University of
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THE EFFECTS OF CLUSTER FENCING ON NATIVE AND INTRODUCED FAUNA

A Thesis submitted by

Geoff Castle, MSc

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ABSTRACT

Apex predators may perform important ecological roles such as the regulation of herbivores and or mesopredators. Removal or loss of apex-predators is thought to cause negative effects for ecosystems, including mesopredator release which may facilitate cascading effects on species at lower trophic levels as predicted by the Trophic Cascade Hypothesis (TCH). Australia has one of the highest mammal extinction rates on Earth and is in a unique situation because the three largest mammalian carnivores are all introduced species. Dingoes (*Canis familiaris*) are expected by some to suppress foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) and indirectly alleviate predation pressure on smaller native fauna, although evidence for these processes remains equivocal. It is therefore critical that the ecological role of dingoes is better understood before potentially unreliable studies are used to inform predator management practices.

I conducted a comprehensive literature review of studies investigating dingo-mesopredator relationships. This review showed that most studies were correlative and therefore had little power to measure the causal roles of dingoes in ecosystems, highlighting the need to undertake better designed experiments. I support the use of stronger-inference studies that manipulate the abundance of dingoes in order to further elucidate the ecological role of dingoes in Australian ecosystems. I therefore undertook a stronger-inference manipulation experiment which removed dingoes from inside two closed (cluster fenced) systems in south-west Queensland where remotely sensed vegetation monitoring, sand plot passive tracking indices (PTI) and spotlight surveys were used to monitor the ecological outcomes of the sustained removal of an apex predator. Following the manipulation, I did not observe a mesopredator release of foxes or cats and I was unable to demonstrate negative relationships between dingoes and these sympatric predators, indicating that the mechanisms underpinning predicted mesopredator releases were absent. My experiments revealed no evidence of lower overall wildlife population abundances within the fences where dingoes were absent and that vegetation trends were almost identical inside and outside the fences. I concluded that although sympatric predators may interact negatively with each other on smaller spatiotemporal scales, these negative interactions did not scale-up to the population level or cause a mesopredator release.

I advocate that future experiments investigating the ecological role of the dingo should transcend the systemic and continued use of low-inference study designs currently being used to investigate the subject. More studies need to incorporate the essential elements of experimental design, especially the use of a measured treatment effect, randomisation and replication of treatments. Studies should also be conducted over longer time intervals (3-5 years), especially when conducted in arid ecosystems, which may also assist in disentangling bottom up and top down effects.

My findings align with other global predator manipulation studies and suggest that the negative effects of trophic cascades are unlikely to occur following the removal of the dingo.

CERTIFICATION OF THESIS

I Geoffrey Paul Castle declare that the Master's Thesis entitled [The Effects of Cluster Fencing on Native and introduced Fauna] is not more than 100,000 words in length including quotes and exclusive of tables, figures, appendices, bibliography, references, and footnotes.

This Thesis is the work of Geoffrey Paul Castle except where otherwise acknowledged, with the majority of the contribution to the papers presented as a Thesis by Publication undertaken by the Student. The work is original and has not previously been submitted for any other award, except where acknowledged.

Date: 30 June 2022

SUPERVISORS

Principal Supervisor: Professor. Geoff Cockfield,
Director (former)
Centre for Sustainable Agricultural Systems
University of Southern Queensland, Toowoomba

Co-supervisor: Dr. Benjamin L. Allen
Senior Research Fellow – Wildlife Research
Centre for Sustainable Agricultural Systems
University of Southern Queensland, Toowoomba

Student and supervisors signatures of endorsement are held at the University.

STATEMENT OF CONTRIBUTION

Paper 1:

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Paper 2:

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DEDICATION

This thesis is dedicated to

Dr David Suzuki
Whose motivating lecture at the Brisbane Power House in 2010 started me on this road.

&

To my dear wife Bernadette and our close friends for their unwavering support.

&

Last but not least, my father Brian who unfortunately did not live to see me finish this research project.

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PROVISIONS

1) Chapters 4 and 5 of this thesis have already been published. Chapter 3 has been formatted with the intention of publishing. As a result, some content may be repeated in multiple chapters.

2) Due to differences in formatting requirements of various journals and the University, there may be some minor stylistic differences between the contents of the unpublished chapters in this thesis and the corresponding published manuscripts. This has also resulted in some inconsistent formatting within this thesis.

3) The contributions of each co-author to each chapter have been listed in the Statement of Contribution section. Where no Author Contributions section is present, the entirety of that chapter's contents are attributed to G. Castle. The use of the pronouns "we" and "our" in the published chapters 4 and 5 reflect this.

