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Running head: reptiles killed by cats in Australia

Abstract

Context. Feral cats *Felis catus* are a threat to biodiversity globally, but their impacts upon continental reptile faunas have been poorly resolved.
Aims. To estimate the number of reptiles killed annually in Australia by cats; to list Australian reptile species known to be killed by cats.
Methods. We used: (1) data from >80 Australian studies of cat diet (collectively, >10,000 samples); and (2) estimates of the feral cat population size, to model and map the number of reptiles killed by feral cats.
Key results. Feral cats in Australia's natural environments kill 466 million reptiles yr^{-1} (95% CI: 271–1006 million). The tally varies substantially between years, depending on changes in the cat population driven by rainfall in inland Australia. The number of reptiles killed by cats is highest in arid regions. On average, feral cats kill 61 reptiles km^{-2} yr^{-1}, and an individual feral cat kills 225 reptiles yr^{-1}. The take of reptiles per cat is higher than reported for other continents. Reptiles occur at a higher incidence in cat diet than in the diet of Australia's other main introduced predator, the European red fox *Vulpes vulpes*. Based on a smaller sample size, we estimate 130 million reptiles yr^{-1} are killed by feral cats in highly modified landscapes, and 53 million reptiles yr^{-1} by pet cats, summing to 649 million reptiles yr^{-1} killed by all cats. Predation by cats is reported for 258 Australian reptile species (about one-quarter of described species), including 11 threatened species.
Conclusions. Cat predation exerts a considerable ongoing toll on Australian reptiles. However, it remains challenging to interpret the impact of this predation in terms of population viability or conservation concern for Australian reptiles, because population size is unknown for most Australian reptile species, mortality rates due to cats will vary across reptile species, and there is likely to be marked variation among reptile species in their capability to sustain any particular predation rate.
Implications. This study provides a well-grounded estimate of the numbers of reptiles killed by cats, but intensive studies of individual reptile species are required to contextualise the conservation consequences of such predation.

Running head: How many reptiles are killed by cats?

Additional keywords: conservation, diet, introduced predator, island, mortality, predation

Introduction

As with most other terrestrial vertebrate groups, many reptile species across the world have declined or become extinct because of invasive predator species, with susceptibility especially pronounced for island-endemic species (Böhm *et al.* 2016; Doherty *et al.* 2016). However, the impacts of introduced predators are generally not well resolved for continental reptile faunas, because there is little information on predation rates or on the consequences of predation rates on the population viability of any reptile species. In Australia, the significance of predation by introduced species upon reptiles is also difficult to evaluate because the reptile fauna is incompletely catalogued. In addition, population trends for reptile species are difficult to discern because there are few substantial population monitoring programs for reptiles (Meiri 2016; Meiri and Chapple 2016; Woinarski 2018). Nonetheless, recent studies have demonstrated severe impacts of introduced predators on at least local populations of some Australian reptiles. For example, high rates of predation on egg clutches by the introduced European red fox *Vulpes vulpes* and pig *Sus scrofa* are implicated in population declines of several species, some threatened, of freshwater turtles (Spencer 2002; Spencer and Thompson 2005; Fordham *et al.* 2006, 2008; Micheli-Campbell *et al.* 2013; Whytlaw *et al.* 2013; Freeman *et al.* 2014; Fielder *et al.* 2015; Robley *et al.* 2016;) and marine turtles (Limpus and Reimer 1994). Predation by the red fox is also a recognised threat to some threatened Australian lizard species (Nielsen and Bull 2016). Furthermore, predation by the red fox has been implicated in complex but substantial changes in some Australian reptile communities (particularly suppression of native reptilian predators) (Olsson *et al.* 2005; Sutherland *et al.* 2011; Read and Scoleri 2015). Introduced predators, probably primarily the wolf snake *Lycodon capucinus*, are also considered to have caused the recent collapse of the endemic reptile fauna of the Australian external territory of Christmas Island, with four of the five native lizard species becoming extinct, or extinct in the wild, over the last decade (Smith *et al.* 2012; Andrew *et al.* 2018).

Here, we assess the extent of predation by the introduced house cat *Felis catus* on the Australian reptile fauna. Cats were introduced to Australia at the time of European settlement (1788) and have since spread across the entire continent and onto most large islands (Abbott 2008; Abbott *et al.* 2014; Legge *et al.* 2017). They have caused severe detrimental impacts on the Australian mammal fauna (Woinarski *et al.* 2015) and are a major source of mortality for Australian birds (Woinarski *et al.* 2017a). There has been far less consideration of their impacts on the Australian reptile fauna. The most substantial assessment was within a recent study of continental-scale variation in the diet of feral cats (Doherty *et al.* 2015). That study reported that: (i) reptiles formed a significant component of the diet of cats (average frequency of occurrence of 24% in cat dietary samples), (ii) there was substantial geographic variation in the occurrence of reptiles in cat diet, with a higher frequency of reptiles in cat dietary samples from hotter, drier areas and in mid-latitudes, and (iii) 157 reptile species had been recorded within the diet of feral cats in Australia, including one threatened species, the recently extinct Christmas Island forest skink *Emoia nativitatis*.

Using a recent assessment of geographic variation in the density, and hence total population size, of feral cats in Australia (Legge *et al.* 2017), information on the number of individual reptiles within cat dietary samples (as distinct from simply the percentage occurrence of reptiles in dietary samples), and a more extensive compilation of cat diet information, we extend the study of Doherty *et al.* (2015) to evaluate the annual tally of reptiles killed by cats in Australia and the spatial variation in this number. This study complements, collates information from many of the studies reported in, and adopts a similar analytical approach to, a recent assessment of the number and species of birds killed by cats in Australia (Woinarski *et al.* 2017a, b). Our objectives are to: (i) examine environmental and geographical variation in the number of reptiles killed by feral cats; (ii) derive an overall estimate of the number of reptiles killed by feral cats annually; (iii) attempt to contextualise this estimate in relation to the overall number of reptiles in Australia; (iv) compare these assessments with the number of birds killed in Australia by cats (Woinarski *et al.* 2017a); (v) compile an updated inventory of Australian reptile species known to be killed by feral cats; (vi) interpret the conservation consequences and implications of these results; and (vii) compare these results with available information from other continents. Our main focus is on feral cats in largely natural environments, but we also include some information on predation of reptiles by pet cats and by feral cats in highly modified environments.

This assessment is of some global significance because the Australian reptile fauna comprises more than 10% of the global reptile complement, most Australian species (>90%) are endemic (Chapman 2009), and the conservation management of reptiles has been notably neglected globally compared with other vertebrate groups (Roll *et al*. 2017).

Methods

Feral cats in natural environments

To determine the numbers of feral cats in Australia, and the spatial variation in cat density, Legge *et al.* (2017) collated and then modelled 91 site-based estimates of feral cat density from largely natural sites widely and representatively scattered across Australia. They concluded that the total number of feral cats in largely natural landscapes in Australia was 2.07 million (varying between 1.4 million in drought and average years to 5.6 million after prolonged and extensive wet periods in inland Australia).

We collated 82 results from Australian studies (with a minimum of 10 cat scat or stomach samples per study) that provided a quantitative assessment of the frequency of occurrence of reptiles in cat stomachs or scats (Table 1). These studies were widely spread across Australia (Fig. 1) and included broad representation of Australian natural environments. Thirty-two of these studies were also included in a previous consideration of continental variation in the diet of feral cats in Australia (Doherty *et al.* 2015). Where multiple studies provided estimates for the same location, these were averaged (weighted by the number of samples examined). Several individual studies reported information from more than one site or from the same site in markedly different conditions: where the source data could be readily resolved to site level, information from these separate sites or conditions was treated as distinct data points in our analyses (as per Table 1), such that the total number of study x site combinations included in our analyses (98) exceeds the number of included studies.

Although the frequency of occurrence of reptiles in the diet of feral cats in Australia generally increases in warmer seasons, consistent with seasonal variation in reptile activity (Paltridge 2002; Yip *et al.* 2015), it was not possible for us to account for seasonal variation in cat diet in this analysis because many of the constituent studies collated here spanned several seasons, or the time of year covered by the sampling was not specified. The studies occurred over the period 1969-2017, but we do not include year in analyses, as any directional trend in diet over decadal scales is unlikely, and Legge *et al.* (2017) found no evidence of trends in cat densities over this period. Inter-annual variation in rainfall is a key driver of the abundance of many species in arid and semi-arid Australia, including feral cats (Legge *et al*. 2017), and we include separate analyses (for the number of reptiles killed by cats) based on modelled densities of cats in years of good rainfall in arid and semi-arid Australia and in years of poor or average rainfall there (Legge *et al*. 2017). Inter-annual rainfall patterns in arid and semi-arid Australia may also influence the abundance of reptile species, but these relationships are more complex and vary among reptile species (Read *et al*. 2012; Dickman *et al*. 2014; Greenville *et al*. 2016).

Collectively, the collated cat dietary studies include 10,744 samples of scats or stomachs . Most studies reported only frequency of occurrence (i.e. the proportion of stomachs or scats that contained reptiles) rather than a record of the number of individual reptiles in those samples. However, in a subset of the studies (Table 1), tallies were given for the number of individual reptiles in those samples that contained reptiles. We assessed whether there was a relationship, across studies, between the number of reptile individuals in those samples that contained reptiles, and the frequency of occurrence of reptiles in those diet samples. We modelled this relationship using a linear least-squares regression model of the form:

$$\log(\text{individuals} - 1) \sim \text{frequency}.$$

Here, we assume that that one stomach or scat sample represents 24 h worth of prey eaten by an individual cat. This is likely to be a conservative under-estimate of the number of prey killed per day because: (i) prey are largely digested after 12 h; (ii) cats typically produce more than one scat per day; (iii) cats may kill some reptiles but not necessarily consume them (‘surplus kill’); (iv) cats may injure hunted animals but not directly kill and consume them, and many of those injured animals will subsequently die (Jessup 2004); and (v) reptile eggs and hatchlings may be rapidly digested and leave little trace (Hubbs 1951; Jackson 1951; George 1978; Davies and Prentice 1980; Read and Bowen 2001; Loss *et al.* 2013). Conversely, cats may also scavenge, so some reptiles included in cat dietary studies are not necessarily killed by the cat that consumed them (Hayde 1992; Molsher *et al.* 2017).

For analysis of the environmental and other factors that may have contributed to variation in the frequency of occurrence and number of reptiles in cat samples, we noted whether the study was from an island or the mainlands of Australia and Tasmania (64 519 km^2), and – if on an island – the size of the island. We derived a composite variable expressing whether the site was an island, and the size of the island:

$$island\ size\ index = \log_{10}\left(\text{minimum}\left\{1, \frac{area}{10000}\right\}\right),$$

where *area* is land mass or island area in km^2. Hence, any land mass or island with area ≥10 000 km^2 (i.e. the Tasmanian and Australian mainlands) has an index of 0. Islands <10 000 km^2 have negative values, which become increasingly negative with decreasing island area. From the reported location of the study, we also determined mean annual rainfall (Australian Bureau of Meteorology 2016b), mean annual temperature (Australian Bureau of Meteorology 2016a), mean tree cover within a 5-km radius (Hansen *et al.* 2003) and topographic ruggedness (standard deviation of elevation within a 5-km radius) (Jarvis *et al.* 2008).

We used generalised linear modelling to examine geographic variation in the frequency of occurrence of reptiles in the diet of feral cats. The response variable was proportional: samples containing reptiles, out of the total number of samples, and hence was analysed using the binomial error family. We examined a set of 40 candidate models representing all combinations of the five explanatory variables described above (island size index, rainfall, temperature, tree cover, ruggedness), including an interaction between rainfall and temperature (to account for a possible negative effect of temperature on water availability). Models were evaluated using a second-order form of Akaike's Information Criterion ($QAIC_c$), which is appropriate for small sample sizes and overdispersed data (Burnham and Anderson 2003). There was evidence of strong overdispersion, so we used the 'quasibinomial' error structure to estimate coefficient standard errors and confidence intervals.

The final model was based on multi-model averaging of the entire candidate set, with each model weighted according to w_i, the Akaike weight, equivalent to the probability of a particular model being the best in the candidate set (Burnham and Anderson 2003). The final model was used to predict the frequency of occurrence of reptiles in cat diet across Australia's natural environments (i.e., excluding areas of intensive land use, such as urban areas and rubbish dumps: following Legge *et al.* (2017)).

The predicted frequency of occurrence of reptiles in cat diets was used to estimate the number of individual reptiles in those cat samples that contained reptiles, using the linear least-squares regression model described earlier (log [individuals – 1] ~ frequency). Multiplying the predicted frequency of occurrence of reptiles in cat samples across Australia by the predicted number of individual reptiles in those cat samples with reptiles provided a spatial representation of the estimated number of reptiles killed per feral cat per day. We multiplied this by the modelled density of cats in natural environments across Australia (Legge *et al.* 2017), and then by 365.25 (days in a year), to provide a spatial representation of the estimated number of reptiles killed by cats km^{-2} yr^{-1}. We summed this rate across the natural environments of Australia to derive the total number of reptiles killed by feral cats.

We followed the approach of Loss *et al.* (2013) and Legge *et al.* (2017) and characterised the uncertainty of the estimated total number of reptiles killed by feral cats using bootstrapping. Bootstrapping is an appropriate approach because we needed to propagate errors through a number of analytical steps (e.g. the estimate of the total feral cat population, the number of reptiles eaten per cat per year). Hence, we simultaneously bootstrapped (20,000 times) the three underlying datasets: (i) cat density; (ii) frequency of reptiles in cat diet samples; and (iii) the number of individual reptiles in cat diet samples containing reptiles. For each random selection of these underlying data, we recalculated the total number of reptiles killed. We report the 2.5% and 97.5% quantiles for the 20,000 values of the total number of reptiles killed.

Based on studies that included identification of reptile species in cat dietary items, we also calculated the mean percentage of reptile items consumed that were native species. From all studies that reported the total number of individual reptiles in cat samples, and the taxonomic identity (to family, genus or species), we also calculated the percentage of cat-killed reptiles by broad reptile group: crocodiles (family Crocodylidae), marine turtles (Cheloniidae and Dermochelyidae), freshwater turtles (Carettochelydidae and Chelidae), geckoes (Carphodactylidae, Diplodactylidae, Gekkonidae), pygopodids (Pygopodidae), agamids (Agamidae), skinks (Scincidae), monitors (Varanidae), blind-snakes (Typhlopidae), pythons (Boidae), file-snakes (Acrochordidae), colubrid snakes (Colubridae) or elapid snakes (Elapidae).

Feral cats in highly modified landscapes

Legge *et al.* (2017) estimated that there are 0.72 million feral cats occurring in the ca. 57,000 km^2 of Australia that comprise highly modified landscapes (such as rubbish dumps, intensive piggeries, urban areas) where food supplementation for feral cats is unintentionally provided by humans. There were only six Australian studies (with >10 samples) that reported frequency of reptiles in the diet of feral cats occurring in highly modified environments (Table 1). This small number provides little scope for assessing variability, so we simply use the average frequency of occurrence of reptiles in samples across these six studies and multiply this mean by the expected number of individual reptiles in cat samples with that frequency, and then by the density (and hence population size) of feral cats in these environments as estimated by Legge *et al.* (2017). We also compare the frequency of reptiles in these samples with those from feral cats in natural environments, using Mann-Whitney *U* tests, but note that the small sample size of dietary studies for cats in highly modified environments constrains the reliability of such comparisons.

Pet cats

From national surveys of pet ownership, the population of pet cats in Australia has been previously estimated at 3.88 million (Animal Medicines Australia 2016). The average number of reptiles killed by pet cats in Australia has been estimated in several studies that have involved cat-owners tallying the number of prey items brought in by pet cats over fixed time periods (Paton 1990; Paton 1991; Paton 1993; Trueman 1991; Barratt 1997; Barratt 1998). There is substantial variation in such tallies according to the amount of time the pet cat is allowed to roam outside (Trueman 1991).

The actual number of kills by pet cats is likely to be appreciably higher than these owner-reported tallies, given that studies elsewhere indicate that pet cats typically return home with a relatively small proportion of prey actually taken (Blancher 2013), with estimates of this proportion from studies on other continents being 12.5% (Maclean 2007), 23% (Loyd *et al.* 2013), and 30% (Kays and DeWan 2004). Here, we average across Australian studies the number of individual reptiles reported by pet owners to be killed by their pet cats per year, and scale this up to account for the number of reptiles killed but not returned to the cat's home, using the mean (22%) from the three studies that provide estimates of this proportion.

Comparison of frequency of reptiles in the diet of feral cats with that of other co-occurring mammalian predators

Australian reptiles face many introduced and native predators in addition to cats. A subset of the feral cat diet studies collated here also included comparable sampling of the diet of other co-occurring mammalian predators, notably the introduced red fox and dingo (including wild dog) *Canis dingo/familiaris*. For studies that included at least 10 samples of feral cats and at least 10 samples of one other mammalian predator species, we compared the frequency of reptiles in samples, using Wilcoxon matched-pairs tests.

List of reptile species reported to be killed by feral cats

From a collation of individual cat dietary studies, Doherty *et al.* (2015) derived a list of Australian reptile species known to be killed by feral cats. We add to that list by incorporating information from additional cat dietary studies, autecological studies of reptiles, and specimens reported as cat-killed from all main museums in Australia. There are some notable caveats and biases in constructing such a list. First, the Australian reptile fauna has been subjected to major taxonomic overhaul in recent decades, resulting *inter alia* in rapid increase in the number of described species (Oliver *et al.* 2009; Cogger 2014; Meiri 2016), and specific names given for reptiles in older studies may now be difficult to reconcile unambiguously with the currently recognised taxonomy. Second, diagnostic morphological characteristics for reptile species in some groups (e.g., many small skinks, blind snakes) are difficult enough to resolve in the field with intact specimens, but such fine species-level resolution will be impossible in many circumstances for the partly digested and fragmented material within cat stomachs or – even more challenging – from reptile scales and skeletal residue in cat scats; thus many reptiles in cat dietary samples have been listed only to family or genus level. Third, many reptile species have highly localised ranges (Rosauer *et al.* 2016; Oliver *et al.* 2017), and there may have been no sampling of cat diet in the small areas that such species occupy.

We also report the conservation status of reptile species recorded to be killed by cats, although we note that conservation status has not yet (as at February 2018) been completed for most Australian species (Böhm *et al.* 2013; Meiri and Chapple 2016).

Results

Feral cats in natural environments

Based on 89 estimates from natural environments in Australia (Table 1; Fig. 1), the overall frequency of occurrence of reptiles in cat scat and stomach samples was 25.6% (95% confidence interval [CI]: 21.0–30.7%), with frequency ranging widely across individual studies, from 0 to 100%.

Generalised linear modelling suggested that two variables were clear predictors of the frequency of reptiles in feral cat diet samples: mean annual rainfall (with higher frequency of reptiles in cat samples in areas with lower rainfall) and mean annual temperature (with higher frequency of occurrence in areas with higher temperature) (Fig. 2). These variables were included in the 17 most highly ranked models, all with a very high level of support ($QAIC_c$ <14.9; Table 2). The best models had R^2 of ≥0.56. Other variables (whether the sample was from an island or mainland, topographic ruggedness, tree cover) had little influence on the frequency of reptiles in cat diet. These modelled relationships were used to project the frequency of reptiles in cat diets across Australia (Fig. 3a).

The number of individual reptiles in cat dietary samples that contained reptiles was correlated with the frequency of reptiles in cat samples (Fig. 4): i.e., when a high proportion of the cat samples in a study contained reptiles, each of those samples with reptiles was likely to include many individual reptiles. There were many notable cases of high numbers of individual reptiles in single cat stomachs, including 24 individual reptiles in a single cat stomach (Muir 1982), 40 (including 34 *Tympanocryptis lineata*) and 21 individual reptiles (including 15 *T. lineata*) (Brooker 1977), at least 19 skinks (Jones and Coman 1981), 32 (including 24 *Ctenophorus pictus*), 22, and 19 reptile individuals (Read and Bowen 2001), 27 individual skinks (all *Pseudomoia pagenstecheri*) (Cahill 2005), 20 individual skinks (all *Ctenotus regius*) (Bayly 1976), and 33, 18 and 17 individual reptiles (Woinarski *et al.* in press).

Spatial analyses revealed a clear contrast in the relative numbers of reptiles killed per km^2 between mesic coastal Australia (with relatively low numbers of reptiles killed, with minimum of 0.1 km^{-2} yr^{-1}) and arid and semi-arid areas of the Australian interior (with relatively high kill-rates, to a maximum of 219 km^{-2} yr^{-1}) (Fig. 3b).

Summing these rates provides an estimate of 466 million reptiles (95% CI: 271–1006 million) killed by feral cats across the natural environments of Australia per year (varying from 250 million [95% CI: 168–501 million] in dry or average years to 1.49 billion in 'wet' years [95% CI: 0.58–3.56 billion]) (Fig. 5a). On average, a feral cat kills 225 reptiles per year (95% CI: 157–344) (Fig. 5b). The average number of reptiles killed by feral cats in natural environments is 61.1 km^{-2} yr^{-1} (95% CI: 35.5–131.8), varying from 32.7 km^{-2} yr^{-1} (95% CI: 22.0–65.6) in dry and average years to 194.7 km^{-2} yr^{-1} (95% CI: 76.2–466.0) in wet years.

For the 41 studies where all the species of reptiles present in cat dietary samples were reported, all reptile species were native. However, two studies from Christmas Island (Corbett *et al.* 2003; Tidemann *et al.* 1994) reported some occurrence of introduced reptile species in cat diet, but information presented in those studies did not allow the calculation of a proportion of all cat-killed reptiles that was native. Given that the two Christmas Island studies are atypical in sampling an area with a relatively high proportion of introduced reptiles, and that introduced reptile species are absent from most sites in studies where reptiles in cat diet samples were not identified to species, it is highly likely that native reptile species in the diet of feral cats comprise close to 100% of all reptiles consumed across most of Australia.

Reptiles killed by cats are taxonomically diverse. Across cat dietary studies that reported the identity and number of all reptiles killed (Table 3), skinks (35.0%), agamids (30.3%) and geckoes (21.5%) comprised the largest proportions of cat-killed reptile individuals. Pygopodids (1.6%), goannas (3.5%), blind-snakes (1.8%), pythons (0.1%), colubrid snakes (0.1%) and elapid snakes (6.2%) comprised smaller proportions, and these studies reported no crocodiles, marine turtles, freshwater turtles or file-snakes in the cat dietary samples (Table 3) – although there are records of cats consuming freshwater turtles and hatchling marine turtles in other studies that provided less quantitative descriptions of cat diet (Supplementary Table A1). There was substantial variation among studies in the relative proportions of different reptile families killed by cats (Table 3).

Feral cats in highly modified landscapes

Of the six studies that reported the frequency of occurrence of reptiles in samples from feral cats in highly modified environments (Table 1), the mean frequency of occurrence of reptiles was 24.7%, similar to, and not significantly different from, that for cats in largely natural environments (mean 25.6%: Mann-Whitney *U* test, $z = 0.47$, $p = 0.64$). Multiplying the reptile frequency in the six studies by the expected number of reptile individuals in samples with reptiles (relationship shown in Fig. 4), by 365.25 (days in a year) and then by the total population size of feral cats in highly modified landscapes (0.72 million: Legge *et al.* (2017)) produces an estimate of 130.0 million reptiles killed per year by feral cats in modified environments.

Pet cats

Pet owners reported an average of 7.8 reptiles observed to be taken home as prey per cat per year in Adelaide from a sample of 166 cats (with the highest rates of predation of reptiles by pet cats in rural areas, followed by country towns and then suburbs) (Paton 1991). In comparable studies, pet owners in Canberra reported an average of 0.6 reptiles taken home as prey per cat per year from a sample of 138 cats (Barratt 1998), and those in Hobart reported an average of 0.6 reptiles per year from a sample of 166 cats (Trueman 1991). Using the average of 3.0 reptiles observed to be taken per cat per year across these studies, and scaling this mean by the average proportion of all kills that are returned home (i.e., 22%), the average number of reptiles killed by individual pet cats is 13.6 yr^{-1}. Hence, with a total Australian population of 3.88 million pet cats, the estimated annual tally of reptiles killed by pet cats is 52.9 million. We note the marked disparity in estimated rates of predation by pet cats on reptiles between the studies by Paton (1991) and those by Barratt (1998) and Trueman (1991), and hence attach low confidence to our collated tally.

Comparison of frequency of occurrence of reptiles in the diet of feral cats with that of other co-occurring mammalian predators

Comparative data on the frequency of occurrence of reptiles in samples of feral cats and other co-occurring mammalian predators are summarised in Table 4. Across 24 studies where the diet of co-occurring cats and foxes was reported, the frequency of occurrence of reptiles was appreciably higher in the diet of cats (mean = 31.1%) than of foxes (mean = 20.0%) (Wilcoxon-matched pairs test $z = 3.46$, $p = 0.0005$). Across 18 studies in which the diet of co-occurring cats and wild dogs (including dingoes) was reported, the frequency of occurrence of reptiles in the diet of cats (26.3%) was higher than that of dogs (16.1%), but not significantly so ($z = 1.50$, $p = 0.14$). Only two studies with sample sizes of >10 samples per predator species have considered the diet of cats and a co-occurring native marsupial predator, in both cases, the spotted-tailed quoll *Dasyurus maculatus* (Burnett 2001; Glen *et al.* 2011). In these studies, the frequency of reptiles was low in both species (mean of 1.0% for cats and 3.9% for quolls).

Reptile species reported to be killed by feral cats

We collated records of 258 Australian reptile species known to be killed by cats (Supplementary Table A1), a substantial increase from the 157 species previously reported by Doherty *et al.* (2015). This tally represents about a quarter of the described Australian terrestrial reptile fauna (997 species are listed in Supplementary Table A1, which excludes sea-snakes), and includes representation of all families with primarily terrestrial species. Varanidae had the highest proportion (47%) of species reported in cat diets, possibly because these are relatively large lizards and are readily identifiable to species in cat dietary samples. Species known to be killed by cats comprised 10-30% of the species complement for most other terrestrial families.

Although there is insufficient information in the collated sources to report on species-level impacts of cat predation, some reptile species have been reported as cat prey from many studies: the tree dtella *Gehyra variegata*, Bynoe's prickly gecko *Heteronotia binoei*, central bearded dragon *Pogona vitticeps*, robust ctenotus *Ctenotus robustus*, broad-banded sand-swimmer *Eremiascincus richardsonii* and curl snake *Suta suta* have all been reported as cat prey in at least ten studies describing cat diet. This may be because these species are targeted by cats, they are common and widespread, and/or relatively many cat dietary studies have been undertaken within their range.

The list of cat-killed reptile species includes four of the 31 Australian terrestrial squamate species listed as threatened by the IUCN (as at February 2018): the Christmas Island forest skink, dwarf copperhead *Austrelaps labialis*, Lord Howe Island skink *Oligosoma lichenigera* and great desert skink *Liopholis kintorei*; eight of the 45 terrestrial squamate species listed as threatened nationally under Australia's *Environment Protection and Biodiversity Conservation Act 1999* (as at February 2018); and one marine turtle and one freshwater turtle listed as threatened nationally (Supplementary Table A1).

Discussion

We provide the most robust estimate to date on the extent of, and geographic variation in, continental-scale predation of reptiles by an introduced species. That take is substantial: feral cats in Australia's largely natural environments kill more than one million reptiles per day, and individual cats take, on average, more than 225 individual reptiles yr^{-1}, with almost all of these killed reptiles being native species (consistent with the generally low proportion of non-native to native reptiles in most parts of Australia).

The incidence of predation on reptiles by feral cats shows marked geographic variation, being significantly higher in hotter and drier regions, consistent with results reported by Doherty *et al.* (2015). Given that cat density also tends to be higher in arid Australia, at least in wetter seasons (Legge *et al.* 2017), the total number of reptiles killed by cats per unit area increases by at least an order of magnitude from Australia's higher rainfall coastal fringe to inland deserts. Although there is little comparable information on geographic variation in the density of reptiles, variation in numbers of reptiles killed by cats is broadly consistent with patterns in the species richness of the Australian reptile fauna, with species richness highest for many groups in more arid areas (Pianka 1969, 1981, 1989; Morton and James 1988; Powney *et al.* 2010; Cogger 2014), with some indication that density of reptiles is also highest in arid areas of Australia (Read *et al*. 2012).

The only previous estimate of the numbers of reptiles killed by cats per area or per year for any site in Australia is that of Read and Bowen (2001) for a site (Roxby Downs) in arid South Australia. They estimated a feral cat density there of 2 km^{-2}, and average kill rate by individual cats of 350 reptile individuals yr^{-1}; hence, they concluded that feral cats in that area consumed 700 individual reptiles km^{-2} yr^{-1}. These estimates are somewhat higher than our modelled estimates for arid Australia, with cat density in that study notably higher than typical values reported in Legge *et al.* (2017).

Our focus was primarily on the numbers of reptiles killed by feral cats in natural environments, and most of the evidence that we collated refers to this component of the Australian cat population. With much less evidence, we also estimated the numbers of reptiles killed by pet cats at 53 million yr^{-1} and by feral cats in highly modified environments at 130 million yr^{-1}, hence summing to 649 million reptiles yr^{-1} (i.e. ca. 1.8 million reptiles day^{-1}) killed by all components of the Australian cat population.

It is difficult to contextualise and interpret our estimates of the annual take of Australian reptiles by cats in terms of conservation impact, consequences to the population viability of any reptile species, or relative to other causes of reptile mortality – because very few studies have assessed such parameters (Braysher 1993). There are remarkably few studies that provide robust information on population size or density for any Australian reptile species, or the overall density of reptiles. At an arid site in South Australia, Read *et al*. (2013) used mark-recapture analyses to estimate densities for six common reptile species (of skinks and geckoes), with these varying from 85 to nearly 400 individuals ha^{-1}. Ehmann and Cogger (1985) collated the few available density estimates for individual Australian reptile species across a broader environmental range, and Cogger *et al.* (2003) used these to estimate that the average density (across all reptile species) in Australia was 200 individual reptiles ha^{-1}, giving a national tally of 154,000 million reptiles. These are clearly bold extrapolations, but they are the only available estimates of density and the total numbers for Australian reptile assemblages. Albeit recognising the meagre evidence base, these tallies indicate that cats kill ca. 0.4% of Australian reptiles per year.

Cogger *et al.* (2003) also provided an estimate for one other major source of reptile mortality in Australia, the number of reptile individuals killed by land clearing. Based on their estimates of average reptile density, and a then annual rate of vegetation clearance of ca. 4500 km^2 in Queensland (the Australian state with highest rate of loss of native vegetation), they concluded that this clearing resulted in the loss of 89 million individual reptiles per year. The national rate of deforestation has declined, unevenly, since then, and in 2013-2014 was ca. 2000 km^2 yr^{-1} (Evans 2016). However, deforestation in Queensland increased again in 2015-2016, with 40 million reptiles estimated to be killed there in each of those years (Cogger *et al.* 2017). These annual rates of loss of reptiles due to habitat clearance are appreciably less than our estimates of the numbers of reptiles lost annually to cat predation (ca. 649 million). However, we recognise that such a comparison has interpretational constraints: clearing results in permanent loss of habitat suitability and reduction in reptile density, whereas a larger annual tally of reptiles killed due to cat predation may have far less acute or longer-term impact on individual reptile species or communities than habitat loss.

Our collation includes records of more than 250 Australian reptile species killed by feral cats, including 10 species nationally listed as threatened. The actual number of reptile species killed by cats is likely to be appreciably higher than this tally, given that many cat dietary studies have not reported reptile prey to species level, many Australian reptile species are highly localised and there have been no cat dietary studies in many parts of Australia. Cats consume a broad taxonomic spectrum of Australian reptiles, but may prey selectively on some species or species-groups. In a comparison of actual abundance and frequency of prey in cat dietary samples at a site in inland Queensland, Kutt (2012) concluded that cats preyed selectively on reptile species in the size range 10-50 g, and less so in the size ranges 50-100 g and 100-3500 g, and selected against reptile species <10 g. However, such a size preference is challenging to relate to impacts on individual species because many reptile species exhibit marked size changes over their lifetime. At a site in arid South Australia, Read and Bowen (2001) found that cats ate fewer individuals of the reptile species (relative to their actual abundance) associated with stony plains than for species associated with sand dunes, and concluded that this was because, at the local scale, cats were more abundant in the latter habitat. They also noted some differences in cat predation rates between similarly-sized co-occurring reptiles, and considered that this was possibly due to different defence responses, with reptile species that responded vigorously to potential attack (such as the gecko *Underwoodisaurus milii* and some large elapid snakes) experiencing lower rates of predation.

Given cat hunting behaviour and geographic variation in their density, reptile groups likely to be most affected by cat predation are those that: (i) are relatively long-lived and have low rates of reproduction (because these may be most affected by any factor causing increase in mortality rates); (ii) have high predictability in activity, such as those with permanent burrows or latrine sites (because the ambush strategy typically employed by cats will be most effective with such prey types: Moore *et al.* (2018)); (iii) occur in habitats with relatively open ground vegetation and/or in sites subject to frequent and extensive fire (because cats may occur more commonly in such areas and hunt most effectively in them: Leahy *et al.* (2015); McGregor *et al.* (2015); (iv) are colonial or semi-colonial (because cats may develop effective search images for such species and target them selectively); (v) are predominantly terrestrial, rather than arboreal or fossorial (although cats can hunt in trees and can dig up prey: Saunders (1991); (vi) do not occur in rugged rocky areas (because cat density and hunting efficiency may be least in such habitats: Hohnen *et al.* (2016); and (vii) occur mainly in arid or semi-arid areas. Several genera of large Australian skinks (*Bellatorias, Cyclodomorphus, Egernia, Eulamprus, Liopholis, Nangura, Tiliqua*) and agamids (e.g. *Pogona*) exhibit many of these characteristics (Chapple 2003; Moore *et al.* 2018), and hence can be expected to show the most pronounced impacts from cat predation. Impacts may also be severe for some reptile species that occur on islands where breeding seabirds occur in part of the year, allowing for high cat densities, but where few other prey items are available at other times of the year.

Although when averaged across Australia the rate of predation by cats on reptiles may indicate (albeit with very low confidence) that a small proportion of the national reptile population is killed by cats each year, cases of very high (and selective) predation pressure are evident in some reported instances of large numbers of individual reptiles (often mostly of one species) in stomachs of single cats (Woinarski *et al.* in press). Such high predation rates may well lead to local depletion of populations of some cat-targeted reptile species. There are few relevant studies that have assessed rates of mortality, and their causes, for individual reptile species in Australia. Sweet (2007) radio-tracked 50 individuals of *Varanus tristis* and *V. scalaris* in Kakadu National Park, northern Australia, over a 10-month period, and recorded predation by cats for six of these individuals, by far the largest source of mortality for those marked individuals. A radio-tracking study of two large elapid snakes in south-eastern Australia also found that cats were a major source of mortality (Whitaker and Shine 2000), and a recent study of the threatened great desert skink also concluded that mortality due to feral cats was higher than that due to any other predator (Moore *et al.* 2018). In a less quantitative study, Read and Bedford (1991) considered threats to the highly localised snake *Austrelaps labialis*, recorded its occurrence in samples from pet cats and consequently suggested 'cat predation rates on threatened pygmy copperheads may be significant due to the large domestic and feral cat population in the Mt Lofty Ranges'. While such studies suggest that a relatively high proportion of individuals may be killed by cats, few studies have demonstrated population-level impacts, partly because such evidence may require long-term research and intensive monitoring.

While introduced predators may have direct detrimental impacts on some reptile species, they may also have more diffuse community-level impacts. A small number of Australian studies have considered reptile assemblages in areas where contrasting management has led to marked differences in the abundance of foxes (Olsson *et al.* 2005; Sutherland *et al.* 2011), cats (Stokeld *et al.* 2016) or both foxes and cats (Moseby *et al.* 2009; Read and Scoleri 2015). These studies indicate that many components of these reptile assemblages change markedly due to the impacts of introduced predators, most likely through their suppression of previously apex reptilian predators (Jessop *et al.* 2016). Given that the rate of predation by cats is higher than that by foxes (this study; Catling (1988); Read and Bowen (2001)), cats occur over much more of Australia than do foxes, and may often also be at higher abundance than foxes (Read and Bowen 2001), it is plausible that feral cats have had major impacts on reptile communities across much of Australia. However, these impacts may be complex and highly interactive, as predation by cats may also have resulted in marked decreases in some native bird, mammal and reptile species that also prey on reptiles, hence the net impact of cats on individual reptile species and reptile assemblages may be very difficult to assess.

The results reported here for the extent of predation by cats on Australian reptiles can be compared with a recent study of the extent of predation by cats on Australian birds (Woinarski *et al.* 2017a), and also of the extent of predation on reptiles by cats in other continents. Although mammals are typically the main component of cat diet in most areas of Australia, as elsewhere in the world (Doherty *et al.* 2015, 2017), feral cats in largely natural environments in Australia include a high and broadly similar proportion of birds and reptiles in their diet (overall frequency of 31.6% and 25.6%, respectively: Woinarski *et al.* (2017a)). Unlike for reptiles, cat predation on Australian birds is highest on islands, especially smaller islands. This is largely because cats on many Australian islands prey heavily on dense populations of breeding seabirds, and may also be because many islands do not support mammalian prey. As with reptiles, more birds are killed by cats in hot and dry regions (at least in good rainfall years), although this pattern is notably more pronounced for reptiles than for birds. Nationally, the total number of reptiles killed by all cats in Australia is substantially higher than the number of birds killed by cats (649 million vs. 377 million).

There are no comparable robust assessments of the extent of cat predation on reptiles for other continents. In a recent review of the impacts of cats on wildlife in the contiguous USA, based on analysis of predation rates reported in a series of collated studies, Loss *et al.* (2013) located only one such study of un-owned cats that reported on reptile predation, with that *per capita* rate (59 reptile individuals cat^{-1} yr^{-1}: Parmalee (1953)) appreciably lower than that reported here (225 reptile individual cat^{-1} yr^{-1}). However, estimates of the numbers of feral (or 'free-roaming') cats are far higher for the US (30-80 million) than for Australia (2.1 to 6.3 million: Legge *et al.* (2017)), so the overall take of reptiles by cats for the US (median 478 million, with a range between 258 and 822 million: Loss *et al.* (2013)) is comparable to that reported here for Australia. In their collation, Loss *et al.* (2013) also noted only one comparable study from Europe, which reported a rate of predation by un-owned cats of 4.15 reptile individuals cat^{-1} yr^{-1}: Biro *et al.* (2005)). Although this is a very sparse base for comparison, it suggests that the *per capita* rate of predation on reptiles by feral cats in Australia is likely to be substantially higher than for North America and Europe. This possibly reflects the strong association between high frequency of reptiles in cat diets (and high densities of reptiles) and hot and dry climate zones (Fig. 2; Doherty *et al.* (2015)), given that most of North America and Europe is cooler and wetter than Australia.

Our results suggest that cat predation may be a major source of mortality for Australian reptiles. However, much of the interpretation of this result is constrained by shortcomings in evidence: our study did not seek to assess whether predation by cats is leading to chronic ongoing depletion in the 'standing crop' of Australian reptiles. There are some priority areas of research that could most effectively address those shortcomings. One priority is for more autecological research (including assessments of demographic factors including the rate of predation and other mortality factors), particularly for some reptile genera with traits that render them likely to be susceptible to cat predation. Such an approach will allow for an assessment of the extent to which mortality rates due to cat predation affect population viability and size. Another priority is for targeted assessments of responses of reptile species at sites with contrasting management of feral cats (such as predator-proof exclosures or broad-scale baiting). Our study is based on collations of cat dietary studies spaced widely across Australia, but we recognise that some environments (notably rainforests) and regions were relatively under-sampled, and additional studies in such sites would increase the representativeness of our analysis. Another priority for research is to contextualise the threat posed by cats relative to mortality due to other threat factors, and to better understand the interactions between cat predation and those factors. A final priority is to substantially increase the extent and coverage of population monitoring in Australian reptile species, to provide more information on reptile population trends, and timely warning of declines that may have conservation significance (Woinarski 2018).

Cat predation may also subvert the assumed conservation security provided to native reptiles by the conservation reserve system, given that feral cats occur in similar density within and outside Australia's reserve system (Legge *et al.* 2017). Hence conservation of reptiles likely to be susceptible at population scale to predation by cats will require targeted and effective control of cats rather than simply inclusion of those susceptible species within the reserve system.

The loss of about 1.8 million native reptiles per day due to predation by cats provides further evidence of the potential conservation impact of this introduced predator on Australian biodiversity, and underscores the value of efforts now being made to manage feral cat populations (e.g., through local-scale exclosures, enhanced island biosecurity, broad-scale predator control programs) and the predation pressure they exert (e.g. management of fire and grazing pressure), especially targeting conservation management for species whose population viability is most vulnerable to cat predation (Commonwealth of Australia 2015; Department of the Environment 2015).

Conflicts of interest

The authors declare no conflicts of interest

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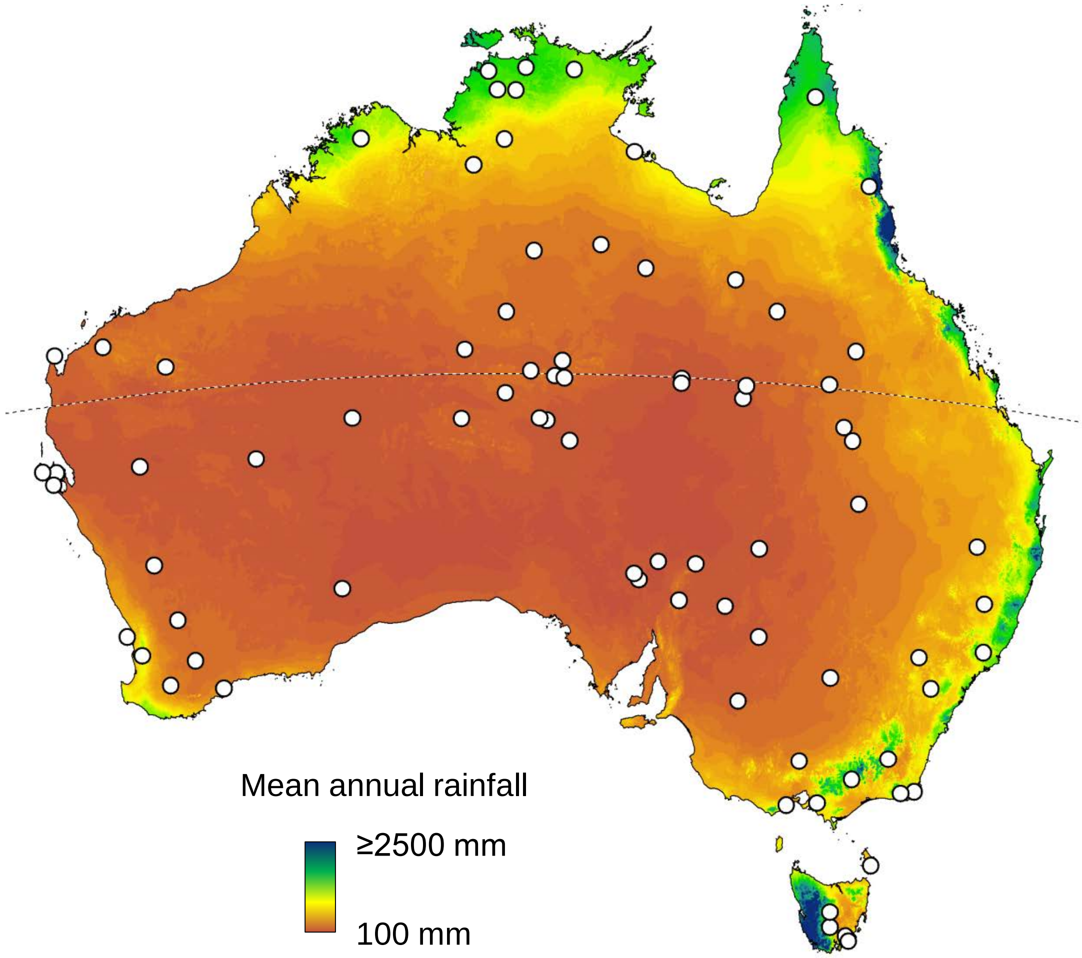

Figure 1. Occurrence of cat dietary studies collated in this study. There are 89 studies in natural vegetation (76 on the Australian mainland, three in Tasmania and 10 on smaller islands, including Macquarie and Christmas Islands, not shown on map). There are another six studies in highly modified environments (such as rubbish dumps). The map background shows mean annual rainfall (Australian Bureau of Meteorology, 2016). The dashed line indicates the Tropic of Capricorn.

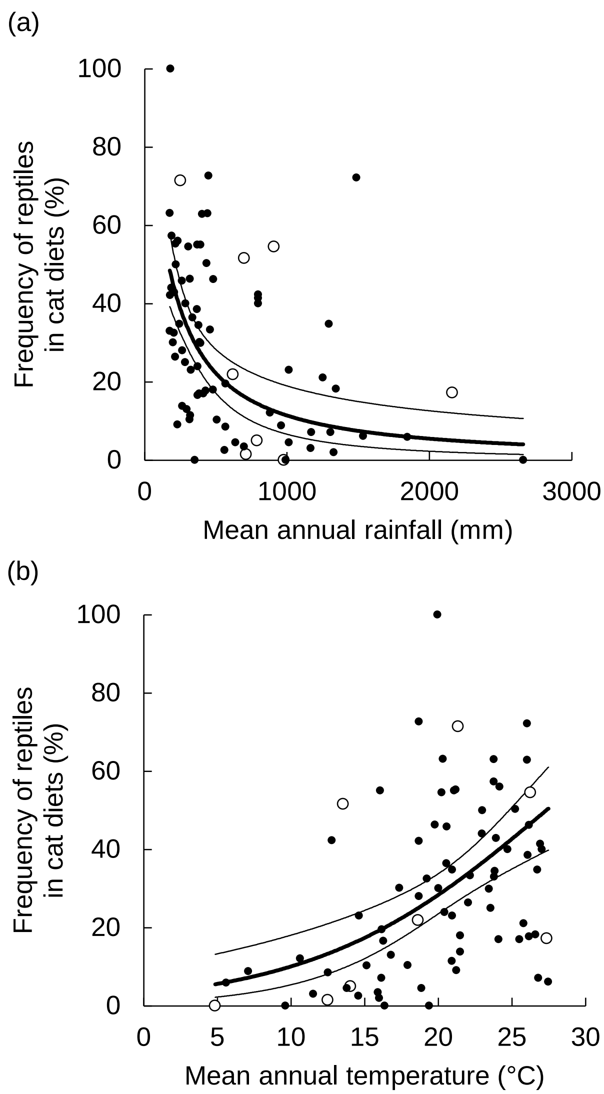

Figure 2. Variation in the frequency of reptiles in cat samples in relation to (a) mean annual rainfall and (b) mean annual temperature in Australia. Observations from the mainland, comprising Tasmania and greater Australian mainland, are indicated by filled circles, while those from islands smaller than Tasmania (64,519 km^2) are indicated by unfilled circles. Regression lines represent the predictions of generalised linear models (quasibinomial errors), with 95% confidence intervals.

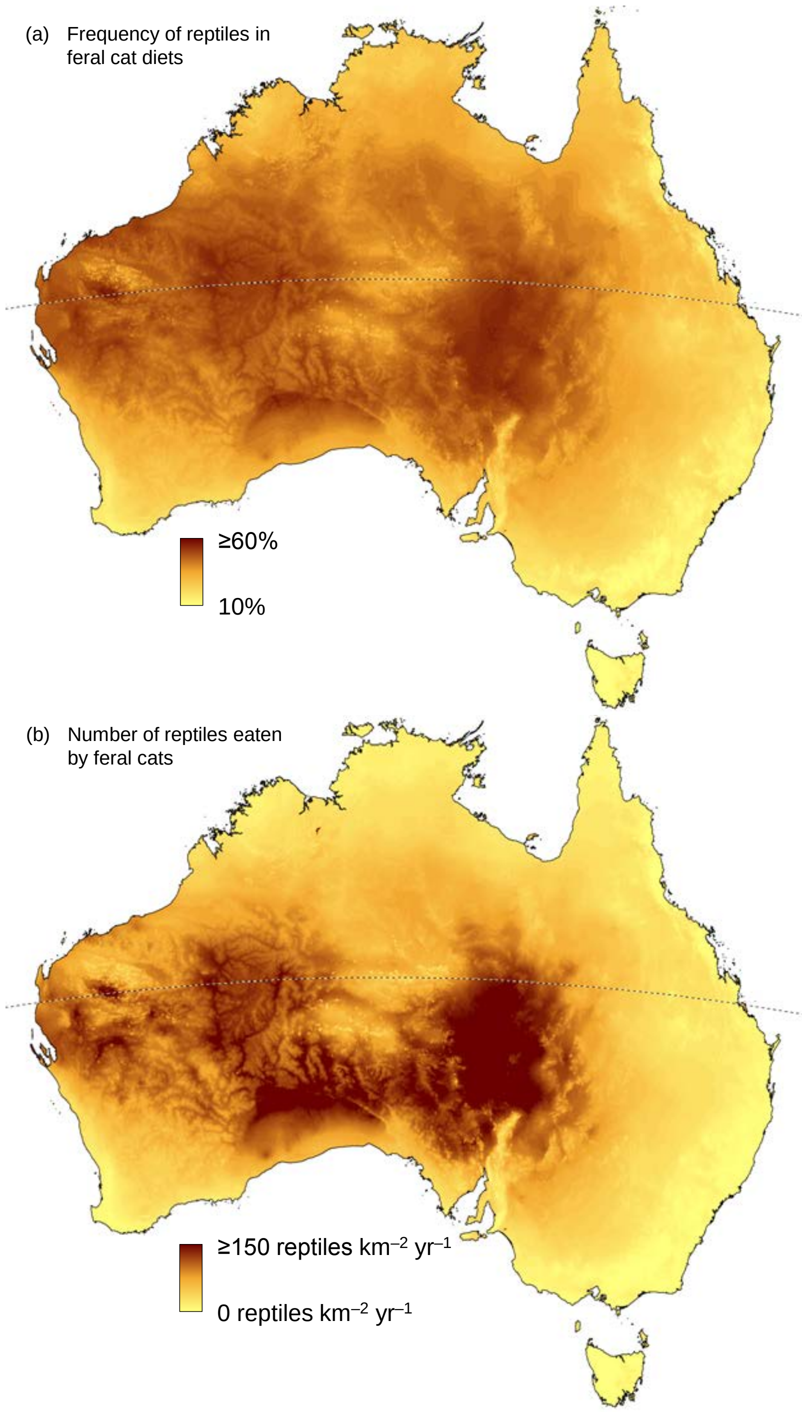

Figure 3. Model projections of (a) the frequency of reptiles in cat diets, and (b) the number of reptiles killed by cats each year, in natural environments throughout Australia. For (a) predictor variables in the regression model are: mean annual rainfall; mean annual temperature; tree cover; and ruggedness, weighted according to Akaike weights (w_i) for the candidate models (Table 2). The dashed lines indicate the Tropic of Capricorn.

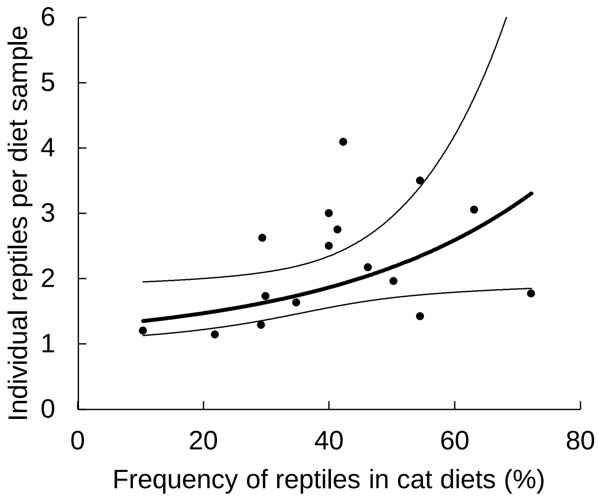

Figure 4. The modelled relationship between the number of individual reptiles in those samples containing reptiles and the frequency (incidence) of reptiles in cat dietary samples, according to a linear least-squares regression model of the form: log (individuals – 1) ~ frequency.

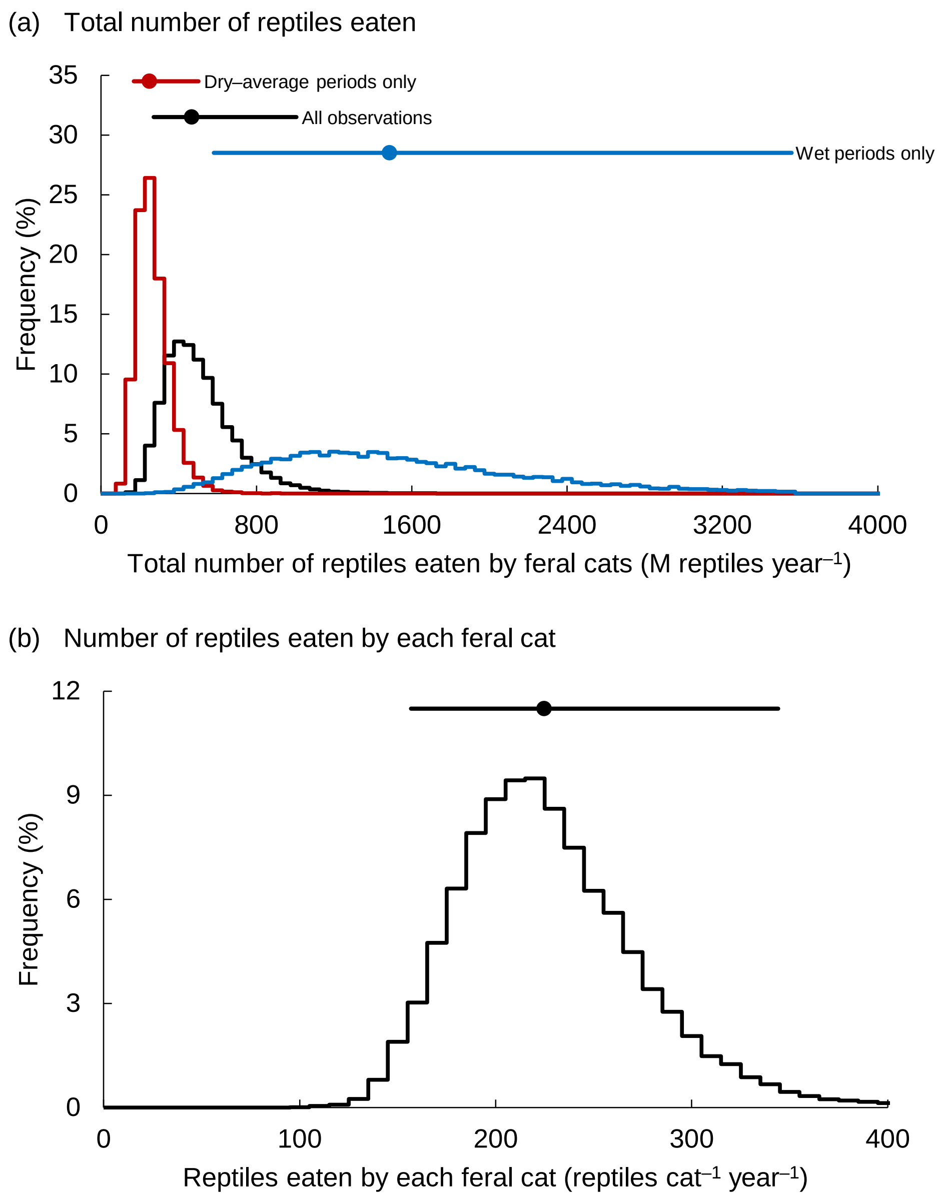

Figure 5. Uncertainty in (a) the total number of reptiles eaten, and (b) the number of reptiles eaten by each feral cat, based on bootstrapping of the dataset 20,000 times. At the top of each panel is the mean (filled circle) and 95% confidence bounds (lines). In (a), this is shown separately for analyses with cat density observations from wet periods, dry–average periods, and including all observations (wet and dry–average) (as defined in Legge *et al*. 2017).

Table 1. Collation of accounts of the frequency of reptiles in the diet of feral cats in Australia (limited to those studies with >10 samples). N – sample size; NG – relevant information not given in source; 'island' indicates island smaller than Tasmania. Abbreviations for Australian jurisdictions: NSW New South Wales; NT Northern Territory; Qld Queensland; SA South Australia; Tas Tasmania; Vic Victoria; WA Western Australia.

Location	**% frequency of occurrence of reptiles in diet (N)**	**% native reptiles /all reptiles in diet**	**Mean no. of individual reptiles in samples with reptiles**	**Sample type**	**Site type**	**Source**
Kanandah, Nullarbor, WA	42.1% (76)	100%	NG	stomachs	mainland, natural	Algar and Friend (1995)
Purple Downs, SA	100% (14)	100%	NG	stomachs	mainland, natural	Bayly (1976)
Farina, SA	55.0% (21)	NG	NG	stomachs	mainland, natural	Bayly (1978)
Wedge Island, Tas.	1.5% (527)	100%	NG	scats	island, natural	Beh (1995)
East Gippsland, Vic	4.5% (22)	NG	NG	scats	mainland, natural	Buckmaster (2011)
Wet Tropics, Qld	0% (123)	NG	NG	scats	mainland, natural	Burnett (2001)
Gibson Desert, WA	42.1% (19)	NG	NG	scats	mainland, natural	Burrows *et al.* (2003)
Various sites, Tas.	8.8% (45)	NG	NG	stomachs	mainland, natural	Cahill (2005)
Yathong, NSW	30.1% (112)	100%	NG	stomachs	mainland, natural	Catling (1988)
Collation across many sites, Vic.	2.5% (128)	NG	NG	stomachs	mainland, natural	Coman and Brunner (1972)
Kakadu, NT	8.0% (49)	NG	NG	scats	mainland, natural	Corbett (1995)
Erldunda, NT	55.3% (38)	NG	NG	stomachs	mainland, natural	Corbett (1995)
Christmas Island	3.3% (92)	NG	NG	scats	island, natural	Corbett *et al.* (2003)
SW Wheatbelt, WA	10.3% (39)	NG	NG	stomachs	mainland, natural	Crawford (2010)
Ningaloo/Cape Range, WA	40% (10)	100%	3.00	stomachs	mainland, natural	F. Delanzy, T. Thomson and M. Vanderklift (unpubl.)
Dirk Hartog Island	71.4% (14)	100%	NG	stomachs	island, natural	Deller *et al.* (2015)

Location	% frequency of occurrence of reptiles in diet (N)	% native reptiles /all reptiles in diet	Mean no. of individual reptiles in samples with reptiles	Sample type	Site type	Source
Oberon, NSW [natural area]	12.1% (33)	NG	NG	scats	mainland, natural	Denny (2005)
Oberon, NSW [rubbish dump]	8.3% (48)	NG	NG	scats	mainland, modified	Denny (2005)
Tibooburra, NSW [natural area]	45.8% (144)	NG	NG	scats	mainland, natural	Denny (2005)
Tibooburra, NSW [rubbish dump]	46.2% (119)	NG	NG	scats	mainland, modified	Denny (2005)
Dwellingup, WA	7.1% (14)	NG	NG	stomachs	mainland, natural	C. Dickman (unpubl.)
Katherine - NT	41.4% (29)	100%	2.75	stomachs	mainland, natural	C. Dickman (unpubl.)
Kellerberrin - Durokoppin, WA	10.4% (48)	100%	1.20	stomachs	mainland, natural	C. Dickman (unpubl.)
Mt Isa - Cloncurry, Qld	46.2% (26)	100%	2.17	stomachs	mainland, natural	C. Dickman (unpubl.)
Rottnest Island, WA	21.9% (32)	100%	1.14	scats	island, natural	C. Dickman (unpubl.)
Charles Darwin Reserve, WA	46.3% (123)	NG	NG	scats	mainland, natural	Doherty (2015)
Burt Plain NT	36.4% (33)	100%	NG	stomachs	mainland, natural	G. Edwards (unpubl.)
Daly Basin bioregion, NT	18.2% (11)	100%	NG	stomachs	mainland, natural	G. Edwards (unpubl.)
Finke bioregion, NT	34.8% (23)	100%	NG	stomachs	mainland, natural	G. Edwards (unpubl.)
Great Sandy Desert, NT	25.0% (16)	100%	NG	stomachs	mainland, natural	G. Edwards (unpubl.)
Hamilton Downs, NT	72.7% (187)	NG	NG	scats	mainland, natural	G. Edwards (unpubl.)
MacDonnell Ranges, NT	23.9% (109)	100%	NG	stomachs	mainland, natural	G. Edwards (unpubl.)
Mitchell Grass Downs, NT	17.7% (192)	100%	NG	stomachs	mainland, natural	G. Edwards (unpubl.)

Location	% frequency of occurrence of reptiles in diet (N)	% native reptiles /all reptiles in diet	Mean no. of individual reptiles in samples with reptiles	Sample type	Site type	Source
Pine Creek bioregion, NT	7.1% (14)	100%	NG	stomachs	mainland, natural	G. Edwards (unpubl.)
Tanami, NT	18.0% (61)	100%	NG	stomachs	mainland, natural	G. Edwards (unpubl.)
Irving Creek & Hale River, NT	11.4% (35)	NG	NG	scats	mainland, natural	Foulkes (2002)
Barrington Tops, NSW	2.0% (49)	NG	NG	scats	mainland, natural	Glen *et al.* (2011)
Flinders Ranges, SA	14.0% (50)	NG	NG	stomachs	mainland, natural	Hart (1994)
Great Dog Island, Tas	51.6% (91)	100%	NG	scats	island, natural	Hayde (1992)
Flinders Ranges, SA (prior to rabbit control)	15.2% (70)	100%	NG	stomachs	mainland, natural	Holden and Mutze (2002)
Flinders Ranges, SA (post rabbit control)	13.1% (288)	NG	NG	stomachs	mainland, natural	Holden and Mutze (2002)
Anglesea, Vic	0.6% (159)	NG	NG	scats	mainland, modified	Hutchings (2003)
Karijini NP, WA	17.0% (88)	NG	NG	scats	mainland, natural	Johnston *et al.* (2013)
Flinders Ranges, SA	8.0% (60)	NG	NG	scats	mainland, natural	Johnston *et al.* (2012)
Flinders Ranges, SA	29.2% (24)	NG	1.29	stomachs	mainland, natural	Johnston *et al.* (2012)
Macquarie Island, Tas	0% (41)	NG	NG	stomachs	island, natural	Jones (1977)
Macquarie Island, Tas	0% (756)	NG	NG	scats	island, natural	Jones (1977)
Mallee, Vic	13.0% (131)	NG	NG	stomachs	mainland, natural	Jones and Coman (1981)
Kinchega NP, NSW	28.0% (65)	NG	NG	stomachs	mainland, natural	Jones and Coman (1981)
Eastern Highlands, Vic	3.0% (117)	NG	NG	stomachs	mainland, natural	Jones and Coman (1981)
Phillip Island, Vic	5.0% (277)	NG	NG	stomachs	island, natural	Kirkwood *et al.* (2005)
Inland NE Qld	63.0% (169)	100%	2.61	stomachs	mainland, natural	Kutt (2011)

Location	% frequency of occurrence of reptiles in diet (N)	% native reptiles /all reptiles in diet	Mean no. of individual reptiles in samples with reptiles	Sample type	Site type	Source
Lambert station, SW Qld	18.0% (49)	NG	NG	stomachs	mainland, natural	Lapidge and Henshall (2001)
Mt Field and Tasman Peninsula, Tas	0% (27)	NG	NG	stomachs	mainland, natural	Lazenby (2012)
Piccaninny Plains, Qld	72.2% (18)	NG	1.77	stomachs	mainland, natural	McGregor *et al.* (2016)
northern Simpson Desert, Qld	57.3% (377)	NG	NG	scats	mainland, natural	Mahon (1999)
'Pastoral' (mostly Pilbara and Murchison), WA	44.0% (50)	100%	NG	stomachs	mainland, natural	Martin *et al.* (1996)
'Rural' (mostly wheatbelt), WA	0% (31)	NG	NG	stomachs	mainland, natural	Martin *et al.* (1996)
Mitchell grass downs, Qld	50.3% (187)	100%	1.96	stomachs	mainland, natural	Mifsud and Woolley (2012)
Lake Burrendong, NSW	3.4% (600)	NG	NG	scats	mainland, natural	Molsher *et al.* (1999)
Fitzgerald NP, WA	19.5% (41)	NG	NG	stomachs	mainland, natural	O'Connell (2010)
Blackall, Qld	46.7% (30)	100%	NG	stomachs	mainland, natural	R. Palmer (unpubl.)
Davenport Downs, Qld	42.9% (184)	100%	1.93	scats & stomachs	mainland, natural	R. Palmer (unpubl.)
Denham Dump, WA	45.3% (53)	NG	NG	scats	mainland, modified	R. Palmer (unpubl.)
Diamantina Lakes, Qld	56.0% (257)	100%	NG	scats & stomachs	mainland, natural	R. Palmer (unpubl.)
Great Western Woodlands, WA	36.4% (11)	100%	NG	scats	mainland, natural	R. Palmer (unpubl.)
Inglewood, Qld	4.5% (22)	100%	NG	scats	mainland, natural	R. Palmer (unpubl.)
Monkey Mia, WA	42.1% (19)	100%	NG	scats	mainland, modified	R. Palmer (unpubl.)

Location	**% frequency of occurrence of reptiles in diet (N)**	**% native reptiles /all reptiles in diet**	**Mean no. of individual reptiles in samples with reptiles**	**Sample type**	**Site type**	**Source**
Muncoonie Lakes, Birdsville, QLD	18.5% (27)	100%	NG	scats	mainland, natural	R. Palmer (unpubl.)
Mulyungarie, SA	35.0% (40)	NG	2.21	stomachs	mainland, natural	R. Palmer (unpubl.)
North Kimberley, WA	21.1% (19)	100%	NG	scats	mainland, natural	R. Palmer (unpubl.)
Offham, SW Qld	43.5% (23)	100%	2.00	stomachs	mainland, natural	R. Palmer (unpubl.)
Pannawonica, WA	38.5% (13)	100%	NG	scats	mainland, natural	R. Palmer (unpubl.)
Kintore, NT	62.9% (70)	NG	NG	scats	mainland, natural	Paltridge (2002)
Tennant Creek (Tanami Desert), NT	72.4% (76)	NG	NG	scats	mainland, natural	Paltridge (2002)
Barkly Tablelands, NT	17.0% (c*)	NG	NG	stomachs	mainland, natural	Paltridge *et al.* (1997)
Tanami, NT	20.0% (b*)	NG	NG	stomachs	mainland, natural	Paltridge *et al.* (1997)
Watarrka, NT	23.0% (a*)	NG	NG	stomachs	mainland, natural	Paltridge *et al.* (1997)
West (Pellew) Island, NT	54.5% (11)	NG	3.50	scats	island, natural	Paltridge *et al.* (2016)
Simpson Desert, NT	9.1% (44)	NG	NG	scats	mainland, natural	Pavey *et al.* (2008)
Roxby Downs, SA	32.0 (127)	NG	NG	stomachs	mainland, natural	Pedler and Lynch (2016)
Roxby Downs, SA	29.4% (360)	100%	2.62	stomachs	mainland, natural	Read and Bowen (2001)
Heirisson Prong, WA	13.8% (109)	NG	NG	stomachs	mainland, natural	Risbey *et al.* (1999)
Sandford, Tas	8.5% (47)	NG	NG	scats	mainland, natural	Schwarz (1995)
Simpson Desert, Qld	33.0% (42)	NG	NG	scats	mainland, natural	Spencer *et al.* (2014)
Kakadu, NT	4.8% (84)	NG	NG	scats	mainland, natural	Stokeld *et al.* (2016)
Darwin, NT [urban/rural]	5.6% (18)	100%	1.00	stomachs	mainland, modified	D. Stokeld (unpubl.)
Kakadu/Wardekken, NT	34.8% (23)	100%	1.63	stomachs	mainland, natural	D. Stokeld (unpubl.)

Location	% frequency of occurrence of reptiles in diet (N)	% native reptiles /all reptiles in diet	Mean no. of individual reptiles in samples with reptiles	Sample type	Site type	Source
Top End, NT	40.0% (10)	100%	2.50	stomachs	mainland, natural	D. Stokeld (unpubl.)
Southern NT	54.5% (22)	100%	1.42	stomachs	mainland, natural	Strong and Low (1983)
Christmas Island	31.0% (93)	NG	NG	scats & stomachs	island, natural	Tidemann *et al.* (1994)
Croajingalong, Vic	23.0% (48)	NG	NG	scats	mainland, natural	Triggs *et al.* (1984)
Armidale, NSW	42.3% (26)	100%	4.09	scats	mainland, natural	van Herk (1980)
Kosciuszko, NSW	5.9% (17)	NG	NG	scats & stomachs	mainland, natural	Watson (2006)
Witchelina, SA	63.1% (404)	100%	3.05	stomachs	mainland, natural	Woinarski *et al.* (in press)
Matuwa (Lorna Glen), WA	26.4% (337)	NG	NG	scats	mainland, natural	Wysong (2016)
Western Qld (‘boom’ period)	23.0% (152)	100%	1.46	stomachs	mainland, natural	Yip *et al.* (2015)
Western Qld (‘bust’ period)	60.0% (35)	100%	2.90	stomachs	mainland, natural	Yip *et al.* (2015)

Footnote: *sample sizes not given for separate areas in text, but a+b+c=390.

Table 2. Models explaining variation in frequency of reptiles in cat diets in natural environments throughout Australia, and the results of the model selection procedure. The models are shown ranked in ascending order of the model selection criterion, $\Delta QAIC_c$, which is the difference between the model's $QAIC_c$ value and the minimum AIC_c value in the candidate set. w_i is the Akaike weight, or the probability of the model being the best in the candidate set. Models which are well-supported relative to the null model (within 2 $QAIC_c$ units) are shaded grey; models with limited support ($\Delta QAIC_c > 5$), or lower support than the null model, are not included in the table.

Model	$\Delta QAIC_c$	w_i	R^2
~ $\log_{10}$ (rainfall) + temperature	0.0	0.29	0.56
~ $\log_{10}$ (rainfall) * temperature	1.5	0.14	0.57
~ $\log_{10}$ (rainfall) + temperature + tree cover	2.1	0.10	0.56
~ $\log_{10}$ (rainfall) + temperature + ruggedness	2.3	0.09	0.56
~ island size index + $\log_{10}$ (rainfall) + temperature	2.3	0.09	0.56
~ $\log_{10}$ (rainfall) * temperature + tree cover	3.7	0.05	0.57
~ $\log_{10}$ (rainfall) * temperature + ruggedness	3.8	0.04	0.57
~ island size index + $\log_{10}$ (rainfall) * temperature	3.8	0.04	0.57
~ island size index + $\log_{10}$ (rainfall) + temperature + tree cover	4.4	0.03	0.56
~ $\log_{10}$ (rainfall) + temperature + tree cover + ruggedness	4.4	0.03	0.56
~ island size index + $\log_{10}$ (rainfall) + temperature + ruggedness	4.6	0.03	0.56

Table 3. Percentage of all reptiles identified in cat dietary samples by reptile family for studies reporting the identity and numbers of all reptiles consumed by feral cats. 'Freq.Occ.' is the % of cat samples that contained reptiles. 'No. reptiles' is the total number of reptile individuals reported in cat dietary samples in the study. Reptile families: Geckoes (Carphodactylidae, Diplodactylidae, Gekkonidae); Pygop. (Pygopodidae); Agam. (Agamidae); Scinc. (Scincidae); Varan. (Varanidae); Typhl. (Typhlopidae); Colub. (Colubridae); Boid. (Boidae); Elap. (Elapidae). Note that none of the listed studies included crocodiles, marine or freshwater turtles, or file-snakes as cat dietary items.

Location	**Source**	**Freq.Occ.**	**No. reptiles**	**Geckoes**	**Pygop.**	**Agam.**	**Scinc.**	**Varan.**	**Typhl.**	**Colub.**	**Boid.**	**Elapid.**
Wedge Island, Tas	Beh (1995)	1.5	8	0	0	0	100	0	0	0	0	0
Ningaloo/Cape Range, WA	Delanzy, Thompson & Vanderkift (unpubl.)	40.0	12	66.7	8.3	0	8.3	16.7	0	0	0	0
Mt Isa, Qld	Dickman (unpubl)	46.2	26	11.5	3.8	30.8	34.6	0	3.8	0	0	15.4
Katherine - VRD, NT	Dickman (unpubl)	41.4	33	39.4	6.1	3	45.5	0	3	0	0	3
Rottnest Island, WA	Dickman (unpubl)	21.9	10	10	0	0	70	0	0	0	0	20
Kellerberrin - Durokoppin, WA	Dickman (unpubl)	10.4	6	0	0	33.3	66.7	0	0	0	0	0
Dwellingup, WA	Dickman (unpubl)	7.1	1	0	0	0	100	0	0	0	0	0
Great Dog Island, Tas	Hayde (1992)	51.6	47	0	0	0	93.6	0	0	0	0	6.4
Flinders Ranges, SA	Johnston et al. (2012)	29.2	9	0	0	0	100	0	0	0	0	0
Phillip I., Vic	Kirkwood et al. (2005)	5.0	20	0	0	0	100	0	0	0	0	0
Inland NE Qld	Kutt (2011)	63.0	277	35.7	2.2	34.3	15.5	5.1	0	0	0.4	6.9
Picanniny Plains, Qld	McGregor et al. (2016)	72.2	23	8.7	0	21.7	73.9	0	0	0	0	0
Mitchell grass downs, Qld	Mifsud & Woolley (2012)	50.3	131	9.2	2.3	51.9	20.6	0	2.3	0	0	13.7
Offham, Qld	Palmer (unpubl.)	43.5	20	30.0	0	15.0	45.0	5.0	0	0	0	5.0
Blackall, Qld	Palmer (unpubl.)	46.7	27	63.0	0	18.5	3.7	0	0	0	0	14.8
Mulyungarie, Qld	Palmer (unpubl.)	35.0	31	54.8	0	16.1	3.2	0	0	0	0	12.9
West (Pellew) Island, NT	Paltridge et al. (2016)	54.5	21	9.5	0	33.3	47.6	0	0	4.8	0	4.8
Roxby Downs, SA	Read & Bowen (2001)	29.4	305	21.6	0.7	24.9	45.6	3.3	2.3	0	0	1.6
Heirisson Prong, WA	Risbey et al. (1999)	13.8	15	33.3	0	33.3	33.3	0	0	0	0	0
Armidale, NSW	van Herk (1980)	42.3	25	12	0	4	84	0	0	0	0	0

Witchelina, SA	Woinarski et al. (in press)	63.1	442	17.4	1.6	34.8	30.5	5.7	3.8	0	0.2	5.9
Western Qld (boom period)	Yip et al. (2015)	23.0	50	8	2	60	22	2	0	0	0	6
Western Qld (bust period)	Yip et al. (2015)	60.0	54	13	3.7	31.5	33.3	3.7	0	0	0	14.8
Total individuals			*1588*	*342*	*25*	*481*	*555*	*55*	*28*	*1*	*2*	*99*

Table 4. Australian studies reporting the frequency (%) of reptiles in the diet of cats and co-occurring mammalian predators. Studies are included only where at least 10 samples were reported for cats and at least one other predator. The sample size is given in parentheses.

	Co-occurring predators			Location	Source
Feral cat	Fox	Dog/dingo	Spotted-tailed Quoll		
55.0 (21)	10.7 (29)			Farina, SA	Bayly (1978)
0 (123)		1.5 (282)	2.2 (1252)	Wet Tropics, Qld	Burnett (2001)
42.1 (19)	41.0 (22)			Gibson Desert, WA	Burrows *et al.* (2003)
30.1 (112)	23.3 (288)			Yathong, NSW	Catling (1988)
55.3 (38)	11.4 (44)	11.9 (285)		Erldunda, NT	Corbett (1995)
46.3 (123)		5.4 (37)		Charles Darwin reserve, WA	Doherty (2015)
11.4 (35)	0 (26)	5.5 (310)		Irving Creek & Hale River, NT	Foulkes (2002)
2.0 (49)	12.6 (95)	2.9 (68)	5.6 (168)	Barrington Tops, NSW	Glen *et al.* (2011)
14.0 (50)	1.7 (105)			Flinders Ranges, SA	Hart (1994)
13.1 (288)	9.5 (774)			Flinders Ranges, SA (post rabbit control)	Holden and Mutze (2002)
17.0 (88)		46.6 (73)		Karijini NP, WA	Johnston *et al.* (2013)
3.0 (117)		6.0 (166)		Eastern Highlands, Vic	Coman (1972); Jones and Coman (1981)
5.0 (277)	0 (147)			Phillip Island, Vic	Kirkwood *et al.* (2005)
18.0 (49)	2.5 (38)			SW Qld	Lapidge and Henshall (2001)
57.3 (377)	36.6 (382)			Simpson Desert, Qld	Mahon (1999)
50.3 (187)	25.0 (52)			Mitchell Grass Downs, Qld	Mifsud and Woolley (2012)
3.4 (600)	9.2 (261)			Lake Burrendong, NSW	Molsher *et al.* (1999); Molsher *et al.* (2000)
10.1 (217)		33.6 (756)		Astrebla Downs, Qld	R. Palmer (unpubl.)
42.9 (184)		17.9 (28)		Davenport Downs, Qld	R. Palmer (unpubl.)
36.4 (11)	27.8 (18)	2.9 (105)		Great Western Woodlands, WA	R. Palmer (unpubl.)
4.5 (22)	3.8 (53)			Inglewood, QLD	R. Palmer (unpubl.)

18.5 (27)		23.4 (64)	Muncoonie Lakes, Birdsville, Qld	R. Palmer (unpubl.)
43.5 (23)	36.5 (74)		Offham, SW Qld	R. Palmer (unpubl.); Palmer (1995)
38.5 (13)		0.0 (50)	Pannawonica, WA	R. Palmer (unpubl.)
62.9 (70)	65.7 (70)		Kintore	Paltridge (2002)
72.4 (76)	49.1 (53)	76.6 (77)	Tennant Creek	Paltridge (2002)
9.1 (44)	3.2 (63)	22.8 (316)	Simpson Desert, NT	Pavey *et al.* (2008)
29.4 (360)	19.0 (105)		Roxby Downs, SA	Read and Bowen (2001)
13.8 (109)	2.1 (47)		Heirisson Prong, WA	Risbey *et al.* (1999)
31.1 (254)	18.2 (572)	26.3 (236)	Simpson Desert, Qld	Spencer *et al.* (2017)
4.8 (84)		0.1 (1100)	Kapalga, NT	Stokeld *et al.* (2016)
23.0 (48)	3.0 (937)	3.0 (412)	Croajingalong, Vic	Triggs *et al.* (1984)
63.1 (404)	68.6 (51)	0 (11)	Witchelina, SA	Woinarski *et al.* (in press)
26.4 (337)		2.5 (353)	Matuwa (Lorna Glen)	Wysong (2016)