Check for updates

Received: 24 September 2021 | Revised: 4 February 2022 | Accepted: 8 February 2022

DOI: 10.1111/ddi.13497

RESEARCH ARTICLE

Diversity and Distributions WILEY

Counting the bodies: Estimating the numbers and spatial variation of Australian reptiles, birds and mammals killed by two invasive mesopredators

Alyson M. Stobo-Wilson[1,2] | Brett P. Murphy[1] | Sarah M. Legge[1,3,4] | Hernan Caceres-Escobar[3] | David G. Chapple[5] | Heather M. Crawford[6] | Stuart J. Dawson[6,7] | Chris R. Dickman[8] | Tim S. Doherty[9] | Patricia A. Fleming[6] | Stephen T. Garnett[1] | Matthew Gentle[10,11] | Thomas M. Newsome[12] | Russell Palmer[13] | Matthew W. Rees[14] | Euan G. Ritchie[15] | James Speed[10] | John-Michael Stuart[6] | Andrés F. Suarez-Castro[3,16] | Eilysh Thompson[15] | Ayesha Tulloch[9] | Jeff M. Turpin[17] | John C.Z. Woinarski[1,18]

[1]Research Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, Northern Territory, Australia

[2]CSIRO Land and Water, Winnellie, Northern Territory, Australia

[3]Centre for Biodiversity and Conservation Research, School of Biological Sciences, University of Queensland, St. Lucia, Queensland, Australia

[4]Fenner School of Environment and Society, The Australian National University, Canberra, Australian Capital Territory, Australia

[5]School of Biological Sciences, Monash University, Clayton, Victoria, Australia

[6]Terrestrial Ecosystem Science and Sustainability, Harry Butler Institute, Murdoch University, Perth, Western Australia, Australia

[7]Department of Primary Industries and Regional Development, Invasive Species and Environment Biosecurity, South Perth, Western Australia, Australia

[8]Desert Ecology Research Group, School of Life and Environmental Sciences A08, University of Sydney, Sydney, New South Wales, Australia

[9]School of Life and Environmental Sciences, University of Sydney, Sydney, New South Wales, Australia

[10]Pest Animal Research Centre,

Abstract

Aim: Introduced predators negatively impact biodiversity globally, with insular fauna often most severely affected. Here, we assess spatial variation in the number of terrestrial vertebrates (excluding amphibians) killed by two mammalian mesopredators introduced to Australia, the red fox (*Vulpes vulpes*) and feral cat (*Felis catus*). We aim to identify prey groups that suffer especially high rates of predation, and regions where losses to foxes and/or cats are most substantial.

Location: Australia.

Methods: We draw information on the spatial variation in tallies of reptiles, birds and mammals killed by cats in Australia from published studies. We derive tallies for fox predation by (i) modelling continental-scale spatial variation in fox density, (ii) modelling spatial variation in the frequency of occurrence of prey groups in fox diet, (iii) analysing the number of prey individuals within dietary samples and (iv) discounting animals taken as carrion. We derive point estimates of the numbers of individuals killed annually by foxes and by cats and map spatial variation in these tallies.

Results: Foxes kill more reptiles, birds and mammals (peaking at 1071 km^{-2} $year^{-1}$) than cats (55 km^{-2} $year^{-1}$) across most of the unmodified temperate and forested areas of mainland Australia, reflecting the generally higher density of foxes than cats in these environments. However, across most of the continent – mainly the arid central and tropical northern regions (and on most Australian islands) – cats kill more animals than foxes. We estimate that foxes and cats together kill 697 million reptiles annually in Australia, 510 million birds and 1435 million mammals.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2022 The Authors. *Diversity and Distributions* published by John Wiley & Sons Ltd.

Invasive Plants and Animals, Biosecurity Queensland, Toowoomba, Queensland, Australia

[11]School of Agriculture and Environmental Science, University of Southern Queensland, Toowoomba, Queensland, Australia

[12]Global Ecology Lab, School of Life and Environmental Sciences, University of Sydney, Sydney, New South Wales, Australia

[13]Department of Biodiversity, Conservation and Attractions, Bentley, Western Australia, Australia

[14]Quantitative & Applied Ecology Group, School of Ecosystem and Forest Sciences, The University of Melbourne, Parkville, Victoria, Australia

[15]Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Burwood, Victoria, Australia

[16]Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogota, D.C., Colombia

[17]School of Environmental and Rural Science, University of New England, Armidale, New South Wales, Australia

[18]School of Ecosystem and Forest Sciences, University of Melbourne, Parkville, Victoria, Australia

Correspondence
Alyson M. Stobo-Wilson, CSIRO Land and Water, PMB 44, Winnellie Northern Territory, 0822, Australia.
Email alyson.stobowilson@gmail.com

Funding information
Conservation Ecology Centre; Centre of Excellence for Environmental Decisions, Australian Research Council, Grant/Award Number: DE170100599 and DP210100323; Australian Geographic Society; Victorian Environmental Assessment Council; Australian Government's National Environmental Science Program via the Threatened Species Recovery Hub; Centre for Invasive Species Solutions, Australian Government; Department of Biodiversity Conservation and Attractions, Western Australian Government; Holsworth Wildlife Research Endowment

Editor: José Brito

Main conclusions: This continental-scale analysis demonstrates that predation by two introduced species takes a substantial and ongoing toll on Australian reptiles, birds and mammals. Continuing population declines and potential extinctions of some of these species threatens to further compound Australia's poor contemporary conservation record.

KEYWORDS
biodiversity conservation, dietary ecology, domestic cat (*Felis catus*), invasive mesopredator, invasive species, mortality, predation, red fox (*Vulpes vulpes*), threatened species

1 | INTRODUCTION

Invasive predators impact biodiversity globally, including causing declines and extinctions of many animals, especially of island-endemic species (Doherty et al., 2016; Medina et al., 2011). Some invasive predators exert broad-scale and continuous predation pressure on native wildlife, with continental-scale analyses demonstrating that they can kill billions of animals every year, potentially leading to mortality rates that native prey populations cannot sustain (Brzeziński et al., 2020; Loss et al., 2013). Consequently, in many areas of the world, there is a strong management imperative to mitigate or eliminate the impacts of invasive predators on native fauna, including through broad-scale lethal predator control, eradication of predators from islands where threatened prey animals occur or might be

translocated, removal of predators from fenced reserves, reintroducing or maintaining native apex predators or conserving habitat structure to reduce hunting efficiency (Christensen et al., 2021; Doherty et al., 2015, 2017; Russell et al., 2015).

Since British colonisation in 1788, the introduced red fox *Vulpes vulpes* (hereafter 'fox') and domestic cat *Felis catus* (hereafter 'cat') have had, and continue to have, major detrimental impacts on Australian biodiversity. These mesopredators are thought to be the primary cause of extinction for at least 20 animal species, and responsible for the ongoing declines of many others (Abbott et al., 2014; Woinarski, Braby, et al., 2019; Woinarski et al., 2015).

In Australia, the management of foxes and cats is a priority conservation concern (Department of the Environment, 2015; Department of the Environment Water Heritage & the Arts, 2008). Across mainland Australia, there are areas in which broad-scale baiting of foxes (and other wild canids) has been implemented for many years (Robley et al., 2009; Saunders et al., 2010), a smaller number of areas with comparable cat control (e.g., Comer et al., 2020), as well as some relatively small areas where fencing excludes both predators (Legge et al., 2018). Otherwise, the vast majority of Australia has no effective management of invasive predators. Without management, the impacts of foxes and cats on Australian biodiversity are likely to be severe, widespread and ongoing.

A recent series of related papers, building on large datasets of dietary studies, have documented the number of species (and their biological traits) of Australian vertebrates killed by cats (Woinarski et al., 2018, 2020; Woinarski, Woolley, et al., 2017; Woolley et al., 2019), and the number of species (and their traits) of Australian reptile, bird and mammal species killed by foxes (Stobo-Wilson, Murphy, Crawford, et al., 2021; Stobo-Wilson, Murphy, Legge, et al., 2021; Woinarski et al., 2021). This allows the complement of species eaten by these two predator species to be compared, and the species eaten by one or both predators to be tallied. These studies have demonstrated a high degree of dietary overlap between foxes and cats in the vertebrate species consumed, but also some differences, with foxes taking, on average, larger prey than cats, highlighting their impacts are both compounded and complementary.

A parallel set of analyses evaluated the total numbers of individual vertebrates killed annually by cats in Australia (Murphy et al., 2019; Woinarski, Murphy, et al., 2017; Woinarski et al., 2018), including by pet cats (Legge et al., 2020). Here, we build upon these recent papers by addressing the following research questions:

1. Does spatial variation in the density of foxes in Australia differ from that of cats?
   We predict the density of foxes will vary across their Australian range, and that there will be regions where the density of foxes is higher than cats, and vice-versa
2. What is the estimated number of individual Australian reptiles, birds and mammals killed annually by foxes?
   We predict there to be a greater number of individuals consumed by foxes in those regions of Australia where fox densities are predicted to be higher.
3. How does the number and spatial pattern of animals killed by cats compare to that of foxes across Australia?
   We predict there to be a greater overall number of individuals consumed by cats relative to foxes due to the greater geographic range of cats. Additionally, we predict there to be a separation of impact between foxes and cats across Australia, with a greater number of individuals consumed by cats in regions of Australia where cat densities are predicted to be higher.
4. What is the combined toll of animals killed by cats and foxes across Australia?
   We predict there to be significant cumulative predation pressure by foxes and cats across large regions of Australia.

Our study — the first to quantify the continental-scale death toll imposed by both cats and foxes on vertebrate prey — aims, in part, to help direct management efforts to areas where impacts may be most acute and the benefits of investment may be most substantial. We know of no comparable study at this scale that describes and compares the death toll, across multiple vertebrate prey groups, imposed by two co-occurring introduced predators.

2 | METHODS

2.1 | Background: the fox and cat in Australia

Foxes were introduced to south-eastern Australia from the 1840s (Abbott, 2011), and populations became established from about 1874 (Fairfax, 2019). Foxes now occupy about 6.2 million km^2 (>80%) of mainland Australia, absent only from monsoonal northern Australia. They also occur on about 50 Australian islands (totalling 3,265 km^2). In contrast, cats now occur across >99% of mainland Australia and Tasmania (a total area of 7.6 million km^2) and are present on about 100 islands (with total area of about 90,000 km^2) (Legge et al., 2017). Cat introduction and spread preceded that of foxes by about 30–50 years (Abbott, 2008).

Foxes are opportunistic, omnivorous predators (Cavallini & Volpi, 1995; McIntosh, 1963) that consume a broad range of vertebrates, invertebrates and plant material (mostly fruits and seeds) (Fleming et al., 2021). Although their diet is also broad, cats are obligate carnivores (Woinarski et al., 2019). Foxes are slightly larger than cats (mean adult weight ca. 6 kg cf. 4.5 kg; Van Dyck & Strahan, 2008) and thus have larger daily dietary intake requirements. Estimated daily dietary intake for non-lactating foxes ranges from about 370–530 g (Lockie, 1959; Sargeant, 1978; Saunders et al., 1993), rising to 1113 g for lactating vixens (Saunders et al., 1993). This compares to estimates of 200–300 g for cats (Jones, 1977; Plantinga et al., 2011).

2.2 | Numbers of animals killed by foxes: approach and assumptions

The approach taken to estimate the number of individual animals killed by cats in Australia has been described previously (Murphy

et al., 2019; Woinarski, Murphy, et al., 2017; Woinarski et al., 2018). We used similar methods to estimate the number of reptiles, birds and mammals killed by foxes. The approach comprised the following steps: (i) prediction of spatial variation in fox density across Australia; (ii) compilation of existing data from studies that report the frequency of occurrence (FOO) of taxonomic groupings (prey groups) of animals in fox dietary samples (i.e., the proportion of dietary samples that contain a specified item), and then modelling spatial variation in FOO; (iii) assessment of the numbers of individual animals (of particular prey groups) in fox dietary samples that contain that prey group and (iv) a discount for the number of food items that appear in fox dietary samples, but were likely scavenged (i.e., as carrion) rather than killed by the fox.

We do not estimate tallies of the numbers of frogs taken by foxes, given that these have been recorded in relatively few fox dietary samples, and because their digestibility makes scat samples an unreliable method for interpreting the extent of predation on frogs (Woinarski et al., 2020). Hence, prey groups considered were reptiles, birds, mammals and the following subsets of mammals: all native mammals; native rodents; dasyurids (Family Dasyuridae); possums and gliders (Suborder Phalangerida); macropods and potoroids (Suborder Macropodiformes); all introduced mammals; lagomorphs (European rabbit *Oryctolagus cuniculus* and the much more spatially restricted European brown hare *Lepus europaeus*); introduced rodents (mostly house mouse [*Mus musculus*] and black rat [*Rattus rattus*]) and livestock (mostly sheep *Ovis aries*, cattle *Bos taurus* and *B. indicus*, and goat *Capra hircus* – farmed or feral). The following subsets of mammals were also considered but were identified in <30% of fox diet studies and thus were not modelled as separate prey groups: bandicoots and bilbies (Order Peramelemorphia); koalas *Phascolarctos cinereus*; wombats (*Lasiorhinus* spp., *Vombatus ursinus*); bats (Order Chiroptera); monotremes (*Tachyglossus aculeatus* and *Ornithorhynchus anatinus*); marsupial moles (*Notoryctes* spp.); numbats (*Myrmecobius fasciatus*); dingoes and dogs *Canis dingo/familiaris*; and cats.

Broadly, our analytical approach assumes that the annual number of individual animals of each prey group killed by foxes at a location can be estimated from the product of the density of foxes at that location, the average number of individuals of that prey group in a single fox stomach at that location and the number of days in a year. We then assumed that these local estimates can be summed to derive national estimates. There are several assumptions underlying, or caveats qualifying, this procedure:

1. All animals in fox dietary samples were killed by the fox that consumed them. This assumption may lead to some over-estimation in the kill rate by foxes because foxes will consume pre-killed animals (carrion). In response, we develop and apply a discount factor for animals consumed as carrion (see later section).
2. Foxes consume all animals that they kill. This assumption may lead to an under-estimation in the kill rate because foxes frequently surplus kill [i.e., do not consume animals they kill, as has been reported many times for foxes in Australia (Abbott et al., 2014; Short et al., 2002)].
3. What is present in a fox scat or stomach represents what is eaten by a fox in the preceding 24 h, and hence can be expressed as the daily kill rate by that fox, following the logic used in analogous cat dietary studies (e.g. Murphy et al., 2019). Based on studies of the passage rate of food items in the fox digestive tract (e.g., Witt, 1980), this assumption is likely to be highly conservative, with digestion rate of most prey types typically being <24 h. However, some prey items may be cached for later consumption or consumed over several days, such that the presence of that prey item in a fox dietary sample may not mean that the animal was killed within the 24-h period preceding sample collection (Macdonald, 1976).
4. Fox density and the incidence of any prey group in fox diets at any site are temporally invariant. However, fox density at any location varies seasonally (due to highly seasonal reproduction), and in some parts of Australia, fox density changes in response to control programmes and to rainfall patterns (and the consequential variation in prey abundance) (Dickman et al., 2014). Furthermore, the diet of foxes also varies seasonally or with rainfall conditions (Green, 2003; Green & Osborne, 1981; Pavey et al., 2008; Wilson & Wolrige, 2000), between sex and age groups (Forbes-Harper et al., 2017) and in response to pest control programmes (that reduce fox and/or prey abundance) (Newsome et al., 2014; Roberts et al., 2006). Hence, there may be temporal variation in the take of prey groups by foxes at any location. However, there is no systematic bias in this respect in the set of our compiled studies: the constituent studies included sampling across one or many seasons, and with or without control programmes (although such information is not always stated in the studies themselves), and our modelling across studies does not include any factors relating to seasonal condition or management.
5. We assume that eggs are detected in proportion to the number consumed. Many studies have demonstrated high rates of predation by foxes on clutches of reptile and bird eggs and have concluded that, for some reptile and bird species, the major impact of fox predation is likely to be through predation of eggs (Thompson, 1983). However, eggs were likely to be severely under-recorded in the fox dietary studies we collated because they are highly digestible and thus difficult to discern in fox stomachs and scats, and because foxes often only consume egg contents (Dawson et al., 2016; Spencer et al., 2021). Consumption rates of eggs will therefore be under-estimated in our data collation and reporting.

2.3 | Fox density analysis

We developed a fox density layer by building a predictive model based on a dataset of 437 published and unpublished observations of fox density (ten from highly modified environments) spread across the fox's Australian range (Figure S1b). A variety of methods were used to estimate density, but the most common were spotlighting, track

counts and counts of active dens (used for 70%, 9% and 6% of density observations, respectively). The fox density estimates included areas with and without fox control. However, given that our aim was to predict fox density across Australia, and we do not have a spatial layer describing area with and without fox control across Australia, we simply included both subsets of data in the analysis. To avoid pseudoreplication, density estimates from the same location were averaged, reducing the dataset to 44 spatially distinct density estimates, including six from highly modified environments (Figure S1b). To analyse the fox density data, we took the same approach as that used by Legge et al. (2017) for modelling cat density across Australia.

We used least-squares linear regression models incorporating all combinations of six climatic and environmental variables, determined for each location, giving a total of 64 models. The variables were mean annual temperature (Australian Bureau of Meteorology, 2016a), mean tree cover within a 5-km radius (Hansen et al., 2003), topographic ruggedness within a 5-km radius (Jarvis et al., 2008), distance from the coast (distance from coast was used instead of the island [yes/no] variable that was used in the original complementary cat analysis), mean human population density within a 5-km radius (Australian Bureau of Statistics, 2014) and vegetation disturbance within a 5-km radius (Australian State of the Environment, 2017) (see Table S1 for a detailed description of each parameter). Mean annual rainfall (Australian Bureau of Meteorology, 2016b) was originally considered as a predictor variable, but preliminary analysis highlighted that this variable was strongly correlated with vegetation cover ($r > .7$) and moderately correlated with several other variables ($r > .5$), so it was ultimately excluded from analyses. We $\log_{10}$-transformed distance to coast and human population density. Fox density was log-transformed prior to analysis to ensure normality of model residuals.

Models were evaluated using Akaike's information criterion corrected for small samples sizes (AIC_C). The final model was based on multi-model averaging of the entire candidate set, with each model weighted according to the Akaike weight (Burnham & Anderson, 2003).

The final model was used to predict fox density across the fox's distributional range at 1 km^2 resolution (Figure S1). Note that the fox is largely absent from far northern Australia, and to demarcate the northern range limit we used fox presence records, based on specimens or sightings, from the Atlas of Living Australia (ALA) database (www.ala.org.au), following Stobo-Wilson, Murphy, Legge, et al. (2021). For the mainland, we identified bioregions (Department of Sustainability Environment Water Population & Communities, 2013) in which the fox is present (i.e., bioregion has recent [post-1970] fox records), and added islands where the fox is known to occur based on the database of Legge et al. (2018).

To estimate the total population of foxes in Australia, we predicted density for every 1 × 1 km cell across the fox's distributional range and then calculated the sum of the estimates across all cells. We characterised the uncertainty of the total fox population by bootstrapping the dataset 10,000 times and recalculating the population based on each random selection of the data. We report the 2.5% and 97.5% quantiles for the 10,000 bootstrapped values of total predicted population.

2.4 | Fox diet analysis: variation in FOO

We compiled data from 89 studies of fox diet in Australia (with several studies including multiple sites, such that the total number of sites with samples was 168) that reported the FOO of reptiles (73 studies), birds (79 studies) or mammals (88 studies) in fox dietary samples. The total number of samples comprised 49,458 scats or stomachs (Table S2). These studies were widely spaced across the geographic range of the fox in Australia and sampled diverse environments (Figure S1a). Some studies excluded empty stomachs from FOO calculations; where this was the case, we recalculated FOO to apply to all collected samples. We also noted whether the dietary sampling was from fox scats or fox stomachs as previous studies have indicated that different prey groups (e.g., birds, livestock) are more likely to be detected in fox stomachs than in fox scats (Cavallini & Volpi, 1995; Fleming et al., 2021). Note that this collation of fox dietary studies has also largely been used by Fleming et al. (2021) to describe characteristics of the diet of foxes in Australia, and more details of the collated dataset are described in that paper.

The categorisation of mammal prey in the compiled fox dietary studies varied, with a range of categories used. For example, some studies reported FOO for: (i) each mammal species; (ii) major taxonomic groups; (iii) all mammals combined; (iv) different size classes of mammals or (v) native *vs.* introduced mammals. Where published studies included only data summaries, we sought primary data (i.e., records of mammal occurrence in individual scats or stomach samples) from the data custodians. Where the raw data were unavailable, we followed Murphy et al. (2019) and used combinatorial probability to group FOO values reported for individual species or groups into higher taxonomic units, given that frequency values are not additive. For example, if a dietary study reported FOO for possum species A ($\text{frequency}_{\text{possum A}}$) as 0.8, possum species B ($\text{frequency}_{\text{possum B}}$) as 0.2 and possum species C ($\text{frequency}_{\text{possum C}}$) as 0.1, we estimated the overall FOO for possums ($\text{frequency}_{\text{possum}}$) as:

$$\text{frequency}_{\text{possum}} = 1 - \left(\left(1 - \text{frequency}_{\text{possum A}}\right) \times \left(1 - \text{frequency}_{\text{possum B}}\right) \times \left(1 - \text{frequency}_{\text{possum C}}\right)\right),$$

in this case 0.86.

All analyses were run in R version 4.4.4 (R Core Team, 2021). Prior to modelling, we followed the protocol for data exploration provided by Zuur et al. (2010). All continuous predictor variables were centred and standardised by deducting the mean and dividing by twice the standard deviation (Gelman, 2008).

For each fox diet study site, we determined the values of the six climatic and environmental variables described above to assess their effects on the FOO of animals in fox diet samples. To accommodate the potentially different detectability of animals from scat versus

stomach samples, we also considered the proportion of dietary samples that were from scats (cf. stomachs) in each study, as a predictor variable.

We used generalised linear models (GLMs), within the binomial error family, to examine geographic variation in the FOO of each prey group in the diet of foxes. The response variable was the proportion of fox diet samples (scats and/or stomachs) containing the prey group. Using the binomial error family, the GLMs incorporated lower precision from observations based on a small number of samples. We examined a set of 128 candidate models representing all combinations of the seven explanatory variables described above (temperature, vegetation cover, ruggedness, distance to coast, human population density, vegetation disturbance, proportion of scat samples). Models were evaluated using a second-order form of Akaike's information criterion ($QAIC_c$), which is appropriate for small sample sizes and over-dispersed data (Burnham & Anderson, 2003). There was evidence of strong overdispersion, so we used the 'quasibinomial' error structure to estimate coefficient standard errors and confidence intervals. We applied model averaging to the entire candidate set to account for model uncertainty, with each model weighted according to its Akaike weight. We identified highly influential variables by calculating relative variable importance (RVI), defined as the sum of Akaike weights for all models containing a given predictor variable. Variables with a RVI value ≥0.73 (equivalent to an AIC_c difference of 2; Richards, 2005) were retained in the best model, which was used to identify the most influential predictor variables and visualise variable effects. Model averaged coefficients from the entire candidate set were used to predict the FOO of each prey group in fox diets across Australia. The proportion of scat samples was retained as a variable here only if it was found to have a negative influence on the prey groups FOO (i.e., the prey group was less likely to be detected in scat than in stomach samples).

Four fox diet studies for island sites were included in analyses (three studies from Phillip Island and one from Bennison Island; see Figure S1a). We modelled the FOO of all prey groups in fox diets both including and excluding these islands to ensure that island sites did not bias the results. We found that including island sites did not alter the most influential predictor variables identified for any of the prey groups and therefore retained all sites in our analyses (see Table S3).

2.5 | Fox diet analysis: variation in number of individual prey animals, and proportions of native species, within samples

In 18 studies that analysed fox stomachs only, tallies were given for the number of individual reptiles in those samples that contained reptiles. We found a significant positive correlation between the FOO for reptiles and the number of individual reptiles identified in fox stomachs and therefore used the predicted FOO of reptiles in fox stomachs to estimate the number of individual reptiles in those diet samples that contained reptiles, using a linear least-squares regression model ($\log_{10}$ [individuals − 0.99] ~ $\log_{10}$ [frequency]) (see Figure S4a). Of the fox dietary studies that reported the species of reptiles consumed (n = 47), none reported consumption of introduced reptile species. Hence, our fox predation tallies assume all reptiles killed were native.

In 21 studies that analysed fox stomachs only, tallies were given for the number of individual birds in those samples that contained birds. We found no significant relationship between the FOO of birds and the number of individual birds in fox stomachs across these studies, so we used the mean number of individual birds within fox stomach samples across studies (1.2 birds) to estimate the number of individual birds in diet samples that contained birds. For the studies in our collation that also reported on the species of birds occurring in fox scats or stomachs (n = 38), we calculated the proportion of native and of introduced birds (relative to all birds) in those samples. Note that far more fox dietary studies reported simply on the occurrence of 'birds' in samples rather than on the species of bird consumed, so our fox predation tallies report on overall consumption of birds rather than breaking this tally down to groups of bird species.

In 22 studies that analysed fox stomachs only, tallies were given for the number of individual mammals in those samples that contained mammals. There was a significant positive correlation between FOO of mammals and the number of individual mammals identified in fox stomachs. We therefore used the predicted FOO of mammals in fox stomachs to estimate the number of individual mammals in those diet samples that contained mammals, using the same approach described above for reptiles (see Figure S4b).

2.6 | Discount for consumed items scavenged (i.e., consumption of carrion) rather than killed

Foxes frequently consume carrion (see Appendix S1 and references therein). To account for potential consumption of carrion in our calculations, we used an expert elicitation approach to estimate the proportion of each taxonomic group in fox dietary samples that were likely taken as carrion. We report only estimates of the number of animals killed by foxes (i.e., the total estimated consumption less the proportion taken as carrion).

2.7 | Estimates of tolls taken by foxes

To spatially represent the estimated number of animals killed per fox per day, we multiplied the modelled FOO of each prey group in fox diets across Australia by the number of individuals in fox diet samples containing that prey group, discounting the number of animals estimated to be consumed as carrion. We then multiplied this by the

modelled density of foxes across Australia, and then by 365.25 (days in a year), to provide a spatial representation of the estimated number of animals killed by foxes per km^2 per year. We summed this rate across the extent of the fox's distributional range in Australia to derive the total number of animals killed by foxes.

We followed the approach of Murphy et al. (2019) to characterise the uncertainty of the estimated total number of animals killed by foxes, using bootstrapping. Bootstrapping is an appropriate approach because we needed to propagate errors from a number of analytical steps. Hence, we simultaneously bootstrapped (10,000 times – which was the maximum feasible given computational constraints) the underlying datasets: (i) fox density; (ii) frequency of the prey group in fox samples and (iii) the mean number of individuals of that prey group in fox diet samples containing that prey group. For each random selection of these underlying data, we recalculated the total number of animals killed. We report the 2.5% and 97.5% quantiles for the 10,000 estimates of the total number of animals killed. We also include the uncertainty associated with the estimate of the proportion of animals consumed as carrion. We did this by sampling a normal distribution and then applying an inverse-logit transformation to the realised value (to constrain the values [of proportion consumed] between 0 and 1). By adjusting the mean and standard deviation of the underlying normal distribution, we ensured that the median and 10% and 90% quantiles of the final values (constrained between 0 and 1) closely matched the best guess and upper and lower standardised credible intervals.

2.8 | Comparison of tolls of animals taken by foxes and cats

The recent analyses of the numbers of animals killed by cats in Australia (Murphy et al., 2019; Woinarski, Murphy, et al., 2017; Woinarski et al., 2018) considered three components of the overall Australian cat population: pet cats, feral cats in highly modified environments (e.g., urban areas) and feral cats in largely natural environments [as defined by Legge et al. (2017)]. A comparable subdivision is not used in our assessment of fox diet because foxes are not kept as pets, and because we included parameters relating to habitat modification in our modelling. We compare tallies (and spatial variation in these tallies) of animals killed by foxes with those killed by (i) feral cats from largely natural environments and (ii) feral cats (in natural and modified environments) as well as pet cats, with the latter component based on an updated estimate of the numbers of animals killed by Australia's pet cats (Legge et al., 2020).

We did not include a discount term for the proportion of animals consumed by cats that were taken as carrion, because many studies have shown that cats take much less carrion than do foxes (Christensen et al., 2013; Forsyth et al., 2014; Read et al., 2016). Nonetheless, cats do some scavenging (e.g. Cunningham et al., 2018; Fleming et al., 2020), so our cat tallies may be marginal overestimates in this regard.

3 | RESULTS

3.1 | Fox density and population size cf. cats

We found a significant negative relationship between fox density and mean annual temperature, and a significant positive relationship between fox density and human population density (see Table S4, Figure S2). The best-supported model of fox density had high model fit (R^2 = .66; Table S4; Figure S3). Areas that have the highest predicted density of foxes include the coastal belt across south-eastern Australia, south-western Australia and parts of coastal South Australia (Figure 1a). In contrast, cat density (in years of average rainfall) is less variable across their extensive Australian range (Figure 1b). Based on spatially modelled density, we estimate that there are 1.7 million foxes in Australia, at an average density of 0.27 km^{-2}, compared with 6.6 million cats (comprising 2.1 million feral cats in natural landscapes, also at average density of 0.27 km^{-2}, 0.7 million feral cats in highly modified landscapes and 3.8 million pet cats; Table 1) (Legge et al., 2017, 2020).

3.2 | Tolls for individual prey groups

3.2.1 | Reptiles

The mean FOO of reptiles in fox dietary samples was 10.3%. FOO of reptiles in fox diets significantly increased with mean annual temperature (standardised beta coefficient ± standard error [*SE*], 0.84 ± 0.34) and decreased with vegetation cover (−1.19 ± 0.37) and vegetation disturbance (−0.77 ± 0.30; see Figure 2a, Figure S5). The best model for FOO of reptiles in fox diets had an R^2 of .49.

We estimate that 88 million reptiles (95% confidence interval [CI]: 49–170 million) are killed by foxes across Australia each year, with 85 million of these in predominantly natural landscapes. These figures exclude the 4% of reptiles that are estimated to be consumed by foxes as carrion. This estimate of reptiles killed by foxes is less than a fifth of the total estimated to be killed by feral and pet cats across Australia each year (609 million reptiles; Table 1, Figure 3).

3.2.2 | Birds

The mean FOO of birds in fox diet samples was 14.4%. FOO of birds in fox samples was significantly lower when sampling comprised a greater proportion of scats than stomachs (standardised beta coefficients ± *SE* for proportion of scats: −0.43 ± 0.14). The FOO of birds in fox diets significantly increased with vegetation disturbance (0.44 ± 0.11) and mean annual temperature (0.73 ± 0.12) and was higher close to the coast (−0.85 ± 0.11; Figure 2b; Figure S6). The best model for the FOO of birds in fox diet had an R^2 of 0.54.

We estimate that 111 million birds (95% CI: 51–176 million) are killed by foxes across Australia each year, of which 93% are native. These figures exclude the 7% of birds that are estimated to be

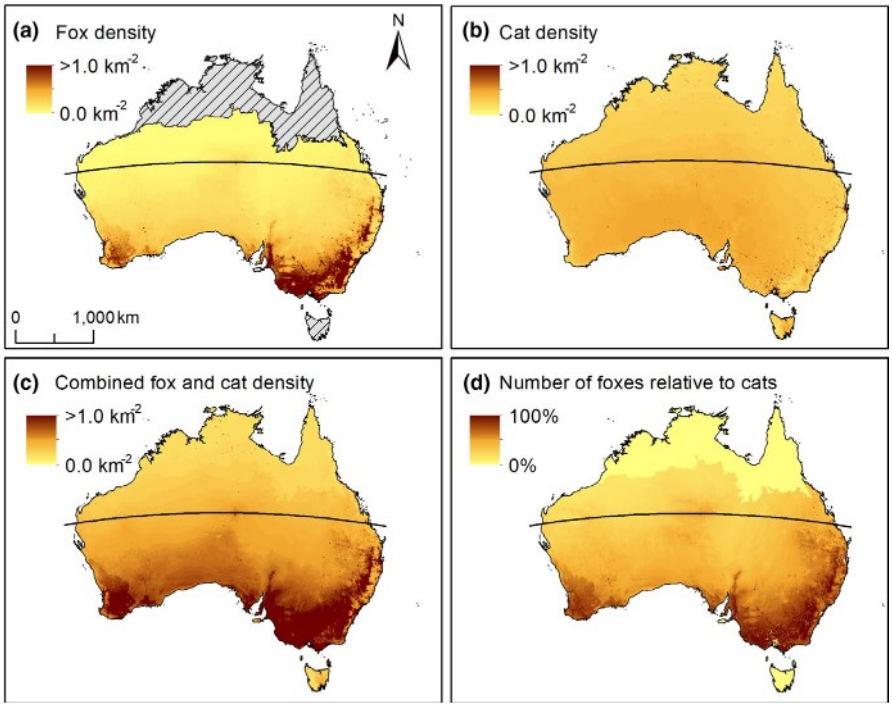

FIGURE 1 (a) The modelled density of foxes throughout Australia, areas outside of the fox's distributional range are hatched and shaded grey. (b) The modelled density of cats (including pet cats) throughout Australia averaged over wet and dry periods. (c) Combined density of foxes and cats (including pet cats) throughout Australia and (d) the proportion of this total that is foxes. The solid black line indicates the Tropic of Capricorn

consumed by foxes as carrion. The estimate of birds killed by foxes is less than a third of the number estimated to be killed by feral and pet cats across Australia each year (399 million; Table 1, Figure 3).

3.2.3 | Mammals

The mean FOO of mammals in fox dietary samples was 70.0% when considering all mammals, 39.5% for native mammals and 37.1% for introduced mammals. The FOO of native mammals in fox diets increased with vegetation cover only (standardised beta coefficients ± *SE* 1.34 ± 0.15; Figure S7). Conversely, introduced mammals were less likely to occur in fox diets as vegetation cover (−1.11 ± 0.15) and human population density increased (−0.61 ± 0.18) and were more likely to occur in fox diets as vegetation disturbance increased (0.73 ± 0.22; Figure S7). Introduced mammals were also significantly less likely to be detected in fox dietary studies that predominantly used scat (rather than stomach) samples (−0.68 ± 0.25). The best models for FOO of native and introduced mammals in fox diets had R^2 of .37 and .46, respectively. The modelled FOO of native and introduced mammals in fox diets show contrasting spatial patterns (Figure 2c,d), with native mammals more likely to occur in fox diets along the forested eastern coastline, while introduced mammals were more likely to occur in fox diets elsewhere.

The estimated number of mammals killed by foxes per year across Australia is 367 million (95% CI: 135–780 million), of which around 29% (108 million [95% CI: 54–344 million]) are native. These figures exclude the 27% of introduced mammals and 19% of native mammals that are estimated to be consumed by foxes as carrion. The number of mammals estimated to be killed by foxes is about half that of those estimated to be killed by feral cats (815 million) and a third of the number of mammals estimated to be killed by feral and pet cats combined (1067 million; Table 1).

Of the mammal subgroups identified in fox diets, rodents had the greatest FOO (22.4%), with an almost equal representation of native rodents (FOO 10.9%) and introduced rodents (FOO 11.6%) (Figure S8a,b). A total of 129 million rodents (95% CI: 90–311 million) are estimated to be killed by foxes each year from natural landscapes (Figure 3). Of this total, around 43% (55 million, 95% CI: 31–147 million) are native. This is only 20% of the number of native rodents estimated to be killed by feral cats each year (268 million). Like cats, lagomorphs were the second most frequently occurring mammal subgroup in fox diets (FOO 19.0%), with 114 million (mostly European rabbits) estimated to be killed by foxes each year (95% CI: 46–259 million) (Figure S8c). This tally is about half that estimated to be killed by feral cats (201 million). The other main introduced prey group was livestock (FOO 12.9%; Figure S8d). Livestock was the only mammal subgroup that was significantly less likely to be detected at a site as the proportion of scat samples increased (standardised beta coefficient ± *SE* −1.16 ± 0.24). After accounting for the 74% of livestock estimated to be consumed by foxes as carrion, we estimate foxes kill 38 million livestock animals (95% CI: 4–122 million) across Australia each year; we had no comparable estimate for cats.

Of the native mammal subgroups, possums and gliders had the largest FOO in fox diet (14.2%), with highest FOO mostly in forested eastern Australia (Figure S8e). Foxes are estimated to kill 40 million (95% CI: 27–121 million) possums and gliders per year (cf. 20 million by feral cats). Macropods and potoroids were reasonably common in fox dietary samples (FOO 9.3%), with highest values in the semi-arid rangelands (Figure S8f); foxes were estimated to kill 29 million (95% CI: 6–96 million) macropods and potoroids annually (cf. 19 million by feral cats) across natural landscapes in Australia (Figure 3).

TABLE 1 Density and population estimates for foxes, feral cats and all cats (including feral and pet cats) throughout Australia, with mean frequency of occurrence (FOO) of all major prey groups, and the estimated numbers eaten for all major prey groups

	Foxes	Feral cats	All cats (including feral and pet)
Average density	0.27 km^{-2}	0.27 km^{-2}	
Total population size (millions)	1.66	2.8	6.6
Mean frequency of occurrence % (minimum-maximum)			
Reptiles	10.3 (0.0–68.6)	25.6 (0.0–100.0)	
Birds	14.4 (0.0–85.0)	31.6 (4.2–92.8)	
Native mammals	39.5 (0.0–100.0)	43.1 (0.0–100.0)	
Introduced mammals	37.1 (0.0–100.0)	31.3 (0.0–100.0)	
Native rodents	10.9 (0.0–88.1)	25.1 (0.0–100.0)	
Introduced rodents	11.6 (0.0–76.0)	14.3 (0.0–62.5)	
Lagomorphs	19.0 (0.0–95.0)	19.6 (0.0–85.0)	
Livestock	12.9 (0.0–92.6)	Not estimated	
Possums and gliders	14.2 (0.0–72.0)	4.3 (0.0–56.0)	
Macropods and potoroids	9.3 (0.0–69.1)	3.5 (0.0–47.4)	
Dasyurids	5.7 (0.0–56.4)	11.7 (0.0–57.1)	
Estimated numbers eaten annually (million) (95% confidence intervals)			
Reptiles	88 (49–170)	466	609
Birds	111 (51–176)	265	399
Mammals	368 (135–780)	815	1067
Native mammals	104 (54–344)	452	
Introduced mammals	264 (109–486)	350	
Native rodents	56 (31–147)	275	
Introduced rodents	80 (46–187)	114	
Lagomorphs	114 (46–259)	202	
Livestock	38 (4–122)	Not estimated	
Possums and gliders	46 (27–121)	21	
Macropods and potoroids	30 (6–96)	19	
Dasyurids	23 (15–67)	84	

Note: Values relating to foxes are from this study. Values relating to cats have been sourced from Legge et al. (2017), Woinarski, Murphy, et al. (2017), Woinarski et al. (2018), Murphy et al. (2019) and Legge et al. (2020). Confidence intervals for the estimated number of animals eaten by cats were not provided by the original sources and therefore have not been provided here. Note that FOO values and tallies are not given for minor mammal prey groups (FOO < 5%).

Dasyurids were less frequent in fox diets (FOO 5.7%), with highest values in forests of south-eastern Australia (Figure S8 g). Foxes kill an estimated 23 million individual dasyurids per year (95% CI: 15–67 million) across natural landscapes, which is 25% of the 84 million estimated to be killed by feral cats annually. The mean FOO of the remaining mammal subgroups in fox diets was bandicoots and bilbies 3.7%, monotremes 0.5%, wombats 0.4%, bats 0.2%, marsupial moles 0.1%, dingoes and dogs 0.4%, and cats 0.5%.

3.3 | Toll of Australian fauna taken by foxes and cats

Collectively, we estimate 697 million reptiles, 510 million birds and 1,435 million mammals are killed by foxes and cats across Australia each year (Table 1), with the greatest predation pressure in urban and peri-urban areas (Figure 4) where cat and fox densities are greatest. However, there are contrasting patterns of spatial variation in tolls of animals taken beyond urban areas, with more animals eaten by foxes than by cats in south-eastern and south-western Australia, and by cats in other regions (Figure 4b).

4 | DISCUSSION

Here, we provide the first estimates of the toll (and its spatial variation) of wildlife taken by foxes at a continental scale. Our evaluation allows for a direct comparison to the toll taken by another co-occurring introduced predator, the cat. Such tolls help contextualise the relative predation threats imposed by both species (Loss et al., 2012), inform public opinion and, hence, better support social licence for agencies to manage the threat (van Eeden et al., 2017; Woinarski, Legge, et al.,

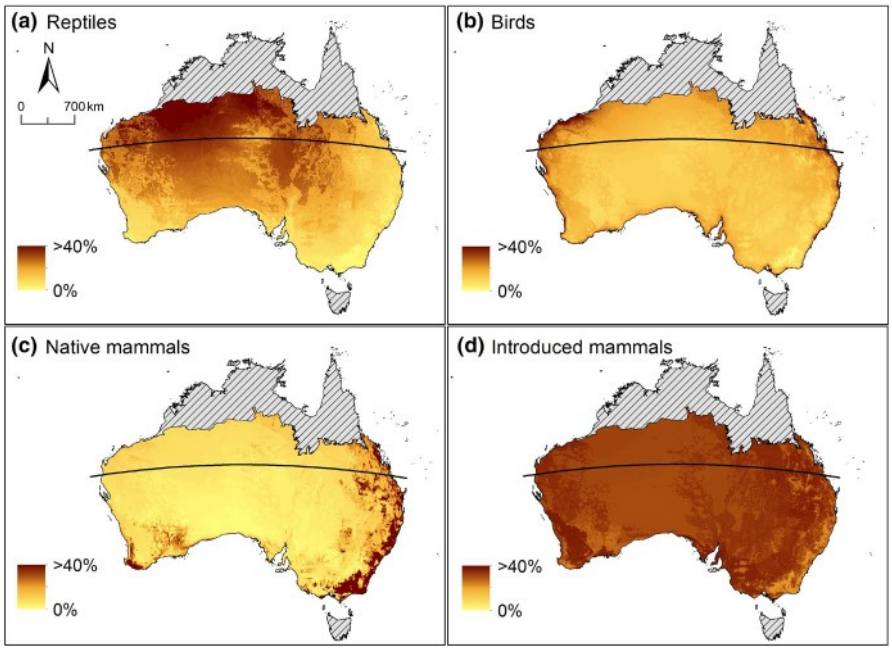

FIGURE 2 Model projections of the frequency of occurrence of (a) reptiles, (b) birds, (c) native mammals and (d) introduced mammals in fox diets throughout Australia. Solid black line indicates the Tropic of Capricorn and hatching indicates areas outside of the fox's distributional range

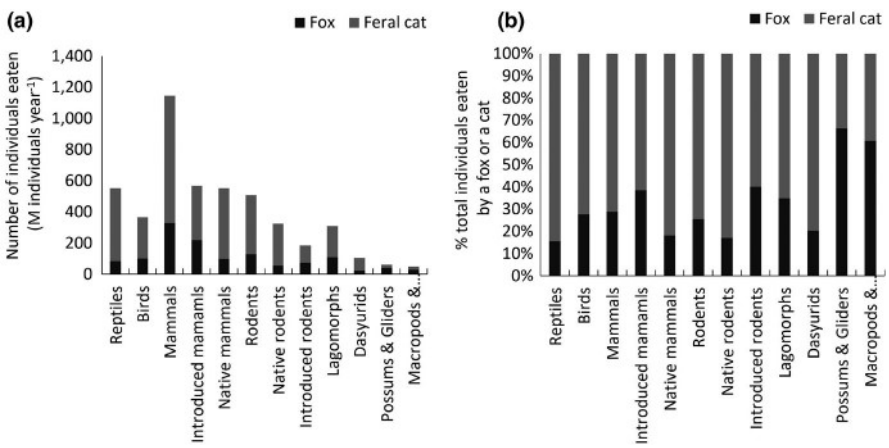

FIGURE 3 (a) The estimated total number of animals, by taxonomic group, killed by foxes (dark grey) and feral cats (light grey) each year in largely natural landscapes across Australia, and (b) the proportion of that total killed by foxes compared to feral cats

2019). In addition, this information can help determine spatial priorities for such management (Januchowski-Hartley et al., 2018).

A key component of our estimate of tolls is the population size (and its spatial variation) of the two predator species. We found that the density of foxes varies markedly across their Australian range, with highest densities in urban areas and in temperate areas of southern mainland Australia and lower densities in warmer and tropical regions. In contrast, feral cat density varies less across their near ubiquitous Australian range (Legge et al., 2017). On average, cats are more abundant than foxes outside of forested and temperate areas in Australia. Our national population estimate for foxes (1.7 million) is much lower than a previous estimate of about 7 million (McLeod, 2004); we attribute this discrepancy to the earlier estimate being based on far fewer studies that were mostly in temperate, urban and/or forested areas where fox density is appreciably higher than in their more extensive arid and semi-arid range (Forsyth et al., 2019; McLeod, 2004).

Foxes are opportunistic omnivores (Cagnacci et al., 2003; Saunders et al., 2010), and the pattern observed here of spatial variation in FOO of different prey groups in fox diet is likely to at least partly reflect spatial variation in the abundance of those prey groups, a result consistent with a national Australian study (Fleming et al., 2021), and regional Victorian study (Davis et al., 2015). Hence, for example, reptiles form a larger proportion of fox diets in arid and semi-arid areas, where reptiles are most abundant; possums form a larger proportion of fox diets in more heavily forested high rainfall areas of temperate Australia, where possums are most abundant. This is similar to patterns of spatial variation in FOO displayed by cats in Australia with, for example, reptiles also forming a larger proportion of cat diet in arid and semi-arid Australia (Woinarski et al., 2018). Much of the difference between the two predator species, in terms of the spatial variation in the relative numbers of prey killed, likely also reflects variation in the relative densities of the two predators. Hence, on average, foxes kill more animals than do cats in south-eastern Australian temperate forests (where they are more abundant than cats), but kill fewer animals in the rest of Australia (where foxes are less abundant).

For most prey groups, the Australian fox population kills many fewer individual animals than do cats. This is a consequence of several

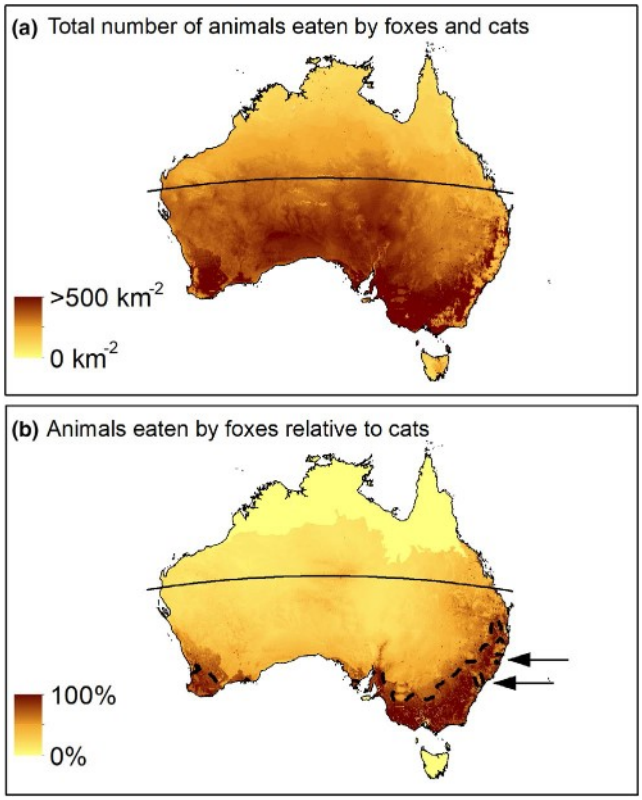

FIGURE 4 (a) The estimated total number of animals (including only reptiles, birds and mammals) eaten by foxes and cats combined each year throughout Australia, and (b) the proportion of this total that is attributable to fox predation; dashed line indicates where the number of animals eaten by foxes versus cats is relatively equal (50%). Solid black line indicates the Tropic of Capricorn

factors: (i) cats occur over a larger area (7.6 million km^2 cf. 6.2 million km^2), resulting in a larger total population of feral cats (2.8 million cf. 1.7 million foxes); (ii) there is an additional component of the Australian cat population, pet cats, that adds considerably to the total toll taken by cats (Legge et al., 2020); (iii) much more of the fox's dietary intake is derived from carrion, so they do not need to make as many kills as cats; (iv) although vertebrates are staples in fox diet, as omnivores they also supplement their diet with more invertebrates and plant material than do cats (Fleming et al., 2021) which are obligate carnivores; (v) although there is extensive overlap between foxes and cats in the vertebrate species eaten, foxes tend to take larger prey items than do cats (Stobo-Wilson, Murphy, Crawford, et al., 2021; Stobo-Wilson, Murphy, Legge, et al., 2021) and so obtain the same volume of food with fewer kills and (vi) birds and reptiles occur less frequently in fox diets than in cat diets. The disparity in numbers of animals killed by foxes relative to cats varies across prey groups, and for a few groups (notably possums and macropods), foxes kill more individuals than do cats. For possums, this is probably because their abundance is highest in areas where fox abundance is generally higher than that of cats; for macropods, this difference may be because foxes are more capable than cats of taking larger animals (e.g., Banks et al., 2000).

The disparities in numbers of animals killed by foxes and cats suggest important differences in the relative impacts of these two predators. Such differences can help set broad management priorities; for example, to direct fox control efforts especially to areas where the toll from foxes is greater than that from cats. However, we note that the modelling on which we base our estimates of total numbers of animals killed is continental in scale, and that there will be much nuance in local conditions, not readily described in our broad-scale assessment. Furthermore, our tallies mostly group taxonomically related prey species, while predation impacts may fall especially on some individual wildlife species, including those whose attributes render them relatively poorly adapted to sustained predation. For example, detailed studies and experimentation have demonstrated that, in some areas, foxes, but not cats, take an unsustainable toll of clutches of some turtle species (Spencer & Thompson, 2005; Spencer et al., 2016), even though across most of Australia, we found that cats take far more reptiles than do foxes. This example also serves as a caveat that our analyses probably under-estimate the consumption of reptiles (and birds), because digested eggs leave little trace in fox stomachs or scats.

Notwithstanding our interest in the comparison between foxes and cats in relative kill rates, the cumulative or compounded impact of these two species is of more conservation concern. Across their vast overlapping range, these two predators are collectively exerting a large and continuous predation pressure on a high proportion of Australian reptile, bird and mammal species (e.gGreenville et al., 2017; Woolley et al., 2019). This ongoing predation pressure is likely to be causing declines in many prey populations, or reducing their resilience to other threats. For example, there are now many examples of increases in native animal populations at sites where foxes and cats have been excluded (Kanowski et al., 2018; Legge et al., 2018; Moseby et al., 2009, 2018), or their populations reduced through broad-scale control (Claridge et al., 2010; Dexter et al., 2007; Dexter & Murray, 2009; Kinnear et al., 1998; Robley et al., 2014), although interactions between these two predators can complicate the conservation outcomes (Marlow et al., 2015). These examples demonstrate that the predation pressure imposed by cats and foxes is likely unsustainable for many Australian animal species in many regions, but with well-planned, targeted management, that pressure can be significantly reduced or even removed.

The separate and combined tolls of these two predators on Australian wildlife could be contextualised more precisely if the numbers of individual animals killed could be expressed as a proportion of the total number of individuals present. However, there are no reliable estimates of the total Australian population of reptiles or mammals. Woinarski, Murphy, et al. (2017) estimated the annual consumption of birds by cats comprised 4% of the Australian bird population of ca. 11 billion. The current study indicates that foxes take another ca. 1% of that total population per year. Such a toll may be sustainable for many species, but the predation pressure falls inequitably across species (Woinarski, Woolley, et al., 2017) and some native vertebrate species may be incapable of sustaining even low rates of predation (Radford et al., 2018).

Our estimates of the numbers of animals killed annually by foxes can also be counterpointed with total population estimates

for two groupings of mammals. Based on aerial surveys, the Australian Government estimates the population of the four largest (and likely most populous) Australian macropods, in those large parts of Australia in which commercial kangaroo harvesting is permitted, likely exceeds 34 million, although actual national populations are likely to be significantly higher as these figures do not include estimates for areas not surveyed (Department of Agriculture Water & the Environment, 2020). Those population estimates also do not include the majority of macropod and potoroid species, which are not harvested. Nonetheless, our estimate of 30 million macropods and potoroids killed by foxes appears to be high relative to this population estimate, although we note that many macropods typically have high annual population growth rates that may therefore be able to sustain predation rates higher than many other cat and fox prey. Our estimate of 38 million livestock killed annually by foxes also appears to be high, as McLeod (2004) estimated that only about 2% of the ca. 35 million lambs (probably the main livestock component killed by foxes in Australia) born in Australia every year are killed by foxes; although Saunders et al. (1995) noted the proportion of lambs taken by foxes in some areas was much higher (10–30%). In this case, our likely over-estimate may be because we under-estimated the proportion of livestock consumed as carrion, and that larger animals (including livestock) killed by foxes are likely to be eaten over multiple days.

In addition to improved knowledge of the population size and its spatial variation for two nationally important threats to biodiversity, our results contribute to a growing global picture of the impacts of introduced predators (Doherty et al., 2016). The focus of national estimates of tolls taken by introduced predators thus far has been on cats, with estimates of their predation tolls including for the USA (Loss et al., 2013), Canada (birds only; Blancher, 2013), Poland (farm cats only; Krauze-Gryz et al., 2019) and China (Li et al., 2021). Generating comparable estimates for other predators, and vulnerable native wildlife populations and locations, could help answer both applied and fundamental questions in predator–prey ecology. Key questions that could be answered include: how does predation pressure vary between the native and introduced ranges of a single species; how does the predation pressure of introduced and native predators differ within a region; what roles do environmental productivity and prey diversity have in shaping predation tolls and which invasive species and locations are highest priority for management attention. In addition to cats and red foxes, other predators that are priorities for studies such as ours are the dog (*Canis familiaris*), pigs (*Sus scrofa*) and mongoose (*Herpestes* spp.) (Doherty et al., 2016), which are widely distributed, implicated in multiple extinctions and with ranges predicted to increase under climate change (e.g. Caley et al., 2011; Louppe et al., 2020).

Our focus in this study is on the number of animals killed by these two introduced predators, and its biogeographic patterning. But we recognise that assessing the relative conservation impact of such rates of mortality is complex. The impacts of cats and foxes may be compensatory rather than simply additive, as many studies have shown interactions between these two predators (Glen & Dickman, 2005; Molsher et al., 2017; Ritchie & Johnson, 2009). Adding to the complexity, there may be some situations where fox and/or cat predation may provide an element of conservation benefit, such as where such predation constrains the abundance of introduced pest species (Courchamp et al., 1999). The losses attributable to predation by cats and foxes should not be viewed in isolation, as the impacts of cat and fox predation interact with (and compound and are compounded by) many other threatening processes, including habitat fragmentation, fire and grazing pressure (Graham et al., 2013; Hradsky et al., 2017; Hradsky, Robley, et al., 2017; Legge et al., 2019). Our results demonstrate that the magnitude of fox and cat predation on Australian wildlife is substantial, and there is justification in maintaining and expanding strategic and targeted programmes aimed at reducing the numbers and hence predation pressure of these two introduced species.

ACKNOWLEDGEMENTS

The data collation, analysis and preparation of this paper were supported by the Australian Government's National Environmental Science Program (Threatened Species Recovery Hub). MR received funding from the Conservation Ecology Centre, Holsworth Wildlife Research Endowment and Victorian Environmental Assessment Council. SD received funding from the Centre for Invasive Species Solutions. DGC (DP210100323), AT (DE170100599), TSD (DP210100323, DE200100157) and EGR (DP180100747) received funding from the Australian Research Council. EGR and ET received funding from Australian Geographic, the Holsworth Wildlife Research Endowment and Deakin University's Centre for Integrative Ecology. We thank Joanna Riley for contributing fox diet data, and Scott Consaul Atkinson for his contribution to collation of fox density information. We wish to collectively acknowledge and pay respect to the past, present and future Traditional Custodians and Elders of Australia and recognise the significance of the continuation of cultural, spiritual and educational practices of Aboriginal and Torres Strait Islander peoples.

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Drayd at https://doi.org/10.5061/dryad.bk3j9kdcz.

ORCID

Alyson M. Stobo-Wilson https://orcid.org/0000-0002-3880-2442
Sarah M. Legge https://orcid.org/0000-0001-6968-2781
Stuart J. Dawson https://orcid.org/0000-0003-4432-3779
Chris R. Dickman https://orcid.org/0000-0002-1067-3730
Tim S. Doherty https://orcid.org/0000-0001-7745-0251

Patricia A. Fleming https://orcid.org/0000-0002-0626-3851
Thomas M. Newsome https://orcid.org/0000-0003-3457-3256
Andrés F. Suarez-Castro https://orcid.org/0000-0002-6621-3821
John C.Z. Woinarski https://orcid.org/0000-0002-1712-9500

REFERENCES

Abbott, I. (2008). The spread of the cat, *Felis catus*, in Australia: Re-examination of the current conceptual model with additional information. *Conservation Science Western Australia*, *7*, 1–17.

Abbott, I. J. (2011). The importation, release, establishment, spread, and early impact on prey animals of the red fox *Vulpes vulpes* in Victoria and adjoining parts of south-eastern Australia. *Australian Zoologist*, *35*(3), 463–533.

Abbott, I., Peacock, D., & Short, J. (2014). The new guard: The arrival and impacts of cats and foxes. In A. S. Glen, & C. R. Dickman (Eds.), *Carnivores of Australia: Past, present and future* (pp. 69–104). CSIRO Publishing.

Australia State of the Environment (2017). *Land VAST classification of Australian vegetation, 2016*. Retrieved from https://data.gov.au/data/dataset/f093534a-cd3d-4284-a084-0dfabb399272

Australian Bureau of Meteorology (2016). *Average Annual and Monthly Maximum, Minimum, and Mean Temperature*. Retrieved from http://www.bom.gov.au/jsp/ncc/climate_averages/temperature/index.jsp

Australian Bureau of Meteorology (2016). *Average Annual, Seasonal and Monthly Rainfall*. Retrieved from http://www.bom.gov.au/jsp/ncc/climate_averages/rainfall/index.jsp

Australian Bureau of Statistics (2014). *Australian population grid, 2011*. Retrieved from https://www.abs.gov.au/ausstats/abs@.nsf/mf/1270.0.55.007

Banks, P. B., Newsome, A. E., & Dickman, C. R. (2000). Predation by red foxes limits recruitment in populations of eastern grey kangaroos. *Austral Ecology*, *25*, 283–291. https://doi.org/10.1046/j.1442-9993.2000.01039.x

Blancher, P. (2013). Estimated number of birds killed by house cats (*Felis catus*) in Canada. [Estimation du nombre d'oiseaux tués par les chats domestiques (*Felis catus*) au Canada]. *Avian Conservation and Ecology*, *8*(2). https://doi.org/10.5751/ACE-00557-080203

Brzeziński, M., Żmihorski, M., Nieoczym, M., Wilniewczyc, P., & Zalewski, A. (2020). The expansion wave of an invasive predator leaves declining waterbird populations behind. *Diversity and Distributions*, *26*, 138–150. https://doi.org/10.1111/ddi.13003

Burnham, K. P., & Anderson, D. R. (2003). *Model selection and multimodel inference: A practical information-theoretic approach*. Springer.

Cagnacci, F., Lovari, S., & Meriggi, A. (2003). Carrion dependence and food habits of the red fox in an Alpine area. *Italian Journal of Zoology*, *70*(1), 31–38. https://doi.org/10.1080/11250000309356493

Caley, P., Tennant, P., & Hood, G. (2011). *Modelling the distribution of vertebrate pests in New South Wales under climate change*. Invasive Animals Cooperative Research Centre.

Cavallini, P., & Volpi, T. (1995). Biases in the analysis of the diet of the red fox *Vulpes vulpes*. *Wildlife Biology*, *1*(1), 243–249.

Christensen, D. L., Harmon, K. C., Wehr, N. H., & Price, M. R. (2021). Mammal-exclusion fencing improves the nesting success of an endangered native Hawaiian waterbird. *PeerJ*, *9*, e10722. https://doi.org/10.7717/peerj.10722

Christensen, P. E. S., Ward, B. G., & Sims, C. (2013). Predicting bait uptake by feral cats, *Felis catus*, in semi-arid environments. *Ecological Management & Restoration*, *14*, 47–53.

Claridge, A. W., Cunningham, R. B., Catling, P. C., & Reid, A. M. (2010). Trends in the activity levels of forest- dwelling vertebrate fauna against a background of intensive baiting for foxes. *Forest Ecology and Management*, *260*, 822–832. https://doi.org/10.1016/j.foreco.2010.05.041

Comer, S., Clausen, L., Cowen, S., Pinder, J., Thomas, A., Burbidge, A. H., Tiller, C., Algar, D., & Speldewinde, P. (2020). Integrating feral cat (*Felis catus*) control into landscape-scale introduced predator control to improve conservation management for threatened fauna: A case study from the south coast of Western Australia. *Wildlife Research*, *47*, 762–778.

Courchamp, F., Langlais, M., & Sugihara, G. (1999). Cats protecting birds: Modelling the mesopredator release effect. *Journal of Animal Ecology*, *68*(2), 282–292. https://doi.org/10.1046/j.1365-2656.1999.00285.x

Cunningham, C. X., Johnson, C. N., Barmuta, L. A., Hollings, T., Woehler, E. J., & Jones, M. E. (2018). Top carnivore decline has cascading effects on scavengers and carrion persistence. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1892), 20181582. https://doi.org/10.1098/rspb.2018.1582

Davis, N. E., Forsyth, D. M., Triggs, B., Pascoe, C., Benshemesh, J., Robley, A., Lawrence, J., Ritchie, E. G., Nimmo, D. G., & Lumsden, L. F. (2015). Interspecific and geographic variation in the diets of sympatric carnivores: Dingoes/wild dogs and red foxes in south-eastern Australia. *PLoS One*, *10*(3), e0120975. https://doi.org/10.1371/journal.pone.0120975

Dawson, S. J., Crawford, H. M., Huston, R. M., Adams, P. J., & Fleming, P. A. (2016). How to catch red foxes red handed: Identifying predation of freshwater turtles and nests. *Wildlife Research*, *43*(8), 615–622. https://doi.org/10.1071/WR16066

Department of Agriculture Water and the Environment (2020). *Kangaroo population estimates*. Retrieved from https://www.environment.gov.au/biodiversity/wildlife-trade/natives/wild-harvest/kangaroo-wallaby-statistics/kangaroo-population

Department of Sustainability Environment Water Population and Communities (2013). *Interim Biogeographic Regionalisation for Australia (IBRA), Version 7 (Regions). Bioregional Assessment Source Dataset*. Retrieved from https://data.gov.au/data/dataset/70bb7ab7-e8a9-4be5-aa73-85bb22c2cb88

Department of the Environment (2015). *Threat abatement plan for predation by feral cats*. Retrieved from https://www.environment.gov.au/biodiversity/threatened/publications/tap/threat-abatement-plan-feral-cats

Department of the Environment Water Heritage and the Arts (2008). *Threat abatement plan for predation by the European red fox*. Retrieved from https://www.environment.gov.au/system/files/resources/1846b741-4f68-4bda-a663-94418438d4e6/files/tap-fox-report.pdf

Dexter, N., Meek, P., Moore, S., Hudson, M., & Richardson, H. (2007). Population responses of small and medium sized mammals to fox control at Jervis Bay, southeastern Australia. *Pacific Conservation Biology*, *13*, 285–292. https://doi.org/10.1071/PC070283

Dexter, N., & Murray, A. (2009). The impact of fox control on the relative abundance of forest mammals in East Gippsland, Victoria. *Wildlife Research*, *36*(3), 252–261. https://doi.org/10.1071/wr08135

Dickman, C. R., Wardle, G. M., Foulkes, J. N., & de Preu, N. (2014). Desert complex environments. In D. Lindenmayer, E. Burns, N. Thurgate, & A. Lowe (Eds.), *Biodiversity and environmental change* (pp. 379–438). CSIRO Publishing.

Doherty, T. S., Dickman, C. R., Johnson, C. N., Legge, S. M., Ritchie, E. G., & Woinarski, J. C. Z. (2017). Impacts and management of feral cats *Felis catus* in Australia. *Mammal Review*, *47*(2), 83–97. https://doi.org/10.1111/mam.12080

Doherty, T. S., Dickman, C. R., Nimmo, D. G., & Ritchie, E. G. (2015). Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. *Biological Conservation*, *190*, 60–68. https://doi.org/10.1016/j.biocon.2015.05.013

Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G., & Dickman, C. R. (2016). Invasive predators and global biodiversity loss. *Proceedings*

of the National Academy of Sciences of the United States of America, *113*, 11261–11265. https://doi.org/10.1073/pnas.1602480113

Fairfax, R. J. (2019). Dispersal of the introduced red fox (*Vulpes vulpes*) across Australia. *Biological Invasions*, *21*(4), 1259–1268. https://doi.org/10.1007/s10530-018-1897-7

Fleming, P. A., Crawford, H. M., Auckland, C. H., & Calver, M. C. (2020). Body size and bite force of stray and feral cats—are bigger or older cats taking the largest or more difficult-to-handle prey? *Animals*, *10*(4), 707. https://doi.org/10.3390/ani10040707

Fleming, P., Crawford, H., Stobo-Wilson, A., Dundas, S., Dawson, S., Dickman, C. R., Dundas, S. J., Gentle, M. N., Newsome, T. M., O'Connor, J., Palmer, R., Riley, J., Ritchie, E. G., Speed, J., Saunders, G., Stuart, J.-M.- D., Thompson, E., Turpin, J. M., & Woinarski, J. (2021). The diet of the introduced red fox *Vulpes vulpes* in Australia: Analysis of temporal and spatial patterns. *Mammal Review*, *51*(4), 508–527.

Forbes-Harper, J. L., Crawford, H. M., Dundas, S. J., Warburton, N. M., Adams, P. J., Bateman, P. W., Calver, M. C., & Fleming, P. A. (2017). Diet and bite force in red foxes: Ontogenetic and sex differences in an invasive carnivore. *Journal of Zoology*, *303*, 54–63. https://doi.org/10.1111/jzo.12463

Forsyth, D. M., Ramsey, D. S. L., & Woodford, L. P. (2019). Estimating abundances, densities, and interspecific associations in a carnivore community. *The Journal of Wildlife Management*, *83*(5), 1090–1102. https://doi.org/10.1002/jwmg.21675

Forsyth, D. M., Woodford, L., Moloney, P. D., Hampton, J. O., Woolnough, A. P., & Tucker, M. (2014). How does a carnivore guild utilise a substantial but unpredictable anthropogenic food source? Scavenging on hunter-shot ungulate carcasses by wild dogs/dingoes, red foxes and feral cats in south-eastern Australia revealed by camera traps. *PLoS One*, *9*(6), e97937. https://doi.org/10.1371/journal.pone.0097937

Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. *Statistical Methods*, *27*, 2865–2873. https://doi.org/10.1002/sim.3107

Glen, A. S., & Dickman, C. R. (2005). Complex interactions among mammalian carnivores in Australia, and their implications for wildlife management. *Biological Reviews*, *80*(3), 387–401. https://doi.org/10.1017/s1464793105006718

Graham, C. A., Maron, M., & McAlpine, C. A. (2013). Influence of landscape structure on invasive predators: Feral cats and red foxes in the brigalow landscapes, Queensland, Australia. *Wildlife Research*, *39*(8), 661–676. https://doi.org/10.1071/WR12008

Green, K. (2003). Altitudinal and temporal differences in the food of foxes (*Vulpes vulpes*) at alpine and subalpine altitudes in the Snowy Mountains. *Wildlife Research*, *30*(3), 245–253. https://doi.org/10.1071/WR02008

Green, K., & Osborne, W. S. (1981). The diet of foxes, *Vulpes vulpes* (L.), in relation to abundance of prey above the winter snowline in New South Wales. *Australian Wildlife Research*, *8*(2), 349–360.

Greenville, A. C., Wardle, G. M., & Dickman, C. R. (2017). Desert mammal populations are limited by introduced predators rather than future climate change. *Royal Society Open Science*, *4*(11), 170384. https://doi.org/10.1098/rsos.170384

Hansen, M. C., DeFries, R. S., Townshend, J. R. G., Carroll, M., Dimiceli, C., & Sohlberg, R. A. (2003). Global percent tree cover at a spatial resolution of 500 m: First results of the MODIS vegetation continuous fields algorithm. *Earth Interactions*, *7*, 1–15.

Hradsky, B. A., Mildwaters, C., Ritchie, E. G., Christie, F., & Di Stefano, J. (2017). Responses of invasive predators and native prey to a prescribed forest fire. *Journal of Mammalogy*, *98*(3), 835–847. https://doi.org/10.1093/jmammal/gyx010

Hradsky, B. A., Robley, A., Alexander, R., Ritchie, E. G., York, A., & Di Stefano, J. (2017). Human-modified habitats facilitate forest-dwelling populations of an invasive predator, *Vulpes vulpes*. *Scientific Reports*, *7*(1), 12291. https://doi.org/10.1038/s41598-017-12464-7

Januchowski-Hartley, S. R., Adams, V. M., & Hermoso, V. (2018). The need for spatially explicit quantification of benefits in invasive-species management. *Conservation Biology*, *32*(2), 287–293. https://doi.org/10.1111/cobi.13031

Jarvis, A., Reuter, H. I., Nelson, A., & Guevara, E. (2008). *Hole-filled SRTM for the globe Version 4 available from the CGIAR-CSI SRTM 90m Database*. Retrieved from http://srtm.csi.cgiar.org

Jones, E. (1977). Ecology of the feral cat, *Felis catus* (L.), (Carnivora: Felidae) on Macquarie Island. *Australian Wildlife Research*, *4*(3), 249–262.

Kanowski, J., Roshier, D., Smith, M. A., & Fleming, A. (2018). Effective conservation of critical weight range mammals: Reintroduction projects of the Australian Wildlife Conservancy. In S. Garnett, P. Latch, D. Lindenmayer, & J. Woinarski (Eds.), *Recovering Australian threatened species: A book of hope* (pp. 269–280). CSIRO Publishing.

Kinnear, J. E., Onus, M. L., & Sumner, N. R. (1998). Fox control and rock-wallaby population dynamics. II. An update. *Australian Wildlife Research*, *25*, 81–88. https://doi.org/10.1071/WR96072

Krauze-Gryz, D., Gryz, J., & Żmihorski, M. (2019). Cats kill millions of vertebrates in Polish farmland annually. *Global Ecology and Conservation*, *17*, e00516. https://doi.org/10.1016/j.gecco.2018.e00516

Legge, S., Murphy, B. P., McGregor, H., Woinarski, J., Augusteyn, J., Ballard, G., Baseler, M., Buckmaster, T., Dickman, C. R., Doherty, T., Edwards, G., Eyre, T., Fancourt, B. A., Ferguson, D., Forsyth, D. M., Geary, W. L., Gentle, M., Gillespie, G., Greenwood, L., … Zewe, F. (2017). Enumerating a continental-scale threat: How many feral cats are in Australia? *Biological Conservation*, *206*, 293–303. https://doi.org/10.1016/j.biocon.2016.11.032

Legge, S., Smith, J., James, A., Tuft, K., Webb, T., & Woinarski, J. (2019). Interactions among threats affect conservation management outcomes: Livestock grazing removes the benefits of fire management for small mammals in Australian tropical savannas. *Conservation Science and Practice*, *1*, e52. https://doi.org/10.1111/csp2.52

Legge, S. M., Woinarski, J. C. Z., Burbidge, A. A., Palmer, A., Ringma, J., Radford, J., Mitchell, N., Bode, M., Wintle, B., Baseler, M., Bentley, J., Copley, P., Dexter, N., Dickman, C. R., Gillespie, G. R., Hill, B., Johnson, C. N., Latch, P., Letnic, M., … Tuft, K. (2018). Havens for threatened Australian mammals: The contributions of fenced areas and offshore islands to protecting mammal species that are susceptible to introduced predators. *Wildlife Research*, *45*, 627–644.

Legge, S., Woinarski, J. C. Z., Dickman, C. R., Murphy, B. P., Woolley, L.-A., & Calver, M. C. (2020). We need to worry about Bella and Charlie: The impacts of pet cats on Australian wildlife. *Wildlife Research*, *47*, 523–539. https://doi.org/10.1071/WR19174

Li, Y., Wan, Y., Shen, H., Loss, S. R., Marra, P. P., & Li, Z. (2021). Estimates of wildlife killed by free-ranging cats in China. *Biological Conservation*, *253*, 108929. https://doi.org/10.1016/j.biocon.2020.108929

Lockie, J. D. (1959). The estimation of the food of foxes. *Journal of Wildlife Management*, *23*, 224–227. https://doi.org/10.2307/3797647

Loss, S. R., Will, T., & Marra, P. P. (2012). Direct human-caused mortality of birds: Improving quantification of magnitude and assessment of population impact. *Frontiers in Ecology and the Environment*, *10*(7), 357–364. https://doi.org/10.1890/110251

Loss, S. R., Will, T., & Marra, P. P. (2013). The impact of free-ranging domestic cats on wildlife of the United States. *Nature Communications*, *4*, 1396. https://doi.org/10.1038/ncomms2380

Louppe, V., Leroy, B., Herrel, A., & Veron, G. (2020). The globally invasive small Indian mongoose *Urva auropunctata* is likely to spread with climate change. *Scientific Reports*, *10*(1), 7461. https://doi.org/10.1038/s41598-020-64502-6

Macdonald, D. W. (1976). Food caching by red foxes and some other carnivores. *Zeitschrift Für Tierpsychologie*, *42*(2), 170–185. https://doi.org/10.1111/j.1439-0310.1976.tb00963.x

Marlow, N. J., Thomas, N. D., Williams, A. A. E., Macmahon, B., Lawson, J., Hitchen, Y., Angus, J., & Berry, O. (2015). Lethal 1080 baiting continues to reduce European Red Fox (*Vulpes vulpes*) abundance after more than 25 years of continuous use in south-west Western Australia. *Ecological Management & Restoration*, *16*(2), 131–141.

McIntosh, D. L. (1963). Food of the fox in the Canberra district. *CSIRO Wildlife Research*, *8*, 1–20. https://doi.org/10.1071/CWR9630001

McLeod, R. (2004). *Counting the cost: Impact of invasive animals in Australia 2004*. Retrieved from https://www.cabi.org/isc/FullTextPDF/2017/20173377647.pdf

Medina, F. M., Bonnaud, E., Vidal, E., Tershy, B. R., Zavaleta, E. S., Josh Donlan, C., Keitt, B. S., Corre, M., Horwath, S. V., & Nogales, M. (2011). A global review of the impacts of invasive cats on island endangered vertebrates. *Global Change Biology*, *17*(11), 3503–3510. https://doi.org/10.1111/j.1365-2486.2011.02464.x

Molsher, R., Newsome, A. E., Newsome, T. M., & Dickman, C. R. (2017). Mesopredator management: Effects of red fox control on the abundance, diet and use of space by feral cats. *PLoS One*, *12*(1), e0168460. https://doi.org/10.1371/journal.pone.0168460

Moseby, K., Copley, P., Paton, D. C., & Read, J. L. (2018). Arid Recovery: A successful conservation partnership. In S. Garnett, P. Latch, D. Lindenmayer, & J. Woinarski (Eds.), *Recovering Australian threatened species: A book of hope* (pp. 259–268). CSIRO Publishing.

Moseby, K. E., Hill, B. M., & Read, J. L. (2009). Arid Recovery – A comparison of reptile and small mammal populations inside and outside a large rabbit, cat and fox-proof exclosure in arid South Australia. *Austral Ecology*, *34*(2), 156–169. https://doi.org/10.1111/j.1442-9993.2008.01916.x

Murphy, B. P., Woolley, L. A., Geyle, H. M., Legge, S. M., Palmer, R., Dickman, C. R., Augusteyn, J., Brown, S. C., Comer, S., Doherty, T., Eager, C., Edwards, G., Fordham, D., Harley, D., McDonald, P. J., McGregor, H. W., Moseby, K., Myers, C., Read, J., … Woinarski, J. C. Z. (2019). Introduced cats (*Felis catus*) eating a continental mammal fauna: The number of individuals killed in Australia. *Biological Conservation*, *237*, 28–40.

Newsome, T. M., Crowther, M. S., & Dickman, C. R. (2014). Rapid recolonisation by the European red fox: How effective are uncoordinated and isolated control programs? *European Journal of Wildlife Research*, *60*(5), 749–757. https://doi.org/10.1007/s10344-014-0844-x

Pavey, C. R., Eldridge, S. R., & Heywood, M. (2008). Population dynamics and prey selection of native and introduced predators during a rodent outbreak in arid Australia. *Journal of Mammalogy*, *89*(3), 674–683. https://doi.org/10.1644/07-MAMM-A-168R.1

Plantinga, E. A., Bosch, G., & Hendriks, W. H. (2011). Estimation of the dietary nutrient profile of free-roaming feral cats: Possible implications for nutrition of domestic cats. *British Journal of Nutrition*, *106*(S1), S35–S48. https://doi.org/10.1017/S0007114511002285

R Core Team (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Radford, J. Q., Woinarski, J. C. Z., Legge, S., Baseler, M., Bentley, J., Burbidge, A. A., Bode, M., Copley, P., Dexter, N., Dickman, C. R., Gillespie, G., Hill, B., Johnson, C. N., Kanowski, J., Latch, P., Letnic, M., Manning, A., Menkhorst, P., Mitchell, N., … Ringma, J. (2018). Degrees of population-level susceptibility of Australian mammal species to predation by the introduced red fox *Vulpes vulpes* and feral cat *Felis catus*. *Wildlife Research*, *45*, 645–657.

Read, J. L., Peacock, D., Wayne, A. F., & Moseby, K. E. (2016). Toxic Trojans: Can feral cat predation be mitigated by making their prey poisonous? *Wildlife Research*, *42*(8), 689–696. https://doi.org/10.1071/WR15125

Richards, S. A. (2005). Testing ecological theory using the information-theoretic approach: Examples and cautionary results. *Ecology*, *86*, 2805–2814. https://doi.org/10.1890/05-0074

Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, *12*(9), 982–998. https://doi.org/10.1111/j.1461-0248.2009.01347.x

Roberts, M. W., Dexter, N., Meek, P. D., Hudson, M., & Buttemer, W. A. (2006). Does baiting influence the relative composition of the diet of foxes? *Wildlife Research*, *33*(6), 481–488. https://doi.org/10.1071/WR05009

Robley, A., Gormley, A., Albert, R., Bowd, M., Smith, A., & Scroggie, M. (2009). *Monitoring and Evaluation of Glenelg Ark – 2004 to 2008. Arthur Rylah Institute for Environmental Research, Technical Report Series No. 183*. Retrieved from https://www.vgls.vic.gov.au/client/en_AU/search/asset/1013162/0

Robley, A., Gormley, A., Forsyth, D., & Triggs, B. (2014). Long-term and large-scale control of the introduced red fox increases native mammal occupancy in Australian forests. *Biological Conservation*, *180*, 262–269. https://doi.org/10.1016/j.biocon.2014.10.017

Russell, J. C., Innes, J. G., Brown, P. H., & Byrom, A. E. (2015). Predator-free New Zealand: Conservation country. *BioScience*, *65*(5), 520–525. https://doi.org/10.1093/biosci/biv012

Sargeant, A. B. (1978). Red fox prey demands and implications to prairie duck production. *Journal of Wildlife Management*, *42*, 520–527. https://doi.org/10.2307/3800813

Saunders, G., Coman, B., Kinnear, J., & Braysher, M. (1995). *Managing vertebrate pests: Foxes*. Australian Government Publishing Service.

Saunders, G. R., Gentle, M. N., & Dickman, C. R. (2010). The impacts and management of foxes *Vulpes vulpes* in Australia. *Mammal Review*, *40*(3), 181–211. https://doi.org/10.1111/j.1365-2907.2010.00159.x

Saunders, G., White, P. C. L., Harris, S., & Rayner, J. M. (1993). Urban foxes (*Vulpes vulpes*): Food acquisition, time and energy budgeting of a generalized predator. *Symposia of the Zoological Society of London*, *65*, 215–243.

Short, J., Kinnear, J. E., & Robley, A. (2002). Surplus killing by introduced predators in Australia—evidence for ineffective anti-predator adaptations in native prey species? *Biological Conservation*, *103*(3), 283–301. https://doi.org/10.1016/S0006-3207(01)00139-2

Spencer, E. E., Dickman, C. R., Greenville, A., Crowther, M. S., Kutt, A., & Newsome, T. M. (2021). Carcasses attract invasive species and increase artificial nest predation in a desert environment. *Global Ecology and Conservation*, *27*, e01588. https://doi.org/10.1016/j.gecco.2021.e01588

Spencer, R.-J., & Thompson, M. B. (2005). Experimental analysis of the impact of foxes on freshwater turtle populations. *Conservation Biology*, *19*(3), 845–854. https://doi.org/10.1111/j.1523-1739.2005.00487.x

Spencer, R.-J., Van Dyke, J. U., & Thompson, M. B. (2016). The ethological trap: Functional and numerical responses of highly efficient invasive predators driving prey extinctions. *Ecological Applications*, *26*(7), 1969–1983. https://doi.org/10.1002/eap.1375

Stobo-Wilson, A. M., Murphy, B. P., Crawford, H. M., Dawson, S. J., Dickman, C. R., Doherty, T. S., Fleming, P. A., Gentle, M. N., Legge, S. M., Newsome, T. M., Palmer, R., Rees, M. W., Ritchie, E. G., Speed, J., Stuart, J.-M., Thompson, E., Turpin, J., & Woinarski, J. C. Z. (2021). Sharing meals: Predation on Australian mammals by the introduced European red fox compounds and complements predation by feral cats. *Biological Conservation*, *261*, 109284. https://doi.org/10.1016/j.biocon.2021.109284

Stobo-Wilson, A. M., Murphy, B. P., Legge, S. M., Chapple, D. G., Crawford, H. M., Dawson, S. J., Dickman, C. R., Doherty, T. S., Fleming, P. A., Gentle, M., Newsome, T. M., Palmer, R., Rees, M. W., Ritchie, E. G., Speed, J., Stuart, J.-M., Thompson, E., Turpin, J., & Woinarski, J. C. Z. (2021). Reptiles as food: Predation of Australian reptiles by introduced red Foxes compounds and complements predation by cats. *Wildlife Research*, *48*(5), 470–480. https://doi.org/10.1071/WR20194

Thompson, M. (1983). Populations of the Murray river tortoise, Emydura (Chelodina): The effect of egg predation by the red fox, *Vulpes vulpes*. *Wildlife Research*, *10*(2), 363–371. https://doi.org/10.1071/WR9830363

Van Dyck, S., & Strahan, R. (2008). *The mammals of Australia*, 3rd ed. Reed New Holland.

van Eeden, L. M., Dickman, C. R., Ritchie, E. G., & Newsome, T. M. (2017). Shifting public values and what they mean for increasing democracy in wildlife management decisions. *Biodiversity and Conservation*, *26*(11), 2759–2763. https://doi.org/10.1007/s10531-017-1378-9

Wilson, B. A., & Wolrige, J. (2000). Assessment of the diet of the fox, *Vulpes vulpes*, in habitats of the eastern Otway Ranges, Victoria. *Australian Mammalogy*, *21*, 201–211. https://doi.org/10.1071/AM00201

Witt, H. (1980). The diet of the red fox. Questions about method. In E. Zimen (Ed.), *The red fox. Symposium on behaviour and ecology* (pp. 65–69). Dr. W. Junk.

Woinarski, J., Braby, M. F., Burbidge, A. A., Coates, D., Garnett, S. T., Fensham, R. J., Legge, S. M., McKenzie, N. L., Silcock, J. L., & Murphy, B. P. (2019). Reading the black book: The number, timing, distribution and causes of listed extinctions in Australia. *Biological Conservation*, *239*, 108261. https://doi.org/10.1016/j.biocon.2019.108261

Woinarski, J. C. Z., Burbidge, A. A., & Harrison, P. L. (2015). The ongoing unravelling of a continental fauna: Decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(15), 4531–4540.

Woinarski, J. C. Z., Legge, S. M., & Dickman, C. R. (2019). *Cats in Australia: Companion and killer*. CSIRO Publishing.

Woinarski, J. C. Z., Legge, S. M., Woolley, L. A., Palmer, R., Dickman, C. R., Augusteyn, J., Doherty, T. S., Edwards, G., Geyle, H., McGregor, H., Riley, J., Turpin, J., & Murphy, B. P. (2020). Predation by introduced cats *Felis catus* on Australian frogs: Compilation of species' records and estimation of numbers killed. *Wildlife Research*, *47*, 580–588. https://doi.org/10.1071/WR19182

Woinarski, J., Murphy, B. P., Legge, S. M., Garnett, S. T., Lawes, M. J., Comer, S., Dickman, C. R., Doherty, T. S., Edwards, G., Nankivell, A., Paton, D., Palmer, R., & Woolley, L. A. (2017). How many birds are killed by cats in Australia? *Biological Conservation*, *214*, 76–87. https://doi.org/10.1016/j.biocon.2017.08.006

Woinarski, J. C. Z., Murphy, B. P., Palmer, R., Legge, S. M., Dickman, C. R., Doherty, T. S., Edwards, G., Nankivell, A., Read, J. L., & Stokeld, D. (2018). How many reptiles are killed by cats in Australia? *Wildlife Research*, *45*(3), 247–266. https://doi.org/10.1071/WR17160

Woinarski, J. C. Z., Stobo-Wilson, A. M., Crawford, H. M., Dawson, S. J., Dickman, C. R., Doherty, T. S., Fleming, P. A., Garnett, S. T., Gentle, M. N., Legge, S. M., Newsome, T. M., Palmer, R., Rees, M. W., Ritchie, E. G., Speed, J., Stuart, J.-M., Thompson, E., Turpin, J., & Murphy, B. P. (2021). *Compounding and complementary carnivores: Australian bird species eaten by the introduced European red fox* Vulpes vulpes *and domestic cat* Felis catus. Bird Conservation International.

Woinarski, J., Woolley, L. A., Garnett, S. T., Legge, S. M., Murphy, B. P., Lawes, M. J., Comer, S., Dickman, C. R., Doherty, T. S., Edwards, G., Nankivill, A., Palmer, R., & Paton, D. (2017). Compilation and traits of Australian bird species killed by cats. *Biological Conservation*, *216*, 1–9. https://doi.org/10.1016/j.biocon.2017.09.017

Woolley, L.-A., Geyle, H. M., Murphy, B. P., Legge, S. M., Palmer, R., Dickman, C. R., Augusteyn, J., Comer, S., Doherty, T. S., Eager, C., Edwards, G., Harley, D. K. P., Leiper, I., McDonald, P. J., McGregor, H. W., Moseby, K. E., Myers, C., Read, J. L., Riley, J., … Woinarski, J. C. Z. (2019). Introduced cats (*Felis catus*) eating a continental fauna: Inventory and traits of Australian mammal species killed. *Mammal Review*, *49*, 354–368.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*(1), 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

BIOSKETCH

The authors of this manuscript are a group of researchers working for various academic and government organisations across Australia but all with research experience in feral predator ecology and management, and conservation management for Australia's declining native fauna.

Author contributions: A. M. S-W. Methodology, Formal analysis, Data curation, Visualisation, Writing- Original Draft preparation, Project administration. B. P. M. Methodology, Formal analysis, Writing- Reviewing and Editing. S. M. L. Investigation, Resources, Writing- Reviewing and Editing. H. C-E. nvestigation, Resources, Writing- Reviewing and Editing. D. G. C. Investigation, Resources, Writing- Reviewing and Editing. H. M. C. Investigation, Resources, Writing- Reviewing and Editing. S. J. D. Investigation, Resources, Writing- Reviewing and Editing. C. R. D. Investigation, Resources, Writing- Reviewing and Editing. T. S. D. Investigation, Resources, Writing- Reviewing and Editing. P. A. F. Data curation, Investigation, Resources, Writing- Reviewing and Editing. S. T. G. Investigation, Resources, Writing- Reviewing and Editing. M. N. G. Investigation, Resources, Writing- Reviewing and Editing. T. M. N. Investigation, Resources, Writing- Reviewing and Editing. R. P. Investigation, Resources, Writing- Reviewing and Editing. M. R. Investigation, Resources, Writing- Reviewing and Editing. E. R. Investigation, Resources, Writing- Reviewing and Editing. J. S. Investigation, Resources, Writing- Reviewing and Editing. J-M. S. Investigation, Resources, Writing- Reviewing and Editing. A. F. S-C. Investigation, Resources, Writing- Reviewing and Editing. E. T. Investigation, Resources, Writing- Reviewing and Editing. A. T. and J-M. S. Investigation, Resources, Writing- Reviewing and Editing. J. T.Investigation, Resources, Writing- Reviewing and Editing. J. C. Z. W. Conceptualisation, Methodology, Investigation, Resources, Writing- Original Draft preparation, Supervision, Funding acquisition.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Stobo-Wilson, A. M., Murphy, B. P., Legge, S. M., Caceres-Escobar, H., Chapple, D. G., Crawford, H. M., Dawson, S. J., Dickman, C. R., Doherty, T. S., Fleming, P. A., Garnett, S. T., Gentle, M., Newsome, T. M., Palmer, R., Rees, M. W., Ritchie, E. G., Speed, J., Stuart, J.-M., Suarez-Castro, A. F., … Woinarski, J. C. Z. (2022). Counting the bodies: Estimating the numbers and spatial variation of Australian reptiles, birds and mammals killed by two invasive mesopredators. *Diversity and Distributions*, 28, 976–991. https://doi.org/10.1111/ddi.13497