4) All scientific species names within this document follow binomial nomenclature guidelines and are sourced from the Australian Faunal Directory (AFD) website (biodiversity.org.au/afd/home) or from the Mammal Diversity Database (mammaldiversity.org).

5) Ethical approvals to undertake the project were provided by the Queensland Department of Agriculture and Fisheries' Animal Ethics Committee (Approval numbers: CA 2016/10/1010, CA 2013/10/728, and CA 2018/10/1232) and the University of Southern Queensland's Animal Ethics Committee (Approval number: 16REA016). This study was completed in accordance with these approvals.

LIST OF ACRONYMS (ALPHABETICALLY LISTED)

i. AIC – Akaikes Information Criteria
ii. BP – Before Present
iii. BNT – Bridled Nailtail Wallaby
iv. CWR – Critical Weight Range
v. DBF – Dingo Barrier Fence
vi. DC–ITC – Dingo Control–Induced Trophic Cascade
vii. DNA – Deoxyribonucleic Acid
viii. ENSO – El Niño Southern Oscillation
ix. IUCN – International Union for Conservation of Nature
x. Kya – Thousand Years Ago
xi. MRH – Mesopredator Release Hypothesis
xii. mtDNA – Mitochondrial DNA
xiii. Mya – Million Years Ago
xiv. NSW – New South Wales
xv. PTI – Passive Tracking Indices
xvi. TCH – Trophic Cascade hypothesis
xvii. TGP – Total Grazing Pressure
xviii. TL – Thermoluminescence
xix. USQ – University of Southern Queensland
xx. YNP – Yellowstone National Park
xxi. 1080 – Sodium Fluoroecetate

CHAPTER 1: INTRODUCTION

The trophic cascade hypothesis is defined by a series of interactions that begin with apex predators and percolate through disturbed ecosystems (Ripple et al. 2016). This hypothesis is based on the keystone role played by apex predators (Wallach et al. 2015) claiming that their presence is essential for maintaining the structure and function of healthy ecosystems (Ritchie et al. 2012). The mesopredator release hypothesis (MRH) is a subset of trophic cascade theory and it predicts that the loss or removal of apex predators will result in an increase in the abundance of lower order predators (Crooks & Soulé 1999; Allen & Fleming 2012). For example, it has been postulated by many scholars that the introduced dingo suppresses the abundance of two other invasive mesopredators, the European fox and the feral cat (Letnic et al. 2009; Wallach et al. 2010; Letnic, Crowther, et al. 2011). It has been argued that the increase in mesopredator abundance occurs in response to the loss of suppression exerted by the apex predator (Prugh et al. 2009). Suppression is believed to occur via two mechanisms, the consumptive effects of direct killing (Kreplins et al. 2021) or the non-consumptive effects associated with competition for shared resources (Brown et al. 1999). Mesopredator release is a global phenomenon that has been well documented in the literature in both terrestrial and marine ecosystems. Swanson et al. (2014) reported the disappearance of African wild dogs (*Lycaon pictus*) from a Serengeti study area between 1966 and 1998 following a threefold increase in the lion (*Panthera leo*) population during the same period. Crooks and Soulé (1999) reported an increase in cats following the loss of coyotes (*Canis latrans*) in California. A seminal study by (Myers et al. 2007) reported significant increases in mesopredatory stingrays in Atlantic ecosystems following the declines in coastal shark populations which led to the decimation of a 100 year old scallop fishery.

TCH predicts that the removal of dingoes from within cluster fenced areas will result in significant increases in fox and cat density (Johnson et al. 2007), an eruption of large herbivores, concomitant declines in small native prey species (Ritchie & Johnson 2009) and reductions in plant biomass (Schmitz et al. 2000).

Evidence for mesopredator release following the decline of dingo populations in Australia, remains mixed and equivocal. Allen and Fleming (2012) concluded that dingoes are just as much a threat to native species as foxes and cats whereas other studies claim dingo presence is essential for protecting small native prey species (Letnic & Dworjanyn 2011; Schroeder et al. 2015). Some studies reported evidence that dingo presence suppressed fox populations (Cupples et al. 2011; Letnic, Ritchie, et al. 2012; Rees, Kingsford, et al. 2019), while others concluded that neither dingo presence or absence was a significant predictive variable of fox occurrence at the landscape scale (Mitchell & Banks 2005; Arthur et al. 2012). Multiple studies have concluded that dingoes suppress feral cats which may act as a buffer to protect native species (Johnson et al. 2007; Kennedy et al. 2012; Gordon et al. 2015), yet many other studies report that while there may be some fine scale avoidance, dingoes and cats predominantly co-exist within the landscape (Colman et al. 2014; Fancourt et al. 2019; Moseby et al. 2019).

Australia is in the unique ecological situation whereby all of the antecedent marsupial apex predators are extinct on the mainland (Black et al. 2012) and have been replaced with three introduced eutherian carnivores, the dingo, the European fox and the feral cat, that share virtually no evolutionary history with Australian endemic fauna (Strauss et al. 2006). Dingoes are a recent arrival that were introduced to Australia approximately 3 500 years ago (Woinarski et al. 2015) whereas cats and foxes, absent before European settlement, were released in the mid to late 19th century (Abbott 2002). Thirty four of Australia's native mammal species have gone extinct since 1788 with the primary cause being identified as predation from these three introduced carnivores (Woinarski et al. 2019). The touted mesopredator release of foxes and cats following the removal of the dingo has been suggested as a major possible cause of biodiversity loss within Australian ecosystems (Duffy et al. 2007; Letnic, Ritchie, et al. 2012; Ritchie et al. 2012). Given Australia's abysmal extinction record, it is unsurprising that investigating dingo-mesopredator relationships has become a major research priority for conservation managers and other stakeholders.

Netting fencing, such as the dingo barrier fence, has been used on a large scale in Australia to protect livestock from introduced carnivores for over 100 years (McKnight 1969). Due to the increasing density and distribution of dingoes inside the dingo barrier fence (DBF) over the last 20 years, there has been a resurgence of predator exclusion fencing called 'cluster fencing' in order to restore the viability of wool production (Chudleigh 2021). Cluster fences allow livestock producers to effectively manage both the total grazing pressure of herbivores and dingo predation upon their livestock (Smith et al. 2020). The construction of these fenced areas combined with the intensive level of lethal dingo control performed inside the enclosures, has created a landscape-scale opportunity to conduct classical predator manipulation experiments designed to elucidate the ecological role of the dingo that have thus far remained logistically prohibitive.

This thesis commences with a broad discussion of the impacts of the dingo since their introduction into Australian ecosystems (Chapter 2). It then examines the current state of MRH research through a critical review of 37 empirical studies published between 2011–2022 (Chapter 3). The review identified several gaps in the knowledge and recommendations for future predator research that could be assessed using cluster-fenced systems engaging in lethal predator control inside the fenced areas. We performed a major study within two such systems that first investigated if a mesopredator release occurred (Chapter 4), before examining the responses of prey species following dingo removal (Chapter 5). Finally, in chapter 6, I holistically discuss the overarching implications of these results obtained from each of these chapters in concert.

CHAPTER 2: BARKING UP THE WRONG TREE! ARE DINGOES REALLY TROPHIC REGULATORS OR JUST ANOTHER INVASIVE PEST SPECIES?

Abstract

Australia has one of the highest mammal extinction rates on Earth, with over 30 endemic mammals going extinct since European settlement in 1788. Approximately 20% of Australia's extant mammalian fauna are threatened with extinction and have experienced significant reductions in abundance and loss of their former distribution, with seven mainland species now persisting only on small offshore islands. Ground foraging native mammals in the critical weight range 35–5500g (CWR) are most vulnerable to extinction because their small body mass predisposes them to predation by feral cats, foxes and dingoes. There has been a growing recognition over the past few decades that apex predators may play a crucial role in maintaining healthy ecosystems by suppressing sympatric predators and large herbivores. This paradigm has fuelled calls to use apex predators as biological conservation tools via the mechanisms of carnivore conservation and reintroductions. Unfortunately, these calls are largely supported by studies that suffer from weaknesses in experimental design that greatly diminish the reliability of their claims. This review summarises the reliability of the empirical research published between 2011–2022 that investigated dingo-mesopredator relationships in Australian ecosystems, and examines the implications of the scientific findings for predator management decisions. We found that 31 of the 37 studies assessed contained significant experimental weaknesses demonstrating that the currently available research investigating the functional role of the dingo remains confounded, and that most of the findings remain unreliable, ambivalent and inchoate. Given that this conclusion was reached in a previous review conducted in 2011, we concluded that minimal progress has been made in

improving the experimental design of the field experiments conducted over the last decade. There have been many calls from the literature advocating the need to conduct more predator manipulation experiments in order to elucidate the true ecological role of dingoes. The consequences of forming conservation decisions based on poor science could result in even more extinctions of native fauna. My findings therefore suggest the precautionary principle should be applied before using dingoes as conservation tools until more robust predator manipulation experiments have been conducted to better study dingo-mesopredator relationships.

Section 1

Global livestock/agriculture production

The inexorable growth in human population has resulted in the global livestock/agricultural sector becoming the largest human land-use system utilising 30% of the planet's non-barren, ice-free surface (Herrero et al. 2013). Over 4 billion sheep *(Ovis aries)*, goats *(Capra hircus),* cattle *(Bos Taurus)* and pigs *(Sus scrofa)* are now farmed by humans worldwide (Robinson et al. 2014). Global biodiversity loss is accelerating with the rate of species extinctions now exceeding the background rate by two-three orders of magnitude (Barnosky et al. 2011). Up to 80% of the world's large terrestrial carnivore populations are experiencing acute decline (Wolf & Ripple 2018) primarily due to habitat loss and human conflict, especially livestock related conflict, which is tolerated by few human societies. The global livestock herd now comprises 20% of the entire terrestrial biomass (Krausmann et al. 2008) and the insatiable demand for animal products is driving the rapid conversion of old growth forests into livestock pastures (Walker et al. 2009).

Global biodiversity is in decline as humans commandeer more and more of Earth's natural resources (Butchart et al. 2010) and large apex predators, characterized by low densities and low reproduction rates, have increasingly become more vulnerable to anthropogenic stressors (Palazón 2017). It has been argued that apex predators play a crucial role in the structure and function of ecosystems (Crooks & Soulé 1999; Beschta & Ripple 2009). Therefore, in order to prevent the negative cascading effects predicted from the loss of apex predators, the mitigation of human-predator conflict has become a global priority for conservation biology (Castle et al. 2021) .

Livestock predation /conflict

Humans have a history of conflict with apex predators that spans millennia (Prugh et al. 2009). Conflicts can occur for a number of reasons including direct killing of livestock or pets (Miller et al. 2015), threats to human life (Dickman et al. 2011), destruction of crops and property (Treves 2009) or a loss of prey base (Wolf & Ripple 2016). These predator-human conflicts, driven mostly by the global demand for livestock, have now pushed many apex predators to the brink of extinction (Ripple et al. 2014). For example, African lion *(Panthera leo)* populations have declined by approximately 50% (Bauer et al. 2015) and experienced a range contraction of over 75% in the last 30-40 years (Everatt et al. 2019). The proximate causes in this case being the expansion of human land usage, especially agriculture (Riggio et al. 2013) and retaliation for the depredation of livestock (Woodroffe & Frank 2005) both real and perceived. The disruption of intraguild predation amongst sympatric carnivores potentially changes the densities of mesopredators and prey species and has been identified as an underlying driver of biodiversity loss (Crooks & Soulé 1999; Terborgh et al. 2001; Beschta & Ripple 2009).

The biological characteristics of apex predators often create conservation challenges due to their proclivity for preying on human livestock and wild game (Treves & Karanth 2003; Smith et al. 2020). Despite this obvious dilemma, governments around the world have implemented various predator-control initiatives designed to reduce livestock predation (Berger 2006), which has often led to the decline and local extirpation of predators (Dickman 2010). In response, a primary non-lethal control strategy gathering momentum has been the use of predator-exclusion fencing.

Fences

Exclusion fences have been utilised globally to physically exclude predators and large herbivores from livestock grazing areas in order to ameliorate predation and or competition and minimise the economic impact of stock and crop losses (Smith et al. 2020). For example, wire netting fences have been used in Australia for over 100 years to exclude dingoes from sheep grazing properties (McKnight 1969). The most famous being the 5,614 kilometre long DBF which helps prevent the migration of dingoes into the pastoral areas of Southern Queensland, New South Wales, Victoria and South Australia, and the 1,206 km State Barrier Fence protecting south-west Western Australia (Fleming et al. 2001). Exclusion fencing has also been used to control herbivores and has been used around some villages in the Niassa Game Reserve in Mozambique to prevent elephants from destroying local croplands (Osborn & Anstey 2002). The fencing can do more than just limit interactions between predators, prey and livestock (Boone & Hobbs 2004), it can also exclude invasive species from critical habitat needed by endangered species and thus create refuges suitable for conservation reintroductions (Moseby & Bice 2004), such as the Arid Recovery Program in South Australia (Royston 2010) where dingoes, foxes and feral cats have been excluded.

Programs focussed on the lethal control of predators can therefore be at odds with conservation biology (Shivik et al. 2003) and optimum strategies chosen to prevent livestock depredation should also benefit wildlife conservation where possible (McManus et al. 2015). The need for sustainable predator-management has been fuelled by the growing awareness that the loss of predators may lead to ecosystem degradation and biodiversity losses (Myers et al. 2007; Estes et al. 2011). Some have suggested the collective intolerance of carnivores, and the selection of strategies where eradication is the essential objective, is an evolutionary hangover from the time when humans occupied the vulnerable position of being the prey species (Breitenmoser 1998).

Predator Management Practices

One of the oldest forms of wildlife management has been the direct killing of predators which has been a hallmark of human development worldwide (Reynolds & Tapper 1996). This long history of anthropogenic persecution is strongly linked to the extirpation of apex predators. For example, wolves *(Canis lupus)* were killed over 2 500 years ago in ancient Greece to protect human livestock (Berger 2006). Numerous studies have documented human-predator conflicts including snow leopards *(Panthera uncia)* in Pakistan (Hussain 2003), African wild dogs *(Lycaon pictus)* in sub-Saharan Africa (Swarner 2004), Andean bears *(Tremarctos ornatus)* in South America, Hyenas *(Crocuta crocuta)* and lions *(Panthera leo)* (Kolowski & Holekamp 2006) in Africa and dingoes in Australia (Allen & Sparkes 2001).

Growing recognition of the ecological, ontological and economic value of apex predators has fuelled the worldwide impetus for predator conservation (del Rio et al. 2001) and the development of a suite of non-lethal methods of mitigating predator-livestock conflict (Shivik 2004; Du Plessis et al. 2018; Smith & Appleby 2018). Such methods of managing predator-livestock conflicts include livestock guardian dogs, predator relocation, night confinement, exclusion fencing (including electrified enclosures) and audio and visual deterrents (Van Eeden et al. 2018).

Section 2

Australian livestock production

Sheep, goats and cattle arrived in Australia with the first fleet on 24 January 1788 (Parsonson 1998) and by 1860 there were more than 15 million sheep and 4 million cattle in the new colony (Henzell 2007). In the 2019–2020 financial year, Australia had almost 25 million cattle, 64 million sheep and lambs and slaughtered 1.6 million goats for exportation (Australian Bureau of Statistics 2021).

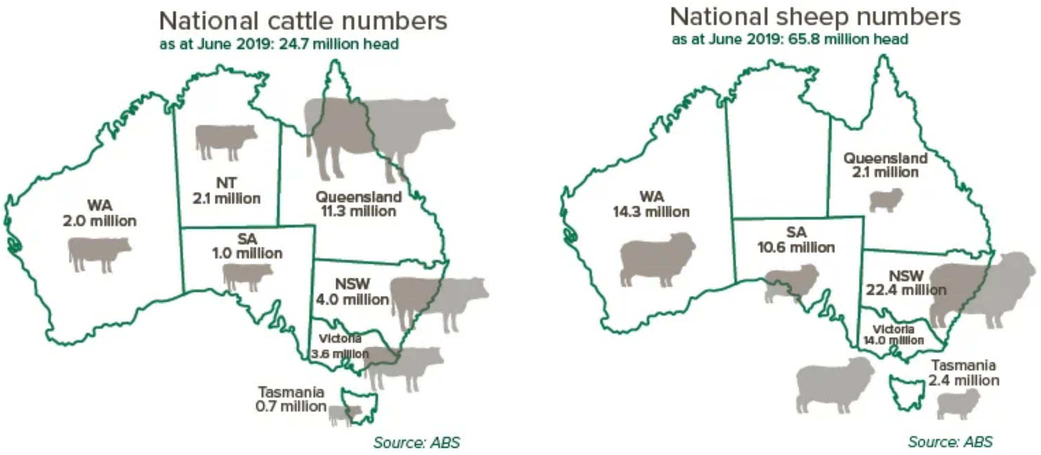

Figure 2.1 National cattle and sheep numbers for 2018–2019 financial year. Source ABS.

In the 2018–2019 financial year the Australian livestock industry turnover was $72.5 billion and employed over 434 000 people (Meat and Livestock Australia 2020). Queensland has been a significant livestock region for over 170 years and continues to be a productive area for sheep, goat and cattle grazing (Allen 2011). Goats were once barely tolerated and viewed as feral herbivores that competed with sheep and cattle for pasture and facilitated land degradation through over-grazing on trees and shrubs (Maas 1998). Today, however, they are grazed alongside sheep and are perceived as a lucrative stock animal (Khairo et al. 2013; Hacker & Alemseged 2014). