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REVIEW

Not all predators are equal: a continent-scale analysis of the effects of predator control on Australian mammals

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ABSTRACT

1. Introduced predators pose threats to biodiversity and are implicated in the extinction of many native species. In Australia, considerable effort is spent controlling populations of introduced predators, including the dingo *Canis dingo* and the red fox *Vulpes vulpes*, to reduce their effects on native species and livestock. Studies describe different outcomes of controlling dingo and fox populations on native species, making biodiversity management decisions difficult for conservation managers.
2. We conduct a meta-analysis to compare the impacts that control programmes targeted towards dingoes and foxes in Australia have on introduced predators and on other mammal species, including native species and prey species.
3. Our results provide evidence that lethal control of dingoes and foxes has different outcomes for different mammalian species. Dingo removal had a negative effect on the abundance of native mammals weighing less than the critical weight range (CWR) of 30–5500 g, and a positive effect on the abundance of mammals above the CWR. Fox abundance increased in response to dingo control, but confidence intervals were large. Fox removal had strong positive effects on ground-dwelling and arboreal mammals. Lethal control of dingoes did not have a significant effect on cats, but where dingoes were removed there was a tendency for foxes to increase, and where foxes were removed there was a tendency for cats to increase.
4. Our results highlight unintended and perverse outcomes of lethal predator control on Australian mammals. Lethal control of dingoes significantly increases abundances of above CWR mammals and significantly decreases abundances of under CWR mammals. Lethal control of foxes significantly increases the abundances of CWR mammals. These findings show how removing dingoes and foxes alters mammal assemblages and provide comprehensive and objective information for conservation managers.

5. We recommend that land management agencies take the results of this study into consideration when planning lethal control programmes targeting dingoes and foxes because, depending on the target canid, these programmes result in different outcomes for other mammal species. Removal programmes targeting dingoes and/or foxes can result in increased abundances of introduced predators and, ultimately, have far-reaching effects on many mammal species.

INTRODUCTION

Globally, introduced predators rank as one of the greatest threats to biodiversity (King 1984, Savidge 1987, Biggins et al. 1999, Johnson 2006, Doherty et al. 2016). Introduced predators have greater impacts on prey species than native predators, and in some cases have driven prey species to extinction because prey species with which they have not coevolved may lack appropriate adaptations to detect and escape novel predators, and thus are particularly vulnerable to predation (Salo et al. 2007, Carthey & Banks 2012). Another reason put forward to explain the severe impacts of introduced predators is that they may thrive in their new environments and thus occur at remarkably high population densities (Moseby et al. 2015, Legge et al. 2017). There are several potential drivers of high population densities of introduced predators. These include release from constraints on population growth posed by competitors and diseases, as well as facilitation that can occur when populations of introduced predators benefit from the presence of high densities of prey (MacDonald & Harrington 2003, Saunders et al. 2010, Sih et al. 2010, Letnic et al. 2012). High rates of encounters between prey and overabundant introduced predators can have catastrophic effects on prey populations (Sinclair et al. 1998).

In many regions, multiple introduced species coexist (Ruscoe et al. 2011, Woinarski et al. 2015). In such circumstances, it can be difficult to parse out the relative importance of their effects on prey species (Ruscoe et al. 2011, Wayne et al. 2017). Coexisting introduced predator species may have additive effects on native prey populations if they have similar prey preferences. However, as a general rule, the impacts that predators have on prey species tend to scale with both the body sizes of the predator and prey species (Sinclair et al. 2003, Letnic et al. 2009a). This is because smaller predators tend to prefer smaller prey than larger predators and vice versa. Thus, we might expect that, in environments where multiple species of introduced predators coexist, their impacts on prey species vary according to their prey preference.

Another factor that can moderate the strength of introduced predators' effects on prey species is the presence of competitive interactions between species. Interactions between coexisting predators may be particularly strong owing to competition for food and, as has been demonstrated in earlier studies, larger predators frequently kill smaller predators (Ripple et al. 2014), suppressing their abundances (Donadio & Buskirk 2006). According to the mesopredator release hypothesis, larger predators can provide a net benefit for populations of the prey of smaller predators (mesopredators) if intraguild killing and interference competitions result in a decrease in the predatory impact of the mesopredator (Letnic et al. 2009a, Read & Scoleri 2015). Such indirect effects can ripple along multiple interaction pathways, and, in doing so, can have profound effects on the composition of species assemblages (Colman et al. 2014).

In order to mitigate the threats that introduced predators pose to native species and livestock, introduced predators in many parts of the world are subjected to population control programmes (Reynolds & Tapper 1996, Gillies & Pierce 1999, Robley et al. 2014). Such control programmes may use selective techniques to remove introduced predators, such as shooting or trapping (Holbrook et al. 2016), or non-selective techniques, such as fencing and the distribution of poison baits (Miller & Miller 1995, Hayward & Kerley 2009). However, the impacts that predator removal programmes have on prey species can be difficult to assess in situations where multiple predators coexist (Ruscoe et al. 2011, Marlow et al. 2015a, Wayne et al. 2017), due to differences in the susceptibility of predator species to the control techniques employed, differences in the prey preferences of predator species (Letnic et al. 2009a) and indirect effects (Ruscoe et al. 2011, Colman et al. 2014).

In Australia, considerable effort is spent on controlling populations of introduced predators: the dingo *Canis dingo*, the red fox *Vulpes vulpes* and the feral cat *Felis catus*. Dingoes (15–25 kg) were introduced to Australia 3500–5000 yBP (years before present) and are likely to have contributed to the extinction of the thylacine *Thylacinus cynocephalus* and the Tasmanian devil *Sarcophilus harrisii* from mainland Australia (Letnic et al. 2012, Crowther et al. 2014). Because dingoes kill livestock, their populations are controlled, primarily by distributing meat baits containing the poison 1080 sodium fluoroacetate (Claridge et al. 2010, Allen 2015). Red foxes (5–7 kg) were introduced to Australia in around 1870 and are thought to be one of the major drivers of the endangerment of native mammals weighing 30–5500 g, also known as the critical weight range (CWR), and ground-nesting birds throughout the continent (Johnson 2006). Like dingoes, foxes are controlled using poisoned 1080 baits to protect native fauna and livestock (Gentle et al. 2007). Dingo and fox populations are also controlled in some areas using a combination of baiting, shooting, trapping, and exclusion fencing. Cats were introduced to Australia in the late 18th century and have been implicated in the endangerment of mammals weighing less than 3000 g (Fisher et al. 2014). Cat populations are difficult to control because cats do not readily take most types of meat bait (Algar et al. 2002), but cats have been eradicated from relatively small areas using a combination of exclusion fencing, shooting, trapping, and poisoning (Moseby et al. 2009).

Because both dingoes and foxes readily take meat baits, many control programmes target both species under the assumption that the impacts of the two predators on prey populations are similar (Claridge et al. 2010, Allen et al. 2013). However, studies investigating the impacts of canid predator control on prey species in Australia have reported unexpected outcomes, such as an increase in the abundance of cats or of certain prey species, due presumably to the existence of interference effects between predators or because of differences in the prey preferences of predator species (Risbey et al. 2000, Colman et al. 2014, Marlow et al. 2015a).

We conduct meta-analyses to compare the impacts that control programmes targeted towards dingoes and red foxes in Australia have had on introduced predators and on other mammal species. We refer to the control programmes as fox/dingo removal. Our specific aims were as follows: 1) to determine the direction and magnitude of the effect that the lethal control of dingoes (mainly via baiting) has on abundance indices of mammals within three weight ranges: under CWR (<30 g), CWR (30–5500 g), and above CWR (>5500 g); 2) to measure the direction and magnitude of the effect that lethal control of dingoes has on abundance indices of dingoes, foxes, and cats; 3) to measure the effects that lethal control of foxes has on abundance indices of mammals within the three weight ranges; and 4) to measure the direction and magnitude of the effect that lethal control of foxes has on abundance indices of foxes and cats. The findings are used to make recommendations for predator control based on the knowledge of how it alters mammal assemblages, with the goal of improving the information available to conservation managers.

METHODS

Literature search

We followed the review approach as outlined in the PRISMA statement as far as possible for our study methodology (Moher et al. 2009). Our study search was conducted on ISI Web of Science and Google Scholar using the keywords ‘red fox baiting Australia’, ‘red fox predation Australia’, ‘dingo baiting’, and ‘dingo predation’ (see Appendices S1 and S2). Based on the results from these searches, we were able to use citations to trace back to other appropriate studies. We only included studies that were published in peer-reviewed journals and that included quantitative data from field-based surveys (Table 1). Database searches for studies pertaining to foxes yielded 196 studies; searches for dingoes yielded 154 studies. From these, we performed backward searches accordingly. Studies were initially collected up until 1 June 2015 and a search update was conducted in July 2017, following the same procedures. A list of studies excluded at the full-text assessment stage is provided (see Appendix S3).

Study selection and eligibility criteria

The eligibility criteria were applied to studies retrieved by independent searches by two of the study authors. For the dingo and fox data sets, we initially included data for analysis if the study passed a set of criteria: 1) the study must have involved the attempted suppression or removal of dingoes or foxes (according to which data set was being populated) and the response of mammalian species (often prey species) to predator removal must have been quantified; 2) studies must have involved before/after or paired control/treatment experimental designs; and 3) dingoes and foxes must have been removed predominantly using 1080 sodium fluoroacetate poison baiting or have been naturally absent from the treatment area (i.e. the treatment area was an island, see Kinnear et al. 2002). We included all terrestrial mammal species where we could extract an effect, regardless of whether the species was introduced or native.

Studies were classified according to the experimental design used by the researchers (before/after or control/treatment). Studies that included data for the same species, but at different study sites, were treated as independent data sets. Wherever possible, we requested additional information about studies from the study authors.

Data extraction and coding

Two authors independently extracted data, and the extracted data were checked and discussed by all five authors. We used electronic callipers and also GraphClick (Arizona Software, Switzerland) to extract relevant effect sizes from published studies reporting effects of dingo or fox baiting on other mammal species or on the target predator itself. Researchers usually reported measures of the abundance or activity of the animal of interest at both the removal and non-removal sites (or before/after removal). If multiple values were reported for the same species, we collected all values and then took the mean of these values for removal and for non-removal. We initially calculated the mean, standard deviation, and sample size from data for each species under removal and non-removal conditions. We used log response ratio (lnRR, the natural logarithm of the ratio between the two means) as our effect size, because it is a more suitable measure of effect than Hedges' d when sample sizes are small (Hedges et al. 1999, Friedrich et al. 2008).

We also collected other information from the studies to use as moderators of potential heterogeneity in the data: 1) publication year; 2) taxonomic information (species, genus, family); 3) sample size of the control and treatment groups; 4) type of mammal (placental, marsupial, or monotreme), mean animal body weight (kg; Menkhorst & Knight 2001), and weight category (under CWR, CWR, above CWR); 5) ecological type (herbivore, arboreal, mesopredator, ground-dwelling); 6) what type of data were reported in the study (index of abundance or true count data); and 7) experiment type (control/treatment or before/after).

Statistical analysis

We performed all statistical analyses within R statistical software, version 3.2.4 (R Core Team 2013). For meta-analytical and meta-regression models, we used the R package metafor (Viechtbauer 2010); for phylogenetic tree construction and plotting, we used the R package ape (Paradis et al. 2004). We created a phylogenetic tree for the mammalian species included in the data set, basing it on the mammalian supertree (Bininda-Emonds et al. 2007). We used study identity as a random factor in multilevel meta-analysis to control for non-independence arising from multiple effect sizes coming from single studies. We also accounted for species non-independence (via shared evolutionary history) by running phylogenetic meta-analytical and meta-regression models (Hadfield & Nakagawa 2010).

To quantify the overall effects of dingo removal on other species of mammal, we first constructed meta-analytic models (intercept-only, with and without phylogeny). We then ran phylogenetic meta-regression that included species average body weight and ecological type (herbivore, arboreal, mesopredator, or ground-dwelling) as moderators. Effects of fox removal on other species were assessed with analogous models: two meta-analytic (intercept-only models, with and without phylogeny) models and a phylogenetic meta-regression model with species mean body weight and ecological type (herbivore, arboreal, mesopredator, or ground-dwelling) as moderators. Body weight of animals was log-transformed and z-transformed before the analyses, so it had a mean of 0 and a standard deviation of 1. Positive estimates of the slope of body weight effect can be interpreted as increased abundance indicators with increasing body weight of species.

We quantified overall heterogeneity for the meta-analytic models using modified I^2 statistics (total variance excluding sampling error variance divided by total variance; Nakagawa & Santos 2012). Values of I^2 above 75% are considered as high levels of heterogeneity (Higgins et al. 2003) and suggest that most of the variability across studies is due to true heterogeneity rather than sampling noise, thus warranting examination of the potential sources of such heterogeneity.

We report mean effect sizes as our point meta-analytic estimates and 95% confidence intervals (CI) of the estimated meta-analytical effects. We considered the point effect estimates statistically significant when their CI did not cross zero.

Sensitivity analyses

To extend our analyses and test robustness of our conclusions, we performed additional analyses on both dingo and fox removal data sets. For the dingo removal experiments, we first looked at the native species (excluding dingo) data subset: we ran meta-analysis, phylogenetic meta-analysis, and then meta-regression with animal weight category (above CWR, CWR, under CWR). We then used data from all species, including dingo, to perform meta-analysis (with and without phylogeny) and a meta-regression using species identity as a categorical predictor. Such 'species model' allows the identification of the most distinct species-specific effects and also allows the assessment of the influence of dingo removal experiments on the abundance indicators of dingo populations. We performed analogous analyses on the data from fox removal studies. We first created a data subset including only native species. For this data subset, we assessed two meta-analytical models and a meta-regression with animal weight category (CWR, under CWR). We then performed meta-analysis on the full data set, including fox, and we also constructed a species meta-regression model using species identity as a moderator (Table 1).

Publication bias

Typical publication bias arises when non-significant results are missing from the collected data due to studies reporting statistically non-significant results being less likely to be published (Rothstein et al. 2006). We assessed publication bias in dingo and fox removal data sets using three methods: 1) visual inspection of symmetry of funnel plots

Table 1. Studies included in the meta-analysis. For each study, the target predator removal species and number of effect sizes extracted per study are provided

No.	Paper reference	Removal of target species	Number of effect sizes
1	Allen (2015)	Dingo	3
2	Allen et al. (2013)	Dingo	3
3	Allen et al. (2014)	Dingo	5
4	Brook et al. (2012)	Dingo	2
5	Burrows et al. (2003)	Dingo	3
6	Caughley et al. (1980)	Dingo	2
7	Colman et al. (2014)	Dingo	9
8	Gordon et al. (2015)	Dingo	3
9	Gordon et al. (2017)	Dingo	3
10	Letnic and Dworjanyn (2011)	Dingo	3
11	Letnic et al. (2009a,b)	Dingo	8
12	Letnic et al. (2017)	Dingo	2
13	Morris and Letnic (2017)	Dingo	2
14	Newsome et al. (2001)	Dingo	6
15	Pople et al. (2000)	Dingo	1
16	Robertshaw and Harden (1986)	Dingo	5
17	Wallach et al. (2010)	Dingo	11
18	Banks (1999)	Fox	1
19	Banks (2000)	Fox	1
20	Coates (2008)	Fox	4
21	Davey et al. (2006)	Fox	5
22	Dexter and Murray (2009)	Fox	5
23	Dexter et al. (2007)	Fox	7
24	Kinnear et al. (1988)	Fox	1
25	Kinnear et al. (1998)	Fox	1
26	Kinnear et al. (2002)	Fox	8
27	Kovacs et al. (2012)	Fox	1
28	Marlow et al. (2015a)	Fox	2
29	Marlow et al. (2015b)	Fox	1
30	Molsher et al. (2017)	Fox	2
31	Pickett et al. (2005)	Fox	1
32	Risbey et al. (2000)	Fox	1
33	Robley et al. (2014)	Fox	4
34	Towerton et al. (2011)	Fox	9

for the raw data and for the residual effect sizes from the meta-analytical models; 2) Egger's regression (Egger et al. 1997); and 3) trim-and-fill analyses (Duval & Tweedie 2000) on 'meta-analytic' residuals, as described by Nakagawa and Santos (2012), and as implemented in the trimfill function in metafor R package.

RESULTS

We extracted 125 effect sizes from 34 papers published between 1980 and 2017. This data set was split into dingo removal and fox removal data sets, according to the target removal species of each paper. These two data sets were analysed independently.

The dingo removal data set comprised 56 effect sizes, reporting effects on 22 species (additionally, there were 15 effect sizes for the dingo itself). There were similar numbers of effect sizes for native species (31 effect sizes) and non-native species (25 effect sizes), and for marsupials and monotremes (26 effect sizes) and placental species (30 effect sizes). The included species represented a broad range of average body weights, spanning 0.015 to 150 kg (mean ± SD: 20.5 ± 30.6). When the animals were placed in the three weight categories in relation to CWR, there were almost equal numbers of effect sizes for the above CWR (26 effect sizes) and CWR (23 effect sizes) categories, and only seven effect sizes in the under CWR category.

The fox removal data set comprised 47 effect sizes. The effects of fox removal were reported for a total of 21 different species (additionally, there were seven effect sizes for the fox itself). In contrast to the dingo data set, most effect sizes were for the native species (37 effect sizes), and only a few effect sizes came from the non-native species (10 effect sizes, including the only mesopredator in the data set – the cat). The data set was dominated by marsupial species (33 of 46 effect sizes). Also, the

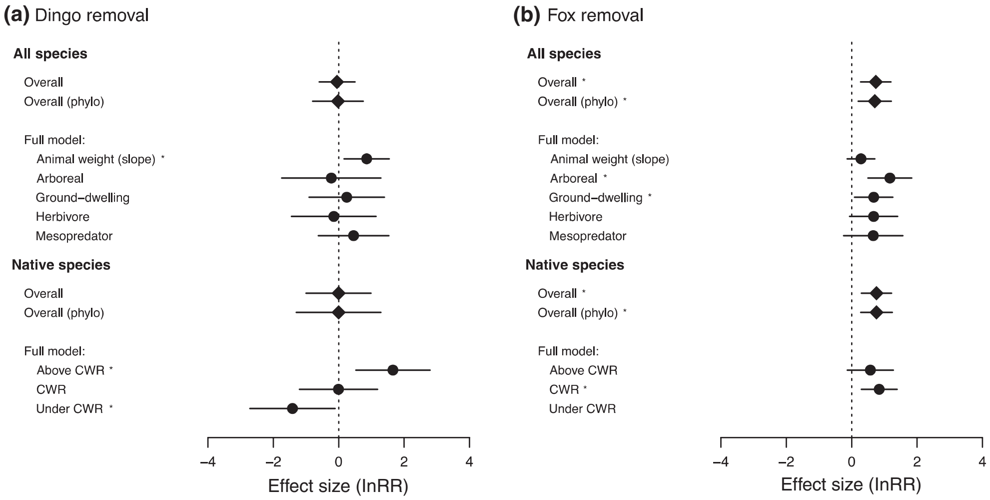

Fig. 1. Effects of dingo removal (a) and fox removal (b) experiments, for all species excluding target species, and for native species only. Overall estimates represent results from meta-analytic models and phylogenetic meta-analytical models (phylo). Full models are phylogenetic meta-regressions with moderators added as fixed effects. Point estimates represent mean intercepts, unless slope is indicated in the brackets. Whiskers represent 95% confidence intervals. Stars indicate estimates that are significantly different from zero (95% confidence intervals not spanning zero).

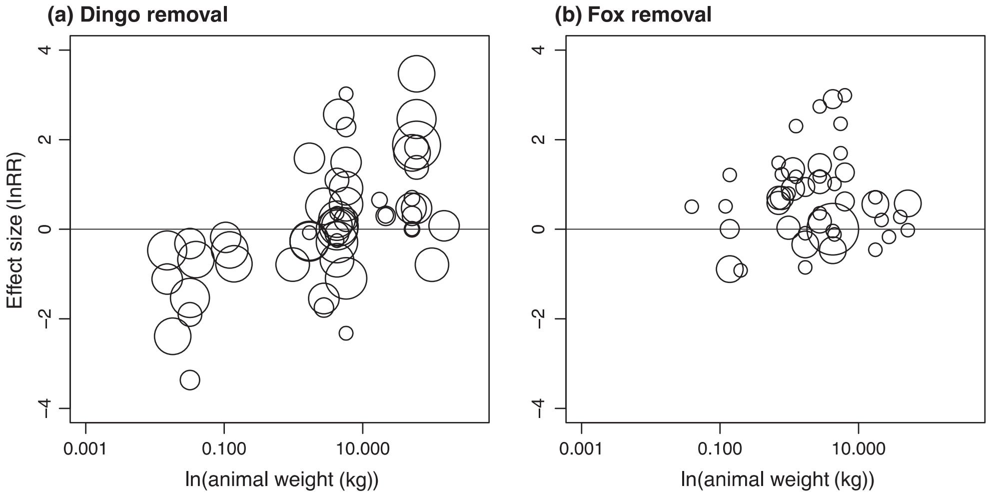

Fig. 2. Effect sizes plotted against animal weights for dingo removal (a) and fox removal (b) experiments. (a) When dingoes were removed, effect sizes are negative for light species and positive for heavy species, indicating decreased abundance of the former and increased abundance of the latter. (b) When foxes were removed, there is no clear linear relationship between effect sizes and body weight; the overall positive effect is mainly driven by species of intermediate weight, indicating a positive effect of fox removal on their abundance. Sizes of the circles are related to the precision of effect sizes; smaller circles bear less weight in the analyses. All species apart from the target species are included in the data sets.

included species represented a narrower range of body weights than those in the dingo data set, spanning 0.039–51.5 kg, and including lighter animals on average (mean ± SD: 7.2 ± 12.3). Thus, the data set was dominated by CWR species (36 effect sizes), and only 11 effect sizes came from above CWR species. There were no species from the under CWR category. The results (parameter estimates) of the meta-analytic and meta-regression models for dingo removal and fox removal studies are presented in Figs 1–3 and Tables 2–7.

Effects of dingo removal on the abundance of mammals

Dingo removal, overall, had negligible effect on other species of mammal (lnRR$_{\text{overall}}$ = −0.049, 95% CI = −0.594 to 0.496; lnRR$_{\text{overall(phylo)}}$ = −0.023, 95% CI = −0.795 to 0.750; Fig. 1a, Table 2). We observed high total heterogeneity in the meta-analytic models (with and without phylogeny = 98.6%; Table 2), which justified exploration of potential moderators with our meta-regression approach.

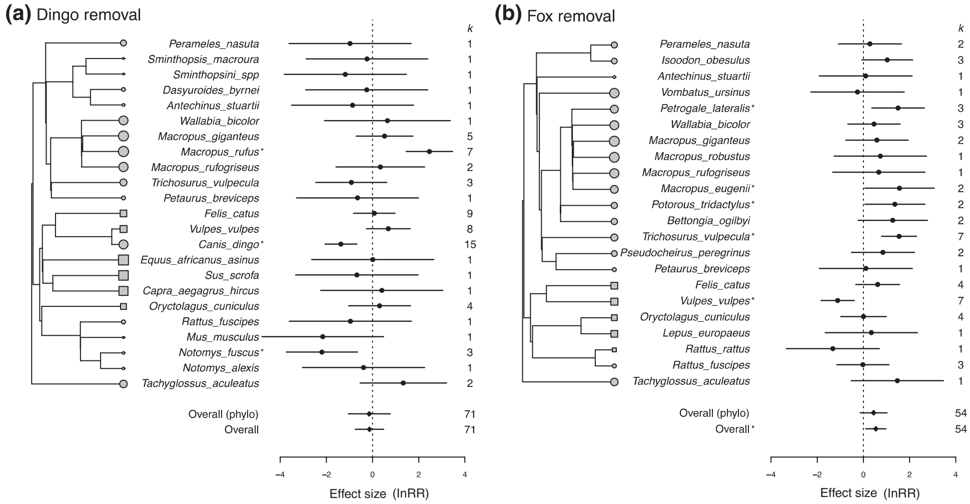

Fig. 3. Effects of dingo removal (a) and fox removal (b) experiments by species, including target species. Phylogenetic trees of relationships among the species are annotated with shapes representing whether each species is native (circles) or non-native to Australia (squares). The size of each shape is proportional to the natural logarithm of species body weight. Forest plots represent mean estimates for each species, along with 95% confidence intervals. Stars indicate estimates that are significantly different from zero (95% confidence intervals not spanning zero). k – number of effect sizes.

In our main meta-regression analysis on the dingo data set, we investigated potential effects of animal weight and ecological type, representing the main ecological groups and key dingo competitors. Heavier species tended to respond to dingo removal by increasing their abundance, while lighter species tended to decline in abundance ($ß_{\text{animal weight}}$ = 0.946, 95% CI = −0.016 to 1.908; Figs 1a, 2, and Table 2). We found no evidence that ecological types, as defined in this study (herbivore, arboreal, mesopredator, ground-dwelling), were related to the magnitude of effects of dingo removal (Table 2). Particularly, there was no statistically significant effect on cat and fox abundance indices. However, foxes ($\text{lnRR}_{\text{Vulpes\_vulpes}}$ = 0.68, 95% CI = −0.271 to 1.632) did show a positive increase in abundance following dingo removal, which is evidenced as the third highest positive response after red kangaroos *Macropus rufus* and short-beaked echidnas *Tachyglossus aculeatus*.

Additional analyses performed on native species data subset (excluding dingo) revealed a very similar picture to that from the data set including all species: there was no overall impact of dingo removal on native species ($\text{lnRR}_{\text{overall}}$ = −0.004, 95% CI = −0.996 to 0.987; $\text{lnRR}_{\text{overall(phylo)}}$ = −0.003, 95% CI = −1.296 to 1.291; Fig. 1a, Table 3). However, the effect on native species was again strongly influenced by species body weight,

Table 2. Meta-analytic and meta-regression models of effects of dingo removal on other species (native and non-native), excluding dingo. M – point estimates (mean); CI.lb – 95% confidence interval lower bounds; CI.ub – 95% confidence interval upper bounds; I^2 – total heterogeneities for each model. Estimates represent intercepts, unless slope is specified in the brackets. Estimates that are significantly different from zero (95% confidence intervals not spanning zero) are highlighted in bold

Model	M	CI.lb	CI.ub	I^2 (%)
Meta-analytic mean	−0.049	−0.594	0.496	98.6
Phylogenetic meta-analytic mean	−0.023	−0.795	0.750	98.6
Meta-regression with animal weight and ecological type category				
Animal weight (slope)	**0.856**	**0.167**	**1.545**	
Arboreal	−0.225	−1.741	1.291	
Ground-dwelling	0.246	−0.905	1.397	
Herbivore	−0.149	−1.442	1.144	
Mesopredator	0.455	−0.622	1.531	

Table 3. Meta-analytic and meta-regression models of effects of dingo removal on native species, excluding dingo. M – point estimates (mean); CI.lb – 95% confidence interval lower bounds; CI.ub – 95% confidence interval upper bounds; I^2 – total heterogeneities for each model. Estimates represent intercepts, unless slope is specified in the brackets. Estimates that are significantly different from zero (95% confidence intervals not spanning zero) are highlighted in bold

Model	M	CI.lb	CI.ub	I^2 (%)
Meta-analytic mean	−0.004	−0.996	0.987	99.0
Phylogenetic meta-analytic mean	−0.003	−1.296	1.291	99.1
Meta-regression with animal weight category				
Above CWR	**1.658**	**0.525**	**2.791**	
CWR	−0.007	−1.202	1.187	
Under CWR	**−1.413**	**−2.716**	**−0.110**	

indicating opposite responses of lighter and heavier species in the data set. Indeed, in meta-regression models, where we used animal weight categories as a predictor, we revealed a large decline of under CWR species (lnRR$_{\text{under-CWR}}$ = −1.413, 95% CI = −2.716 to −0.110; Fig. 1a, Table 3) and also large increase in above CWR species (lnRR$_{\text{aboveCWR}}$ = 1.658, 95% CI = 0.525 to 2.791; Fig. 1a, Table 3) in response to dingo removal. There was a large difference in mean effect magnitude between under and above CWR animals (lnRR$_{\text{aboveCWR-underCWR}}$ = −3.071, 95% CI = −4.489 to −1.654).

Species meta-regression model on the full dingo data set, i.e. including dingo, indicated that some species responded more strongly to dingo removal than others (Fig. 3a, Table 4). Particularly, dingo removal was linked to a dramatic increase in red kangaroo abundance (lnRR$_{\text{Macropus\_rufus}}$ = 2.464, 95% CI = 1.457 to 3.471) and to a decrease in the abundance of the dusky hopping mouse *Notomys fuscus* (lnRR$_{\text{Notomys\_fuscus}}$ = −2.192, 95% CI = −3.735 to −0.648). There was also a tendency towards increased abundance of foxes (lnRR$_{\text{Vulpes\_vulpes}}$ = 0.680, 95% CI = −0.271 to 1.632; if 83% CI was used, it would not cross zero). Finally, our meta-analysis confirmed that dingo removal was effective at reducing the abundances of dingoes (lnRR$_{\text{Canis\_dingo}}$ = −1.373, 95% CI = −2.067 to −0.678).

Table 4. Meta-analytic and meta-regression models of effects of dingo removal on all species, including dingo. M – point estimates (mean) for intercepts; CI.lb – 95% confidence interval lower bounds; CI.ub – 95% confidence interval upper bounds; I^2 – total heterogeneities for each model. Estimates that are significantly different from zero (95% confidence intervals not spanning zero) are highlighted in bold

Model	M	CI.lb	CI.ub	I^2 (%)
Meta-analytic mean	−0.132	−0.749	0.486	98.8
Phylogenetic meta-analytic mean	−0.145	−1.051	0.761	99.0
Meta-regression with species				
Tachyglossus aculeatus	1.330	−0.544	3.205	
Notomys alexis	−0.389	−3.035	2.257	
Notomys fuscus	**−2.192**	**−3.735**	**−0.648**	
Mus musculus	−2.158	−4.796	0.479	
Rattus fuscipes	−0.960	−3.601	1.682	
Oryctolagus cuniculus	0.306	−1.032	1.644	
Capra aegagrus hircus	0.401	−2.245	3.047	
Sus scrofa	−0.678	−3.329	1.973	
Equus africanus asinus	0.008	−2.638	2.654	
Canis dingo	**−1.373**	**−2.067**	**−0.678**	
Vulpes vulpes	0.680	−0.271	1.632	
Felis catus	0.077	−0.819	0.973	
Petaurus breviceps	−0.650	−3.291	1.992	
Trichosurus vulpecula	−0.919	−2.461	0.622	
Macropus rufogriseus	0.338	−1.583	2.259	
Macropus rufus	**2.464**	**1.457**	**3.471**	
Macropus giganteus	0.519	−0.711	1.749	
Wallabia bicolor	0.645	−2.080	3.371	
Antechinus stuartii	−0.866	−3.507	1.776	
Dasyuroides byrnei	−0.251	−2.897	2.395	
Sminthopsini spp	−1.181	−3.827	1.465	
Sminthopsis macroura	−0.240	−2.876	2.395	
Perameles suta	−0.976	−3.620	1.669	

Effects of fox removal on the abundance of mammals

In contrast to results from the dingo data set, fox removal, overall, resulted in increased abundance indices of other species present in the data set (lnRR$_{\text{overall}}$ = 0.737, 95% CI = 0.271 to 1.202; lnRR$_{\text{overall(phylo)}}$ = 0.704, 95% CI = 0.198 to 1.210; Fig. 1b, Table 5). We also observed high total heterogeneity in the meta-analytic models (with and without phylogeny = 87.5 to 87.7%; Table 5), validating exploration of potential moderators via meta-regression models.

Analogous to the meta-regression model for the dingo data set, we included animal weight and ecological type (herbivore, arboreal, mesopredator, and ground-dwelling) as moderators in meta-regression model. In contrast to the results of dingo removal, the effect of fox removal on other mammals was not related to their weight range (ß$_{\text{animal weight}}$ = 0.284, 95% CI = −0.138 to 0.706; Fig. 1b, Table 5). When effect sizes were plotted against animal weights, the largest positive effect sizes were clumped around intermediate values of species body weights (Fig. 2b). Arboreal and ground-dwelling animals responded to fox removal with increased abundance (lnRR$_{\text{arboreal}}$ = 1.168, 95% CI = 0.499 to 1.836; lnRR$_{\text{ground-dwelling}}$ = 0.673,

Table 5. Meta-analytic and meta-regression models of effects of fox removal on other species (native and non-native), excluding fox. M – point estimates (mean); CI.lb – 95% confidence interval lower bounds; CI.ub – 95% confidence interval upper bounds; I^2 – total heterogeneities for each model. Estimates represent intercepts, unless slope is specified in the brackets. Estimates that are significantly different from zero (95% confidence intervals not spanning zero) are highlighted in bold

Model	M	CI.lb	CI.ub	I^2 (%)
Meta-analytic mean	**0.737**	**0.271**	**1.202**	87.7
Phylogenetic meta-analytic mean	**0.704**	**0.198**	**1.210**	87.5
Meta-regression with animal weight and ecological type category				
Animal weight (slope)	0.284	−0.138	0.706	
Arboreal	1.168	0.499	1.836	
Ground-dwelling	0.673	0.090	1.256	
Herbivore	0.671	−0.062	1.405	
Mesopredator	0.659	−0.246	1.564	

Table 6. Meta-analytic and meta-regression models on effects of fox removal on native species. M – point estimates (mean); CI.lb – 95% confidence interval lower bounds; CI.ub – 95% confidence interval upper bounds; I^2 – total heterogeneities for each model. Estimates represent intercepts, unless slope is specified in the brackets. Estimates that are significantly different from zero (95% confidence intervals not spanning zero) are highlighted in bold

Model	M	CI.lb	CI.ub	I^2 (%)
Meta-analytic mean	**0.758**	**0.298**	**1.218**	**83.0**
Phylogenetic meta-analytic mean	**0.760**	**0.276**	**1.243**	**83.1**
Meta-regression with animal weight category				
Above CWR	0.571	−0.134	1.276	
CWR	**0.841**	**0.296**	**1.387**	

Table 7. Meta-analytic and meta-regression models of effects of fox removal on all species, including fox M – point estimates (mean) for intercepts; CI.lb – 95% confidence interval lower bounds; CI.ub – 95% confidence interval upper bounds; I^2 – total heterogeneities for each model. Estimates that are significantly different from zero (95% confidence intervals not spanning zero) are highlighted in bold

Model	M	CI.lb	CI.ub	I^2 (%)
Meta-analytic mean	**0.537**	**0.096**	**0.978**	90.4
Phylogenetic meta-analytic mean	0.440	−0.142	1.023	90.3
Meta-regression with species				
Tachyglossus aculeatus	1.471	−0.527	3.469	
Rattus fuscipes	−0.023	−1.152	1.107	
Rattus rattus	−1.324	−3.338	0.690	
Lepus europaeus	0.343	−1.655	2.341	
Oryctolagus cuniculus	0.004	−0.978	0.987	
Vulpes vulpes	**−1.116**	**−1.833**	**−0.398**	
Felis catus	0.619	−0.328	1.567	
Petaurus breviceps	0.105	−1.909	2.119	
Pseudocheirus peregrinus	0.843	−0.524	2.210	
Trichosurus vulpecula	**1.547**	**0.788**	**2.306**	
Bettongia ogilbyi	1.271	−0.231	2.774	
Potorous tridactylus	**1.364**	**0.063**	**2.666**	
Macropus eugenii	**1.561**	**0.059**	**3.064**	
Macropus rufogriseus	0.666	−1.333	2.664	
Macropus robustus	0.735	−1.264	2.733	
Macropus giganteus	0.584	−0.763	1.932	
Wallabia bicolor	0.458	−0.674	1.590	
Petrogale lateralis	**1.501**	**0.360**	**2.642**	
Vombatus ursinus	−0.257	−2.279	1.765	
Antechinus stuartii	0.098	−1.916	2.112	
Isoodon obesulus	1.033	−0.068	2.135	
Perameles nasuta	0.283	−1.084	1.650	

95% CI = 0.090 to 1.256; Fig. 1b, Table 5), while there were no statistically significant effects on herbivores and mesopredators (cat data only). However, the mean effect on cats was medium–large and had a wide CI (lnRR_{cat} = 0.612, 95% CI = −0.246 to 1.564), suggesting that fox removal is likely to result in increased cat abundance indices, although this effect varies between locations. Notably, if 79% CI was used, it would not cross zero.

Fox removal resulted in overall increases in abundance indices when analyses were performed on native species only ($\text{lnRR}_{\text{overall}}$ = 0.758, 95% CI = 0.298 to 1.218; $\text{lnRR}_{\text{overall(phylo)}}$ = 0.760, 95% CI = 0.276 to 1.243; Fig. 1b, Table 6). The species included in this data subset represented only two of three weight categories; there were no under CWR species. The increased species abundance was especially clear for native species from the CWR category (lnRR_{CWR} = 0.841, 95% CI = 0.296 to 1.387; Fig. 1b, Table 6) and was smaller and not statistically significant for the above CWR category species ($\text{lnRR}_{\text{aboveCWR}}$ = 0.571, 95% CI = −0.134 to 1.276; Fig. 1b, Table 6), although the difference between these two weight categories was small and statistically similar to zero ($\text{lnRR}_{\text{aboveCWR-CWR}}$ = 0.270, 95% CI = −0.469 to 1.009).

Lastly, we noted three species with the strongest increase in abundance indices in the fox removal data set: the common brushtail possum *Trichosurus vulpecula*, the long-nosed potoroo *Potorous tridactylus*, and the black-flanked rock wallaby *Petrogale lateralis*; all with a mean effect size per species of above 1.3 (Fig. 3b, Table 7). Fox removal treatments effectively reduced the abundance indices of foxes ($\text{lnRR}_{\text{Vulpes\_vulpes}}$ = −1.116, 95% CI = −1.833 to −0.398).

Publication bias

We found no evidence of publication bias in dingo removal or in fox removal data sets, when we considered three different approaches to assessing publication bias: 1) the funnel plots (Fig. 4) bear no distinct visual asymmetry; 2) Egger's regression tests did not identify significant asymmetry in the dingo funnel plots of the residuals (t_{69} = −1.252, P = 0.215) and provided evidence for asymmetry in the fox removal data set (t_{52} = 2.895, P = 0.005); and 3) the trim-and-fill analyses found no missing effect studies on the right side of the fox data distributions and 18 for the dingo data set. Such a pattern may not be indicative of publication bias in highly heterogeneous data sets, such as ours.

DISCUSSION

The results of our meta-analysis provide evidence that lethal control of dingoes and lethal control of foxes have different outcomes for other mammal species. The results showed that the effects of removing dingoes and foxes both scaled with the body size of potential prey species, but in different ways. Removal of dingoes had a negative

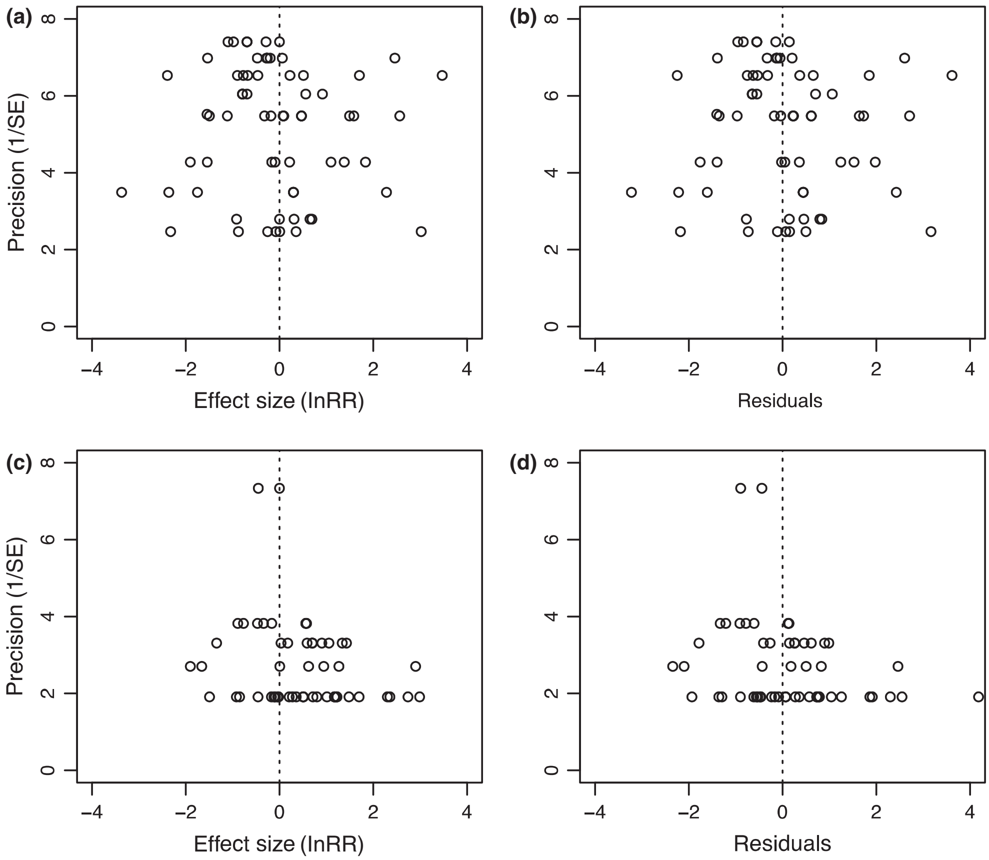

Fig. 4. Funnel plots used to estimate publication bias in the dingo and fox removal data sets. (a) Effect size estimates from the dingo removal data set plotted against their precision; (b) residual effect sizes from the intercept model (phylogenetic meta-analysis) for the dingo removal data set; (c) effect size estimates from the fox removal data set plotted against their precision; (d) residual effect sizes from the intercept model (phylogenetic meta-analysis) for the fox removal data set. Dashed vertical line indicates no effect.

effect on the abundance of native mammals weighing less than the CWR, but mammals weighing more than the CWR increased in abundance where dingoes were removed. On average, dingo removal had no effect on CWR mammals. In contrast, fox removal had a strong positive effect on the abundance of CWR mammals. Arboreal and ground-dwelling mammals responded positively to fox control. Other key findings were that lethal control of dingoes did not have a significant effect on the abundance of cats, but where dingoes were removed there was a tendency for fox abundance to increase, and where foxes were removed there was a tendency for cat abundance to increase.

Our finding that the abundances of mammal species respond in different ways to the lethal control of dingoes and foxes has important implications for biodiversity conservation programmes. In much of Australia, CWR mammals and mammals weighing less than the CWR have become endangered or extinct due to predation by introduced predators (Woinarski et al. 2015, Doherty et al. 2016). To counter the threat posed by introduced predators for native mammals, wildlife agencies have invested considerable effort and funds in programmes in which poison baits are distributed in order to control populations of foxes and dingoes (Fleming 1996, Robley et al. 2014). However, our results suggest that population control programmes directed towards dingoes and foxes have different outcomes for mammal assemblages. It is important to note that most fox control programmes were undertaken in areas where dingoes were rare or absent (Appendix S4) due to the persecution of dingoes by people. The absence of dingoes from sites where poison baiting was targeted towards foxes was evidenced in our results by the absence of dingo abundance as a response variable in studies reporting the effects of fox control programmes. Thus where fox control programmes were conducted, foxes were the apex predator.

On average, the abundance of CWR mammals increased in response to fox control, but CWR mammals showed on average no response to the removal of dingoes. In addition, the abundance of heavy mammals increased and that of light mammals decreased in response to dingo control. We suggest that the disparate responses of CWR mammals and above CWR mammals to dingo and fox removal programmes reflect the different dietary preferences of the predators. CWR mammals are within the optimal prey weight range for foxes (Johnson et al. 2007, Dexter & Murray 2009), but are preyed on less frequently by dingoes (Cupples et al. 2011, Spencer et al. 2014, Davis et al. 2015), and thus may be expected to benefit from fox removal (Saunders et al. 2010, Robley et al. 2014). Similarly, above CWR prey are within the preferred prey weight range for dingoes (Newsome et al. 1983), and thus may be expected to benefit from dingo removal (Colman et al. 2014). Indeed, our results demonstrated that above CWR mammals occur at greater abundances where dingoes have been controlled. Increased abundance of kangaroos and wallabies is an unintended and perverse outcome of dingo control programmes, because these animals compete with livestock for pasture (Caughley 1987, Prowse et al. 2015). To reduce the impacts of kangaroos and wallabies on livestock, culling is undertaken throughout Australia, particularly in areas where dingo populations have been suppressed (Gilroy 1999, Fillios et al. 2010). We recommend that further studies are undertaken to compare the net cost to graziers resulting from controlling dingoes to mitigate stock losses with the cost associated with the irruption of native grazing species resulting from dingo control.

The results of our meta-analysis showed that below CWR mammals responded negatively to the removal of dingoes, but no studies were available to examine the response of below CWR mammals to fox removal. Previous studies have attributed declines in small mammal abundances in areas where dingo populations were controlled to indirect effects resulting from dingo control (Letnic et al. 2009a,b). It has been theorised that red foxes and cats increase in abundance where dingoes are controlled and, as a consequence, their predatory impacts on small mammals increase (Ritchie & Johnson 2009, Letnic & Dworjanyn 2011). It has also been theorised that small mammals benefit from dingoes' suppressive effects on kangaroos, and that when dingoes are controlled, overabundant kangaroo populations destroy habitat and food resources required by small mammals (Colman et al. 2014). The findings of our meta-analysis, that removal of dingoes did not have a significant effect on fox or cat abundance, but did have a positive effect on kangaroo abundance, lend support to the hypothesis that negative effects of dingo control on small mammal populations are due more to indirect effects arising from increased abundance of large herbivores than to mesopredator release (Morris & Letnic 2017, Rees et al. 2017).

Counter to the results of some field studies (Letnic et al. 2009b, Brook et al. 2012), our meta-analysis showed that, on average, dingo control had no significant effect on the abundances of foxes or cats. However, in the case of foxes, there was a moderate increase in abundance in response to dingo control that was significant if an 83% CI was used as the critical alpha value. One explanation put forward to explain the lack of responses by foxes to dingo control is that the primary method of control used in these studies was baiting, and it is well known that foxes also take poison baits laid for dingoes (Fleming 1996, Twigg et al. 2000). Thus, dingo removal may have no net effect on fox populations because lower fox mortality where dingoes have been removed may be offset by fox mortalities resulting from bait consumption (Fleming 1996). However, Johnson and VanDerWal (2009) demonstrated that for dingoes to suppress foxes effectively, dingo abundance needed to exceed a certain threshold level above which their populations are ecologically effective. The existence of such a threshold could help explain the large confidence limits around the effects of dingoes on foxes, and may be due to some studies being conducted in areas where dingo abundances in baited and unbaited areas were either above or below this threshold value, so that the authors did not make comparisons of ecologically effective vs. ecologically ineffective dingo populations.

Previous studies have found cats to show both positive and negative responses to dingo control, which was reflected in our meta-analyses as an overall neutral effect for cats. One explanation put forward to explain the pattern of cat responses to dingo control in previous studies is that cats may be subject to top-down effects by both dingoes and foxes and, thus, may benefit little if dingoes are removed, because foxes are still present in the landscape (Letnic et al. 2009a, Gordon et al. 2015). This explanation is supported by the results of our meta-analysis, which show that cat abundance tended to increase in response to programmes aimed at controlling foxes, which are generally conducted in areas where dingoes have been extirpated. This finding highlights a perverse outcome of fox control and adds weight to the idea that it may be necessary to implement cat control programmes at the same time and place as fox control programmes (Marlow et al. 2015a, Wayne et al. 2017).

In summary, our meta-analysis demonstrates that lethal control of dingoes and of foxes has different and unintended consequences for native and introduced mammals. The goal of dingo control is often to protect livestock, and sometimes CWR mammals (Twigg et al. 2000, Letnic et al. 2012), but it results in increased abundance of large mammals, a tendency for fox abundances to increase, declines in the abundance of small mammals, and it does not, on average, benefit CWR mammals. Fox control, which is primarily undertaken in areas where dingoes were rare or absent, on the other hand, benefits CWR mammals, but has the unintended effect of increasing the abundance of feral cats, which is an issue of great concern as cats have been highlighted as a major threat to many native mammals and birds (Woinarski et al. 2015, Gordon et al. 2017, Wayne et al. 2017).

Our results demonstrate different outcomes for other mammals depending on whether baiting is targeting dingoes or foxes. Land management agencies need to consider whether the goal of their baiting programme is for species recovery or livestock protection, because our results show that removing both dingoes and foxes has far-reaching impacts for multiple mammal species.

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SUPPORTING INFORMATION

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

Appendix S1. PRISMA diagram showing the process of discovery and elimination of publications for the fox removal dataset.
Appendix S2. PRISMA diagram showing the process of discovery and elimination of publications for the dingo removal dataset.
Appendix S3. Excluded full-text studies – fox removal dataset.
Appendix S4. Dingo distribution in Australia and locations of study sites.