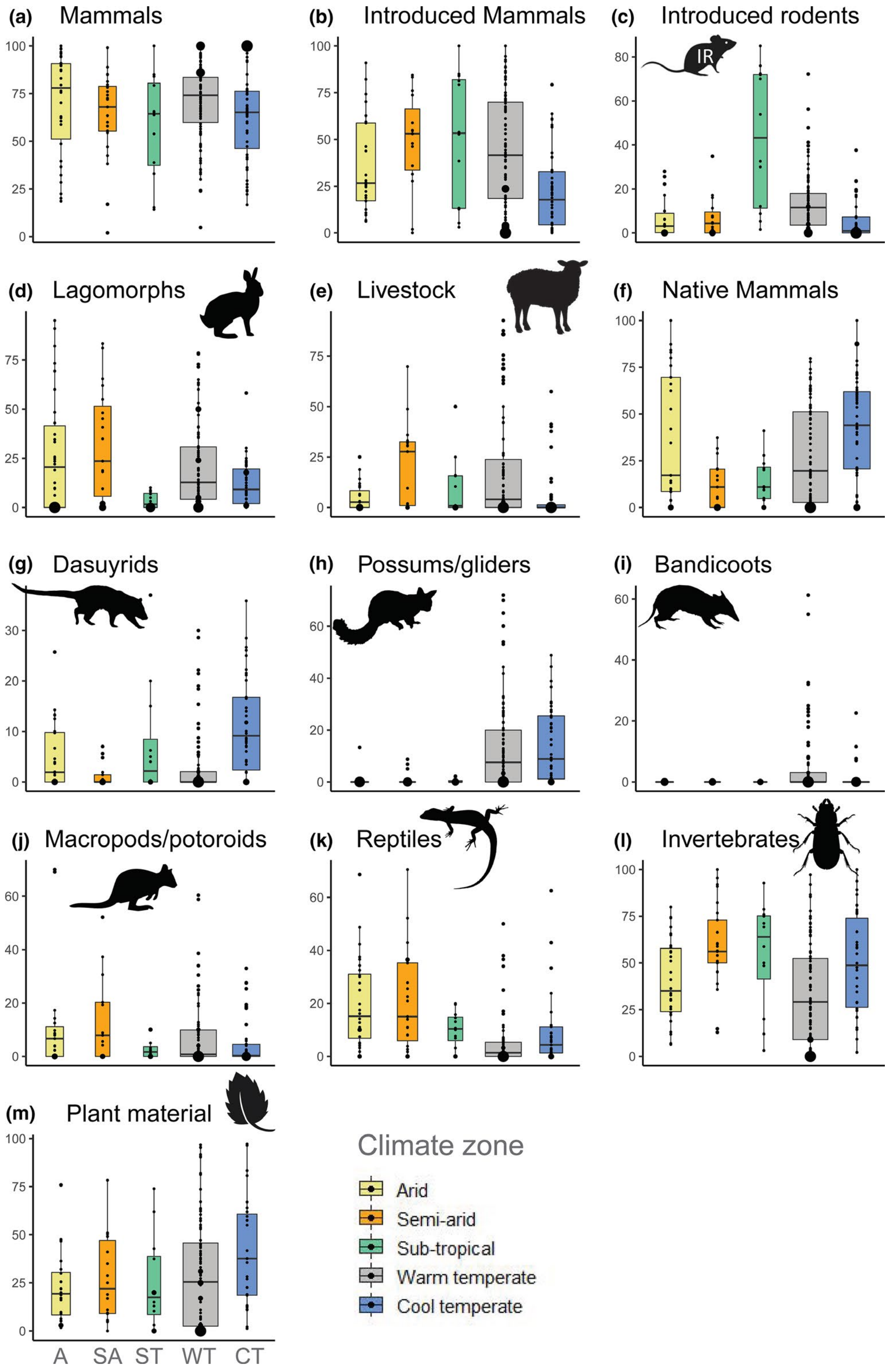

Fig. 5. Frequency of occurrence (FOO) of food categories in the diet of the red fox *Vulpes vulpes* shown by climate zone for those food categories where climate zone was retained in the top model set (AICc/t-AIC < 2). Box plots show the median (horizontal line) quartiles (box) and non-outlier range (whiskers), with width of the columns representing relative sample sizes. Dots represent individual data points (multiple data points are presented with larger dots). [Colour figure can be viewed at wileyonlinelibrary.com]

was more common for cool temperate sites. There was also an influence of mean annual temperature on fox diet composition (PERMANOVA: $R^2 = 0.025$, $P = 0.013$; Table 1, Fig. 4), with all-mammal FOO ($P = 0.001$; specifically introduced rodent FOO: $P < 0.001$, bandicoot FOO: $P < 0.001$, possum/glider FOO: $P < 0.001$, and macropod FOO: $P = 0.004$), reptile FOO ($P = 0.048$), and frog FOO ($P = 0.001$) each positively correlated with mean annual temperature.

There was some effect of human population density (PERMANOVA: $R^2 = 0.029$, $P = 0.006$) on fox diet composition (Table 1, Fig. 4). There were more introduced mammals in fox diets for sites with lower human population ($P = 0.001$); this was typified by the negative relationship between livestock in fox diet for low human population density sites ($P < 0.001$). By contrast, bird FOO increased with human population density ($P < 0.001$), with greater incidence of birds in fox diet recorded around the largest cities. The strongest predictor of plant FOO was similarly a positive relationship with human population density ($P < 0.001$).

Terrain ruggedness had an effect on fox diet composition (PERMANOVA: $R^2 = 0.028$, $P = 0.007$; Table 1, Fig. 4) with a positive correlation between lagomorph FOO and terrain ruggedness ($P = 0.024$) and a negative relationship with the summed native mammal FOO ($P < 0.001$) and bird FOO ($P < 0.001$). Distance to coast also affected fox diet composition (PERMANOVA: $R^2 = 0.019$, $P = 0.042$; Table 1, Fig. 4), with bandicoots more common in fox diet at sites closer to the coastline ($P = 0.022$), but native rodents ($P = 0.011$), dasyurids ($P = 0.010$), invertebrates ($P = 0.005$), and plant material ($P < 0.001$) more common at sites further inland.

In terms of sampling methods, there were significant seasonal effects on fox diet composition (PERMANOVA: $R^2 = 0.078$, $P = 0.003$; Table 1) and specifically for four food categories (Fig. 4). Lagomorphs were more commonly recorded in spring ($P = 0.041$). More invertebrates ($P = 0.001$) were recorded in fox diet for summer samples, and fewer for winter samples ($P < 0.001$). There were also fewer reptiles in winter ($P = 0.032$), while frogs were less commonly recorded in autumn ($P = 0.002$).

There were also effects of year of collection on fox diet composition (PERMANOVA: $R^2 = 0.059$, $P = 0.001$; Table 1, Fig. 4). There was a marked decline in lagomorph FOO (Fig. 6a; $P = 0.003$) and plant material FOO ($P = 0.002$) over time. Lagomorph FOO pre-1996 (29 ± 24%, $n = 70$ data points) decreased by 40% post-RHDV-1 (1996–2010; 17 ± 21%, $n = 60$) and by 78% post-RHDV-2 (2010–2020; 6.4 ± 6.9%, $n = 30$). By contrast, there was an increase in native rodent FOO ($P < 0.001$; Fig. 6a), monotreme FOO ($P < 0.001$), bandicoot FOO ($P = 0.001$), wombat FOO ($P < 0.001$) and macropod/potoroid FOO ($P = 0.003$; Fig. 6a) with year of collection. Lagomorph FOO was included in the top models describing native rodent FOO and macropod/potoroid FOO; furthermore, within studies, there were negative relationships between lagomorph FOO and that of native rodents and macropods/potoroids (Fig. 6b).

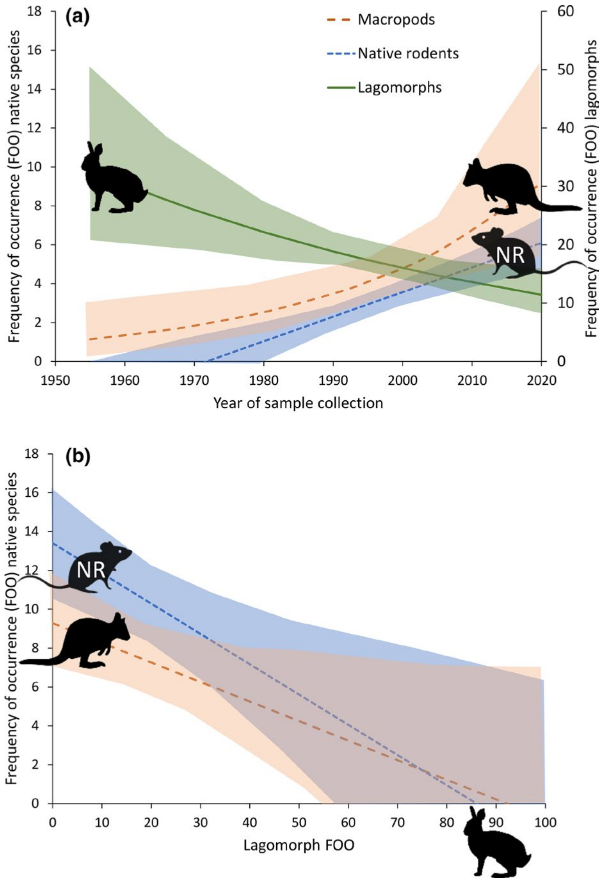

Fig. 6. (a) There was a decrease in lagomorph frequency of occurrence (FOO; principally European rabbit *Oryctolagus cuniculus*) in the diet of Australian red foxes *Vulpes vulpes* with year of study, while two native mammal groups (native rodents [NR] and macropods/potoroids) showed an increase over the same time. (b) There were inverse relationships in the incidence of lagomorphs in fox diet samples with the incidence of native rodents and macropods/potoroids. The graphs show the predicted means (lines) and 95% confidence intervals (shaded areas) of the FOO of each of these prey types (a) with year of study or (b) with lagomorph FOO, holding all other factors retained in the top models constant at a mean value for each. [Colour figure can be viewed at wileyonlinelibrary.com]

Foxes showed no difference in the incidence of introduced rodents in their diet throughout the grain-growing belt of eastern Australia between years with mouse plagues (FOO = 23 ± 20% of samples, $n = 16$ data points) and those without plagues (FOO = 23 ± 25% of samples, $n = 7$; $t_{21} = -0.011$, $P = 0.991$).

There was no overall effect of sample type in the model including all predictor variables (PERMANOVA: $R^2 = 0.016$, $P = 0.063$; Table 1), but individual food categories revealed strong biases. Livestock were 7.2 times more likely ($P < 0.001$), and frogs were 5.8 times more likely ($P < 0.001$) to be recorded for studies that analysed stomach contents rather than scats. By contrast, native rodents (80.5 times, $P < 0.001$), bats (FOO: 0.1 ± 0.6% [0–5.0], $n = 141$; 11.3 times, $P = 0.018$), dasyurids (5.4 times, $P < 0.001$), and possums/gliders (10.0 times, $P = 0.008$) were more commonly recorded for studies that analysed scats rather than stomach contents.

DISCUSSION

Our integrated analysis of 85 Australian fox diet studies reveals marked spatial and temporal patterns. The spatial distribution of these studies covers the Australian geographic range of foxes, while the temporal range spans over seven decades and all seasons. To a large degree, the spatial and temporal patterns in diet reflect marked variation in the distribution and composition of plant and animal communities throughout Australia, as foxes are opportunistic and are likely to eat whatever foods are available at a given time and place. In the following sections, we discuss the biodiversity conservation and pest management implications of these results.

It is no surprise that ecosystem is a strong determinant of fox diet composition, as the ecosystem categories capture landscape differences that are likely to significantly influence the distribution of many plant and animal species. For example, introduced rodents (principally house mice) were most common in fox diet within agricultural landscapes, showing spatial overlap with grain-growing locations (southwest and eastern Australia). Supporting another study that found no relationship between the incidence of house mice in mammal predator scats and mouse density (Sinclair et al. 1990), we found no evidence of more mice in fox diet for years with mouse plagues (compared with years without plague) in mouse plague-prone study sites. However, we note that the mean introduced rodent FOO for these study sites (23 ± 26%) was ~2.3 times greater than the overall mean in other locations (10.1 ± 14.0%), which may suggest that foxes benefit from localised increases in mouse availability even if their exploitation of localised abundances is insufficient to counter the rapid reproductive rate of mouse populations under ideal conditions (Newsome & Corbett 1975, Sinclair et al. 1990).

Another notable ecosystem pattern was the high incidence of native mammals taken by foxes in urban areas. For example, possum/glider FOO for urban landscapes was three times higher (e.g. Wallis et al. 1996, Meek 1998, Coates & Wright 2003, Roberts et al. 2006) than the mean of all other sites (they were also abundant in fox diet from forest sites). In eight urban/peri-urban parks near Melbourne, Victoria, Wallis et al. (1996) recorded three possum and two glider species in fox scats, with up to 72% of fox scats containing evidence of common brushtail possum *Trichosurus vulpecula* at one site, and up to 66% of fox scats containing common ringtail possum *Pseudocheirus peregrinus* at another site. Bandicoot FOO was also three times greater for urban landscapes than for other ecosystems (again noting their abundance in fox diet from forest sites). Additionally, Fleming and Crawford (2019) reported quenda *Isoodon fusciventer* in 61% of fox scats from an urban reserve in Perth, Western Australia. In part, this relatively high take of possums and bandicoots in urban and peri-urban areas may reflect the current low abundance of these native mammals in most arid and semi-arid areas, and the relatively high densities of these three food categories in habitat fragments in some urban settings.

While the strongest influence on fox diet composition was due to ecosystem type, there were also effects of vegetation cover, climate zone, terrain ruggedness and human population density (and lesser influences of distance from the coastline and mean annual temperature at the collection site). For example, the strongest factors associated with bird FOO (see also Woinarski et al. 2021) were terrain ruggedness and vegetation cover, with more birds consumed by foxes in flat, open landscapes. Bird FOO was also positively associated with proximity to humans, being 1.5 times higher in urban areas compared with the overall total, which could reflect increased abundance of synanthropic bird species around human dwellings, increased vulnerability of ground-foraging or ground-roosting birds (Woinarski et al. 2021), or increased likelihood of consuming birds as carrion from road strike. The few fox diet studies on Australian offshore islands used as breeding colonies by seabirds are remarkable, because the predominant prey was birds (rather than mammals); e.g. bird remains were present in more than half of samples from Phillip Island, Victoria (Norman 1971, Kirkwood et al. 2000).

Seasonal patterns in fox diet (in e.g. rabbit young, reptiles, invertebrates) are likely to reflect activity patterns of these prey species. For reptiles, incidence in fox diet varied with climate (see also Stobo-Wilson et al. 2021) and season, both of which are likely to influence reptile activity. In arid and semi-arid Australia, the abundance of mammals is often too low to fulfil the fox's dietary requirements reliably, whereas reptiles are abundant in these ecosystems and therefore become a common component of fox diet (Paltridge 2002, Spencer et al. 2014). A more surprising observation was the relatively high proportion of reptile in fox diets in cooler temperate alpine zones (e.g. Bubela et al. 1998), possibly owing to the relative scarcity of mammals in these regions or the cooler temperatures driving an increase in time spent basking, exposing reptiles to predation or slowing escape (Caldwell et al. 2017).

Changes over time in the incidence of European rabbits and native mammals – prey switching?

Our results support the previous finding that wherever rabbits are common, they are the staple food for foxes (Saunders et al. 1995, Díaz-Ruiz et al. 2013, Soe et al. 2017; see Brown et al. 2020 for current geographic range of lagomorphs). Lagomorphs were the most common mammalian prey group for Australian foxes, averaging 21 ± 22% of fox diet samples overall, but reaching up to 95% of samples for specific studies (Foulkes 2002, Letnic et al. 2011). The incidence of lagomorphs in samples decreased over time, which is likely to reflect the broadscale reduction in rabbit abundance in Australia following episodes of biocontrol since their peak in numbers in the 1920s. Predators with a strong preference for a single prey item switch to alternative prey if or when their preferred prey becomes scarce (Kjellander & Nordström 2003), demonstrating 'prey switching' according to prey availability. Previous studies have set out to test whether alternative prey species are more vulnerable as a result of rabbit removal. Over a period of three years, Saunders et al. (2004) found no evidence of a change in fox diet composition in response to the arrival of RHDV-1 (rabbit FOO 21% for 240 foxes before, compared with 19% for 269 foxes sampled after detection of RHDV-1 in ~1996 in the population). Similarly, in Spain, Villafuerte et al. (1996) recorded no significant decrease in rabbit consumption by foxes despite a ~50% decrease in rabbit density, although subsequent analysis of more extensive 'before-RHDV' samples identified a 68% decrease in incidence of rabbits in fox diet (Ferreras et al. 2011). Using a different model of control, Marlow and Croft (2016) found a 37% reduction in the incidence of rabbits in fox diet in response to destruction of rabbit warrens by 'ripping'. Our long-term dataset also suggests a general reduction in the incidence of rabbits in fox diet following the broadscale biocontrol of rabbits.

While there was a decrease in lagomorph FOO, we recorded increasing incidence of native mammals in fox diet over this same time, particularly native rodents and macropods/potoroids. In addition to these temporal patterns, we recorded negative relationships between the incidence of lagomorphs and these two native prey categories among our studies. Similar inverse relationships across space have been noted between the incidence of rabbits and the FOO for dasyurids and rodents in cat diet (Doherty et al. 2015) and with medium-sized mammals in the diet of dingoes (Doherty et al. 2019). On face value, these diet composition data may suggest greater predation pressure on native mammals in areas subjected to rabbit control (Banks et al. 1998; but see Mutze 2017), although diet composition data reveal nothing about fox density responses to rabbit control. Predator populations can be sustained at high densities due to an abundance of readily accessible prey (e.g. introduced rodents, Singleton et al. 2005; rabbits, McGregor et al. 2020), spilling over to 'hyperpredation' of native species (Pedler et al. 2016).

A decline in abundance of rabbit-dependent predators due to RHDV or other forms of rabbit control has been predicted by modelling (foxes: Pech & Hood 1998; feral cats and foxes: Lurgi et al. 2018), while decreases in both feral cats and foxes have been field-demonstrated (Read & Bowen 2001, Holden & Mutze 2002). Notably, monitoring indicated a greater decline in fox numbers than cat numbers, suggesting that feral cats (which switch to reptiles, birds, and invertebrates; Read & Bowen 2001, Holden & Mutze 2002, McGregor et al. 2020) are less dependent on rabbits than are foxes (which increase their intake of invertebrates and carrion in the absence of rabbits; Read & Bowen 2001, Holden & Mutze 2002). Removing a steady source of food could therefore reduce predator numbers (McGregor et al. 2020), ultimately benefiting native species (Pedler et al. 2016). Removing rabbits from the landscape also allows vegetation recovery (e.g. Sandell 2002) that reduces competition with macropods or provides additional cover for small vertebrates; greater presence in fox diet may therefore also reflect recovering populations of some native mammals (Pedler et al. 2016), although such trends may be localised and for only some species, as many native mammals show ongoing trends for decline (Woinarski et al. 2015, Wayne et al. 2017).

Staple foods

Mammals are clearly a favoured food of foxes, being present in more than two thirds of all diet samples analysed. Invertebrates and plant material were also common. Around a third of Australian fox diet samples contained invertebrates, with a number of studies reporting very high incidence (e.g. FOO > 95%: Frith 1962, Palmer 1995, Berghout 2000, Molsher et al. 2000). Common invertebrate taxa consumed were Orthoptera (grasshoppers and locusts; e.g. Berghout 2000), Chilopoda (centipedes; e.g. Ryan & Croft 1974), and Astacidea (crayfish; e.g. Bubela et al. 1998). Furthermore, roughly a quarter of all fox diet samples contained plant material, principally fruit, grain (i.e. livestock feed), and grass (FOO > 90%: Brunner et al. 1975, Lowe 1989, Stepkovitch 2017, Fleming & Crawford 2019).

Similarly, studies of red fox diet in Europe and North Africa report that invertebrates (especially Orthoptera) and fruit are preferred foods for foxes where available (Doncaster et al. 1990, Dell'Arte & Leonardi 2005, 2009, Rosalino & Santos-Reis 2009) and that these foods are likely to represent a substantial proportion of a fox's energy balance. It is surprising, therefore, that many studies do not record these important components of fox diet.

Supplementary food

Foxes take the offspring of many livestock species, e.g. lambs (Saunders et al. 1995), goat kids (Gentle 2006), and piglets (Fleming et al. 2016). However, adults (e.g. sheep identified from wool length, body parts) and large domestic and feral livestock species (e.g. cattle, camels) have also been recorded in fox diet; this is likely to reflect consumption of carrion. For example, sheep carrion comprised 47–65% of stomach contents volume in livestock production areas in Western Australia (Forbes-Harper et al. 2017). Similarly, most consumption of macropods has been recorded as carrion, although foxes have also been observed to hunt and kill some large macropods (e.g. swamp wallabies *Wallabia bicolor,* adult body mass 13-17 kg, Meek & Wishart 2017; yellow-footed rock wallabies *Petrogale xanthopus,* adult body mass ~6 kg, Lapidge & Henshall 2001), and foxes regulate eastern grey kangaroo *Macropus giganteus* populations through their take of subadults (Banks et al. 2000).

The amount and relatively consistent availability of livestock carrion in production landscapes could, at times, easily meet the entire dietary needs of local fox populations (Berghout 2000, Saunders & McLeod 2007). Pastoral sheep and cattle property owners typically leave livestock carcasses to decompose naturally and, in doing so, supplement scavengers. Similarly, culling of feral species under natural or conservation systems increases carrion availability for predators (Forsyth et al. 2014). Carcass scavenge is also likely to detract from poison-bait desirability and consumption, thereby interfering with current widespread population control methods (Saunders & McLeod 2007). Disposal of livestock carcasses is an expectation for intensive production systems; e.g., subject to local government regulations, outdoor piggeries are required to incinerate, compost, or bury carcasses (Fleming et al. 2016) – having a central disposal pit that could be fenced to exclude foxes may be the cheapest and most commonly used option for disposing of these food resources at a landscape scale.

Foxes also scavenge on windfall fruit from around orchards and vineyards (Lowe 1989), while fruit of many invasive plant species (e.g. basket asparagus *Asparagus aethiopicus;* O'Connor et al. 2019) is consumed and seeds are dispersed by foxes. Just as human refuse can supplement fox populations around human developments (Bateman & Fleming 2012), carrion, fruit, or grain can supplement fox populations under production or natural landscapes, thereby increasing risk of native species and livestock predation, with implications for the management of foxes (Hradsky et al. 2017).

Interactions with other eutherian predators

Some studies reported reasonably high incidence of fox remains in fox diet samples (e.g. Baker & Degabriele 1987), mostly from hair, which is likely to reflect auto-grooming. However, cannibalism is also possible. Substantial bone and tissue in stomach samples were evident in a few samples (fox FOO: 33.3% Crawford et al. unpublished data; 20% J. Speed & M. N. Gentle, unpublished data), with a reasonable volume present (3.5–39 g of stomach contents; Speed & Gentle, unpublished data). This could represent scavenging of foxes culled during intensive control activities or even occasional victims of vehicle strike.

Suppression of cats by foxes via direct predation has been suggested (Christensen & Burrows 1994, Risbey et al. 1999, Marlow et al. 2015), although supporting evidence in Australia is limited. Consumption of cats by foxes has been recorded previously (e.g. Risbey et al. 1999, Paltridge 2002), as well as instances of possible predation without consumption (Paltridge 2002, Molsher et al. 2017). However, in our large collation, we found little incidence of cats in fox diet (FOO 0.43 ± 1.79% [0–18.9], n = 140), suggesting that intraguild predation is rare (Molsher et al. 2017).

Hair from dogs was present in an overall mean of 0.34 ± 1.47% fox diet samples. Compared with the overall mean, the incidence was 5.4 times greater for urban areas (e.g. Wallis & Brunner 1986), suggesting that foxes take domestic dogs rather than dingoes. Dogs in urban areas may be consumed as carrion, foxes could be ingesting hair by consuming scats or incidentally (Brunner et al. 1991) while fighting with dogs, while killing and consuming young (see review by Allen et al. 2012) should also not be ruled out.

Comparison with recent continental-scale reviews of the diets of dingoes (Doherty et al. 2019) and cats (Doherty et al. 2015) in Australia (Fig. 7) reveals that foxes generally have a broader diet than dingoes or cats. Foxes take prey reasonably equally across the full range of prey sizes available to them, with seven food categories present in more than 10% of samples (i.e. FOO) compared with four for dingoes and five for cats. Dingoes show preference for large native mammals (principally macropods), while cats show preference for smaller prey. Invertebrates were recorded in a third of samples for both the fox and cat, but the incidence was lower in dingo diet.

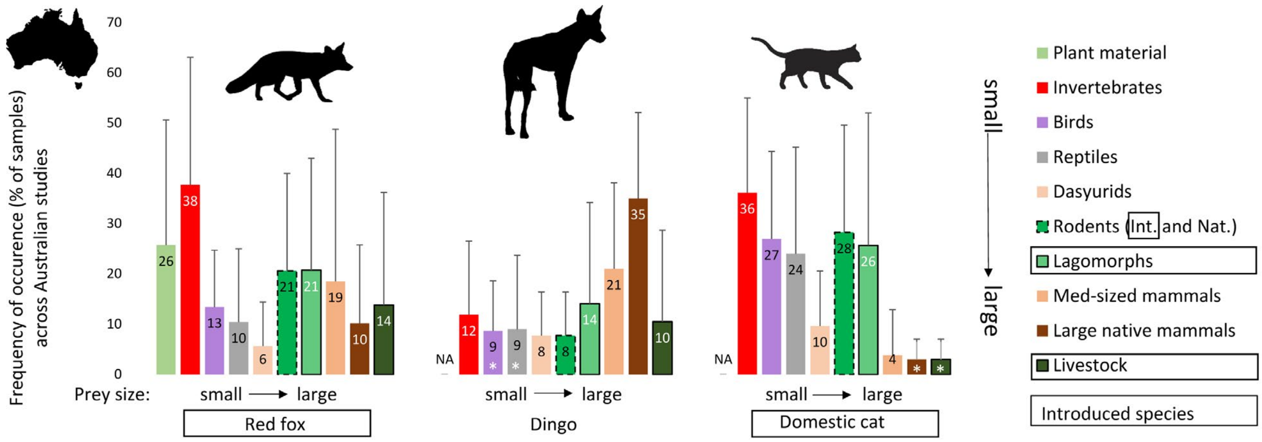

Fig. 7. Frequency of occurrence (FOO) of key prey groups taken by the introduced red fox *Vulpes vulpes* (present study), dingo *Canis familiaris* (Doherty et al. 2019), and introduced domestic cat *Felis catus* (Doherty et al. 2015) in Australia. Food categories are sorted left to right in increasing body size of prey (exception: plant material). Black line around bars: introduced prey species; dashed lines: native and introduced rodents pooled. For dingoes, data on rodents and dasyurids were pooled ('small mammals'; *half the total is represented for each column), and small and large exotic herbivores were grouped as livestock (using our pooling formula – see Appendix S2). For cats, we split carrion between large native mammals and livestock (*). Plant material was present in a quarter of fox diet samples and is also commonly ingested by dingoes and cats, but was not available (NA) for the reviews of diet in those species due to differences in data reporting between studies (T. Doherty, personal communication). Bars represent mean values with standard deviations. [Colour figure can be viewed at wileyonlinelibrary.com]

International comparison of red fox diet

Our study of variation in the diet of the fox across a continent to which it has been introduced provides an intriguing contrast to comparable reviews of the diet of the fox throughout Europe, within its natural range (Díaz-Ruiz et al. 2013, Soe et al. 2017). Common features of both reviews are the broad diet, the marked spatial variation in diet associated with climatic and anthropogenic factors (these factors presumably influence the relative abundance of different prey types), the importance of lagomorphs as a staple food resource, and seasonal variation in dietary composition. Notable differences are also evident: Europe has greater climatic variation, associated especially with latitude, and this gradient has a stronger influence on fox diet than the more nuanced climatic variation found in Australia. The European reviews did not consider longer-term temporal variation in fox diet, although temporal changes in competition and prey availability have influenced red fox diet over different time scales (e.g. Viranta & Kauhala 2011, Lanszki et al. 2018), and long-term temporal patterns and anthropogenic effects are therefore likely.

Sample type influences diet composition analyses

We identified a strong bias in fox diet composition due to sampling method. Livestock were recorded 7.2 times more often from stomachs than from scats, which suggests that when they are consuming large animals (e.g. sheep and cattle), foxes may preferentially consume organs and soft tissues rather than skin, hair, and bones (which are needed for identification of food type from scats). By contrast, small mammals (e.g. native rodents, bats, dasyurids, and possums/gliders) were more often recorded from scats than from stomachs, possibly reflecting that the presence of these species is often quantified on the basis of a few indigestible bones (e.g. jaws, feet) or hair that could be slow to pass through the fox's digestive system. This finding supports the inverse relationship between mammal prey mass and digestibility noted by Ferreras and Fernandez-de-Simon (2019), with a greater digestible proportion for large prey and a greater indigestible proportion for small prey. There was spatial bias in the sampling of stomachs vs. scats, which could also contribute to the observed pattern; for example, there were few stomach samples representing temperate coastal areas. Although multivariate analysis considered sample type and spatial location simultaneously, the unbalanced design would nevertheless influence the outcome to a degree.

Frogs were recorded 5.8 times more often in stomachs than in scats. Frogs are readily digested and have small, soft bones that are difficult to distinguish, contributing to their underestimation in studies using scat analysis (Woinarski et al. 2020). By contrast, birds and reptiles can often be distinguished (and sometimes also identified to species) from only a few hard keratin scales or feathers, and therefore are more likely to be consistently recorded from both scats and stomachs (but see Cavallini & Volpi 1995).

Finally, scat analysis does not inform whether items are eaten as carrion or not. Careful analysis of stomach contents is usually required to quantify carrion consumption, e.g. allowing identification of the presence of maggots, which are highly digestible and unlikely to be detected from scats. Sampling methods therefore need to be taken into account in interpreting dietary composition of this opportunistic canid.

Limitations of this study

Australia's native mammals, especially those in the size range ~35 g to 5.5 kg, have shown marked population declines, extirpations, range contractions, and extinction over the last 200 years (Burbidge & McKenzie 1989, McKenzie et al. 2007, Johnson & Isaac 2009, Woinarski et al. 2015), succumbing to a lethal combination of introduced predators and competitors, altered fire regimes, persecution, habitat destruction, and disease (Johnson 2006, Abbott 2008). The threat foxes pose to Australia's medium-sized mammals is well demonstrated by the recovery of many species following large-scale fox-baiting programmes including 'Western Shield' (Western Australia), 'Southern Ark' (Victoria), and 'Bounceback' (South Australia; Dexter & Murray 2009, Robley et al. 2014, DBCA 2020). Diet analyses, such as those summarised in this review, capture the evidence required to motivate for greater control of invasive predators throughout the continent, although such analysis only provides a retrospective view of the decline of vulnerable prey species.

Notwithstanding the size and distributional breadth of our collation of studies, there are some regional biases, with disparate research effort carried out across land-use categories throughout the continent. Observer and methodological bias could contribute to differences between studies, as small details (e.g. internal morphology of mammal hairs, scale patterns in reptiles, colour patterns in bird feathers) are often needed to distinguish prey species. However, Australian researchers employed contractual services (largely the same three) to analyse an estimated 80-90% of these samples, minimising the likelihood of such bias.

We used recent values for our predictor variables, but many (ecosystem, rainfall, temperature, vegetation cover, VAST class, human population density) are likely to have changed over the seven decades over which the samples were analysed. This would increase the likelihood of type II error for these variables, making our analyses more conservative, and may explain, for example, why vegetation condition (VAST classification) was not an important factor in some analyses.

CONCLUSIONS

1. European red foxes are highly opportunistic and eat just about everything. Their inherent dietary flexibility predisposed foxes to exploiting novel prey following their introduction to Australia. They take vertebrates and invertebrates as live prey or carrion, as well as plant material.
2. Mammals and invertebrates are staple foods, but other foods such as carrion and fruit or grain can incidentally supplement fox populations. This must be a consideration for livestock management, vertebrate population control programmes, and urban weed management.
3. Changes over time in the incidence of European rabbits and native mammals in fox diet could reflect prey switching in the presence of biocontrol of rabbit populations, or recovery of native mammal populations in the wake of rabbit removal (Pedler et al. 2016). As a precautionary principle, population control of foxes, feral cats, and rabbits should be carried out simultaneously, because removal of any one of these species in isolation can have perverse repercussions for native wildlife.

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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. List of studies included in the analyses.
Appendix S2. Food categories and calculation of frequency of occurrence (FOO).
Appendix S3. Summary of predictor variables and their covariation.

Appendix S1. List of studies included in the analyses.

Two teams carried out independent literature searches and collection of data from the primary literature using Web of Science (1900-2020) and Scopus databases for studies on the diet of foxes in Australia using various search strings: (fox OR "*Vulpes vulpes*") AND (diet OR predation OR ecology) AND (Australia). We sourced additional studies from reference lists: book chapters, theses, reports, and unpublished data sets. We contacted authors where their published data did not provide sufficient details for subsequent analyses. We screened studies to ensure that the frequency of occurrence (the proportion of fox dietary samples [stomachs or scats] that contained a given food item, and the most generally used metric of diet composition across our collated studies) of individual food categories was presented or could be calculated, details of sample size were provided and individual datapoints were represented by at least 10 samples.

Australian states where fox diet samples were collected include: New South Wales (NSW), Northern Territory (NT), Queensland (QLD), South Australia (SA), Victoria (VIC), and Western Australia (WA).

Source	Location	*n* scats	*n* stomachs	*n* both‡	Total *n*
Adderton (1998)	Mitchell Park, NSW	56			56
	Scheyville National Park, NSW	163			163
Baker & Degabriele (1987)	Eldorado Hills, VIC	14	26		40
Bayly (1978)	97km east of Farina, SA		29		29
Berghout (2000)	Orange, NSW		148		148
Brown & Triggs (1990)	East Gippsland, VIC	534			534
Brunner et al. (1975)	Sherbrooke Forest Park, Dandenong Ranges, VIC	1888			1888
Brunner et al. (1991)	Dandenong Valley Metropolitan Park, VIC	217			217
Bubela et al. (1998)	Kosciusko National Park, NSW	272			272
Burrows et al. (2003a)	Gibson Desert Nature Reserve, WA			22	22
Catling (1988)	Yathong Nature Reserve, NSW		288		288
Claridge et al. (2010)	Barren Grounds Nature Reserve, NSW	49			49
	Beecroft Penninsula, NSW	42			42
	Ben Boyd National Park, NSW	26			26
	Budderoo National Park, NSW	17			17
	Jerrawangala National Park, NSW	26			26
	Nadgee Nature Reserve, NSW	37			37
	Sydney Water Catchment, Sydney, NSW	73			73
	Wallaga Lake National Park, NSW	26			26
Coates & Wright (2003)	Royal Botanic Gardens Cranbourne, VIC	72			72
Coman (1973)	Central District, VIC		167		167
	Eastern Ranges, VIC		153		153
	Mallee/Wimmera, VIC		293		293
	Northern District, VIC		79		79
	South Gippsland, VIC		92		92
	Western District, VIC		179		179
Corbett (1995)	Central Deserts, NT			44	44
	South east Highlands, VIC			1550	1550
Craik (1979)	Little Desert National Park, VIC	895			895
Crawford (2010)	Boyup Brook, WA		63		63
	Corrigin, WA		18		18

Source	Location	*n* scats	*n* stomachs	*n* both‡	Total *n*
	Darkan, WA		172		172
	Dumbleyung, WA		16		16
	Frankland, WA		24		24
	Gingin, WA		33		33
	Katanning, WA		61		61
	Mt Barker, WA		34		34
	Nyabing, WA		27		27
	Perth, WA		25		25
	Quairading, WA		38		38
	Williams, WA		16		16
	Woodanilling, WA		35		35
Croft & Hone (1978)	Central Plains, NSW		105		105
	Coast, NSW		68		68
	Floodplains, NSW		53		53
	High Country, NSW		268		268
	Slopes, NSW		185		185
	Western NSW		132		132
Cupples et al. (2011)	Nullarbor Desert, SA	52			52
	Simpson Desert, NT	78			78
	Strzelecki Desert, SA	31			31
(Dawson et al. 2016)	Chittering Lakes, WA	234			234
Dickman CR (Unpub. data)	Dwellingup, WA	55			55
	Harry Waring Marsupial Reserve, WA	237	12		249
	Jurien Bay, WA	137			137
Dickman CR, Smith GT (unpub. data)	Wheatbelt, WA	164			164
Diment (2010)	East Gippsland (Southern Ark), VIC	566			566
	East Gippsland, VIC	255			255
Eldridge et al. (2002)	Andado, Lyndavale, & Umbearra Stations, NT	208			208
Fleming & Crawford (2019)	Alison Baird Reserve, Perth, WA	31			31
Foulkes (2002)	Hale River, SA	15			15
	Irving Creek, NT	11			11
Frith (1962)	Round Hill Nature Reserve, NSW	320			320
Glen et al. (2006)	Northern Rivers Region, NSW	48			48
Glen & Dickman (2008)	Marengo & Chaelundi State Forests & North-eastern NSW	207			207
Glen et al. (2011)	Barrington Tops, Eastern Australia, NSW				
Graham et al. (2017)	Brigalow Belt South Bioregion, QLD	46			46
Green & Osborne (1981)	Kosciusko National Park, NSW	1159			1159
Green (2003)	Kosciusko National Park, NSW - Alpine transect	609			609
	Kosciusko National Park, NSW - Subalpine transect	1837			1837
Grossek (1979)	Wyperfeld National Park, VIC	871			871
Harrison (2006); Dickman CR unpub.data	Centennial Park, Sydney, NSW	99			99
Hart (1994)	Flinders Ranges National Park, SA		116		116

Source	Location	*n* scats	*n* stomachs	*n* both‡	Total *n*
Heard (2001)	Mt Meg Flora & Fauna Reserve, VIC	55			55
Holden & Mutze (2002)	Flinders Range National Park, SA		879		879
Kirkwood et al. (2000)	Phillip Island, VIC		289		289
Kirkwood et al. (2005)	Phillip Island, VIC		147		147
Lapidge & Henshall (2001)	Lambert, Acton & Caranna Stations, QLD		38		38
Letnic et al. (2011)	Quinyambie, Strzelecki Desert, SA	31			31
	Winnathee, Strzelecki Desert, SA	74			74
Lowe (1989)	Morialton, SA	702			702
Lugton (1993)	Wentworth, NSW		212		212
Lunney et al. (1990)	Mumbulla State Forest, NSW	613			613
Lunney et al. (1996)	Macleay Gorge System, NSW	146			146
Lunney et al. (2002)	Mumbulla State Forest, NSW	450			450
Mahon (1999)	Simpson Desert, QLD	382			382
Marlow (1992)	Fowler's Gap, NSW	800			800
Martensz (1971)	Tero Creek Station & Gum Poplah Station, NSW		55		55
Meek & Triggs (1998)	Beecroft Peninsula, NSW	116			116
	Bherwerre Peninsula, NSW	157			157
Mifsud & Woolley (2012)	Julia Creek, QLD		57		57
Mitchell & Banks (2005)	Blue Mountains, NSW	250			250
Molsher et al. (2000)	Lake Burrendong, NSW		261		261
Norman (1971)	Cape Woolamai, Phillip Island, VIC	336			336
O'Connor (2020)	Sunshine Coast, QLD	1185			1185
Palmer (1995)	Offham Station, QLD		74		74
Palmer R (unpub. data)	Inglewood, QLD	53			53
	Mt Jackson & Great Western Woodlands, WA	18			18
	Texas, QLD	185			185
Paltridge (2002)	Kintore (Tanami Desert), NT	75			75
	Tennant Creek (Tanami Desert), NT	51			51
Parker (2002)	Arthursleigh, NSW		52		52
Pascoe et al. (2012)	Blue Mountains, NSW	243			243
Pavey et al. (2008)	Simpson Desert, NT	63			63
Purcell (2008)	Southern Greater Blue Mountains World Heritage Area, NSW	962			962
Read & Bowen (2001)	Roxby Downs, SA		92		92
Risbey et al. (1999)	Heirisson Prong, Shark Bay, WA		47		47
Roberts et al. (2006)	Beecroft Jervis Bay, NSW	147			147
	Booderee National Park, Jervis Bay, NSW	122			122
	North Jervis Bay National Park, Jervis Bay, NSW	100			100
	South Jervis Bay National Park, Jervis Bay, NSW	101			101
Rose et al. (1994)	Ku-ring-gai Chase National Park, NSW	133			133
Ryan & Croft (1974)	Kinchega, NSW		99		99
Saunders et al. (2004)	Orange, NSW		509		509
Speed J, Gentle M (unpub. data)	Cowders Creek, QLD		50		50

Source	Location	*n* scats	*n* stomachs	*n* both‡	Total *n*
	Minnel Creek, QLD		16		16
	Miscellaneous sites, south east QLD		20		20
	Talwood, QLD		73		73
Spencer et al. (2014)	Ethabuka & Cravens Peak Reserves, QLD	90			90
Spencer et al. (2017)	Ethabuka Reserve, Simpson Desert, QLD	572			572
Stepkovitch (2017)	Sydney, NSW		114		114
Stuart J-M, Crawford HM, Whiting SD, Fleming PA (unpub. data)	Mundabullangana Station, WA		23		23
Suckling et al. (1976)	Near Myrtleford, VIC			67	67
Thompson E (unpub. data)	Falls Creek, Bogong High Plains, VIC	37			37
	Mt Buffalo, VIC	51			51
	Mt Hotham, VIC	18			18
Towerton (2014)	Goonoo State Conservation Area, NSW	42			42
Triggs et al. (1984)	Croajingalong National Park, VIC	937			937
Turpin J, Riley J (unpub. data)	Great Victoria Desert, WA	26			26
	Porongurup Range, WA	17			17
Wallis & Brunner (1986)	Sherbrooke Forest, VIC: 1975	309			309
	Sherbrooke Forest, VIC: 1981	145			145
	Sherbrooke Forest, VIC: 1985	182			182
Wallis et al. (1996)	Currawong Reserve, VIC	10			10
	Mt Martha, VIC	10			10
	One Tree Hill Reserve & Christmas Hills, VIC	10			10
	Royal Park West, VIC	10			10
	Seaford Foreshore Reserve, VIC	10			10
	The Briars, VIC	10			10
White et al. (2006)	Dandenong Creek Valley, VIC	1317			1317
Wilson & Wolrige (2000)	Eastern Otway Ranges, VIC	143			143
Woinarski et al. (2018)	Witchelina Reserve, SA		51		51
Woolley & Valente (1982)	Cheyne Beach, WA	112			112
	Fitzgerald River, WA	66			66
	Jerdacuttup, WA	234			234
	Stokes National Park, WA	312			312
		23897	6113	1683	31693

‡ Three studies indicated that they analysed both scats and stomachs and these were handled as separate datapoints. Three further studies (Suckling et al. 1976; Corbett 1995; Burrows et al. 2003b) indicated that they analysed both scats and stomachs but presented pooled results. Across all studies, sample sizes were on average three times greater for studies analysing scats compared with those that analysed stomach contents; these three pooled datasets were therefore deemed likely to be principally scats and were classified as 'scats' for the purposes of analyses that required categorical assignment.

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Appendix S2. Food categories and calculation of frequency of occurrence (FOO).

Frequency of occurrence (FOO) values were separately calculated for mammals by broad taxonomic grouping or origin following Murphy et al. (2019).		**Mean ± SD [range] FOO%, *n***	**GLM link function**
Introduced mammals:			
(1)	Introduced rodents – principally house mice *Mus musculus* (~30 g) and black rats *Rattus rattus* (~120 g).	11.1±14.7% [0–76] *n*=150	tweedie
(2)	Lagomorphs (order Lagomorpha) – principally European rabbit (1.5–2.5 kg), scarce records of brown hare *Lepus europaeus occidentalis* (3–5 kg).	20.7±22.3% [0–95] *n*=158	tweedie
(3)	Livestock, including all ungulate species and feral populations of these (i.e. roughly in descending order of reporting frequency: sheep *Ovis aries*, cattle *Bos taurus/indicus*, goat *Capra hircus*, camel *Camelus dromedaries*, pig *Sus scrofa*) (>40kg).	13.8±22.4% [0–92.6] *n*=149	gaussian
(4)	Domestic cats (*Felis catus*) – introduced to the continent ~200 ya (2.5–7.5 kg);	0.4±1.8% [0–18.9] *n*=140	NA
(5)	Dogs/dingoes (*Canis familiaris*) – including dingoes (introduced to the continent some 3,600-5,000 ya), domestic dogs, and their hybrids (14–20 kg).	0.3±1.5% [0–14] *n*=141	NA
Native mammals:			
Eutherians			
(6)	Native rodents (Murinae) – a diverse assemblage of around 70 species, most of which have been present for at least 1 million years (10–700 g) (Geffen et al. 2011).	8.6±15.5% [0–80.97] *n*=147	gaussian
(7)	Bats – fruit bats (Pteropodidae 50 g – 1.5 kg) and microbats (other Chiropteran families 3–145 g) combined.	0.1±0.5% [0–4.98] *n*=141	tweedie
Monotremes			
(8)	Monotremes – short-beaked echidna *Tachyglossus aculeatus*; 2-7 kg) and the platypus (*Ornithorhynchus anatinus*; 0.7 to 2.4 kg).	0.5±1.6% [0–13.3] *n*=142	tweedie
Marsupials			
(9)	Dasyurids – insectivorous/carnivorous marsupials of the family Dasyuridae; most species are small (<30 g).	5.6±8.8% [0–56.35] *n*=142	tweedie
(10)	Marsupial moles (Notoryctidae *Notoryctes* spp., ~34 g).	0.2±1% [0–7.7] *n*=141	NA
(11)	Possums and gliders (Phalangeriformes, 0.01–2.5 kg).	13.3±16.5% [0–72] *n*=142	tweedie
(12)	Bandicoots (Peramelemorphia) (0.23–1 kg).	3.8±10.8% [0–90.9] *n*=142	tweedie
(13)	Koala (Phascolarctidae *Phascolarctos cinereus*, 4–15 kg).	0±0.1% [0–0.8] *n*=141	NA
(14)	Wombats (Vombatidae, 19–32 kg).	0.4±1.1% [0–8] *n*=142	tweedie
(15)	Macropods (Macropodidae, 1–100 kg) and potoroids (Potoroidae, 0.35–3.5 kg).	9.5±13.3% [0–69.09] *n*=138	tweedie
FOOs were also calculated for:			
	all mammal species combined ('summed')	69.6±18.7% [1.9–100] *n*=160	gaussian
	all introduced mammal species ('summed')	39.2±27.7% [0–100] *n*=148	tweedie
	all native mammal species ('summed')	34.6±26.7% [0–100] *n*=148	tweedie
FOO was calculated for other taxa:		13.4±11.3% [0–60] *n*=137	
(16)	Birds (all species pooled).		gaussian
(17)	Reptiles (all species pooled).	10.4±14.6% [0–68.6] *n*=132	tweedie
(18)	Frogs (all species pooled).	1.6±3.6% [0–18.8] *n*=111	tweedie
(19)	Invertebrates (principally arthropods, including insects and crustaceans).	37.7±25.4% [0–100] *n*=130	gaussian
(20)	Plant material (principally fruit and grass).	25.7±24.9% [0–100] *n*=123	gaussian

NA: Scarce species (e.g. domestic cat, dingo/dog, marsupial moles, koala) had insufficient data for analysis by Generalised Linear Modelling (GLM).

Records of fox hair in fox diet (1.5±3.3% [0–21.4] n=140) were considered to represent fur ingested from autogrooming and were not included in diet analyses (although two studies recorded incidence of fox bone and tissues in stomach contents – see discussion).

Where FOO were presented by species but not by taxonomic groupings, we calculated a pooled value using a published approach based on combinatorial probability (Murphy et al. 2019). For example, if a dietary study reported FOO for three possum species (FOO species A = 0.3, species B = 0.2, species C = 0.1), then we estimated the overall frequency for possums (FOO possums) as:

$$\text{FOO possums} = 1 - (1 - \text{FOO}_{\textit{sp.}\,\text{A}}) * (1 - \text{FOO}_{\textit{sp.}\,\text{B}}) * (1 - \text{FOO}_{\textit{sp.}\,\text{C}})$$

$$= 0.496\ (49.6\%)$$

Absences were handled carefully and therefore the numbers of studies varied between diet categories. Absences were particularly important for amphibians and reptiles; where authors did not present data for amphibians or reptiles, but had detailed data across a range of taxonomic groups and did not have an 'other' category – we considered the lack of data for these groups to represent genuine absences (i.e. FOO=0%). We did not make any assumptions about the absence of invertebrates or plant material, and where a study did not present data, these categories were left blank – absences meant that that study was excluded for analysis of overall diet composition (non-metric Multidimensional Scaling Analysis and Permutation Analysis of Variance require a complete dataset) but the data were included in analyses of individual diet items (generalised linear models for each individual diet category).

We only included studies that presented the frequency of occurrence (FOO) of diet categories. Some studies present frequency of occurrence in relation to total prey (often termed relative occurrence) (McIntosh 1963; Purcell 2008; Marlow et al. 2015), but this metric is dependent upon the specific dataset considered, and therefore precludes comparison across studies. Frequency of occurrence (FOO) percentages were extracted directly from the source text, calculated from raw data, or measured from graphs using callipers or Plot Digitizer for Windows (http://plotdigitizer.sourceforge.net/). For the few studies where items were reported as '<1%' FOO, we recorded a value of 0.5%.

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Appendix S3. Summary of predictor variables and their covariation.

Sample type

(1) We recorded the dietary sample types for each study (stomach contents = 1 or scats = 0; proportions of total samples for those studies that used both).

Temporal predictor variables

(2) We recorded the time of year that samples were collected (or back-calculated where raw data were provided) for the four Austral seasons (summer = December–February, autumn = March–May, winter = June–August, spring = September–November). We separated datum points (where sample sizes permitted: $n > 10$ stomachs or scats) for studies that presented their data by season and included a dummy variable (= 1) in one of four season columns ascribing the season when the samples were collected. Where data were specifically stated as collected over two or three seasons, they were similarly recorded as '1' for each season. For studies where no details on time of year of sampling available, all season columns were marked as nil (= 0) for that study.

(3) Year of collection – we recorded dates of commencement and final year of study and calculated the midpoint of sample collection.

Spatial predictor variables

Using the geographic coordinates provided by each study or derived from study site descriptions, we extracted environmental attributes for each study location:

(4) Ecosystem – we used study site descriptions and Köppen classifications (Bureau of Meteorology 2020) to categories each location as: Forest; Woodland; Grasslands; Agricultural (= intensive grain growing – the majority of the Australian continent is pastoral); Urban/peri-urban.

(5) Climate zone – we identified five bioclimatic zones (Arid; Semi-arid; Sub-tropical, Warm temperate; Cool temperate), based on the Köppen classification (**Fig. 1a**), with separation of Temperate into Warm temperate and Cool temperate based on study site description and Temperature/humidity zones (Bureau of Meteorology 2020).

(6) Mean annual precipitation (mm) averaged over 1961-1990 (Australian Bureau of Meteorology 2020b)

(7) Mean annual temperature (°C) averaged over 1961-1990 (Australian Bureau of Meteorology 2020a).

(8) Distance to the coast (km) calculated using GIS as distance to the nearest coastline. Square root-transformed.

(9) Average terrain ruggedness calculated as the standard deviation of elevation within a 5-km radius of the study site (Jarvis et al. 2008). Log-transformed.

(10) Percentage vegetation cover within a 5 km radius of the study site (Hansen et al. 2003) Using values calculated in 2019.

(11) Human population within a 5 km radius of the study site using values calculated in 2019 (Australia Bureau of Statistics 2019). Log-transformed

(12) VAST classification – the Vegetation Assets, States and Transitions (VAST) classification of Australian vegetation categorises the degree of modification of vegetation as, from least to most intact: 0=bare,1= residual, 2=modified, 3=transformed, 5=replaced, 6=removed (see https://data.gov.au/dataset/ds-dga-f093534a-cd3d-4284-a084-0dfabb399272/details for more details). We averaged the scores across a 5 km radius of each study site.

We tested for collinearity using *corvif* in the package 'car' in R. There were strong associations between mean annual precipitation and vegetation cover (Spearman's Rank Order correlations: $R_{S\,158} = 0.875$). Removing precipitation (vegetation cover intuitively has greater relevance for fauna) ensured that all variance inflation factors were less than 5.

	Variance inflation factors (VIF)
Ecosystem	2.169844
Climate zone	4.991471
Mean VAST class (5km radius)	2.757514
Mean annual temperature	3.547666
Distance from coastline (km)	2.764510
Terrain ruggedness (5km radius)	3.261152
Vegetation cover (5km radius)	4.347812
human population (5km radius)	1.305254

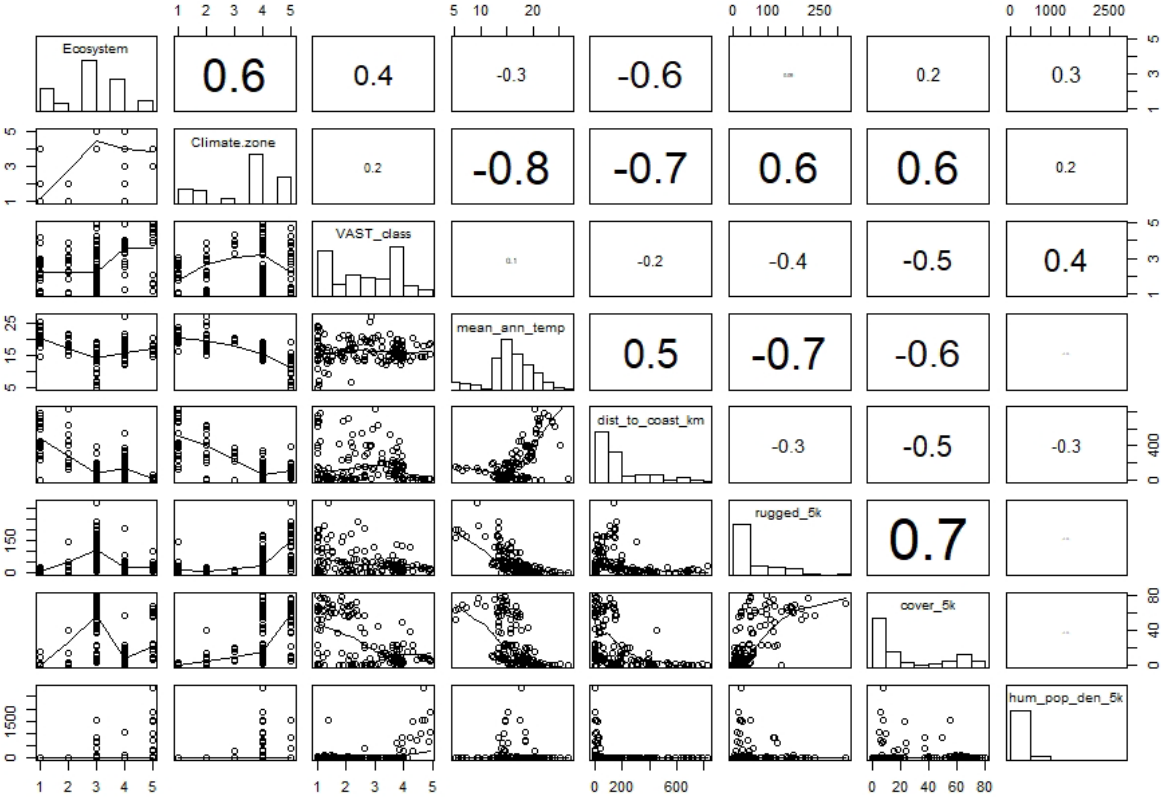

Fig. S3. Spearman's Rank Order correlations between environmental variables tested in this study.

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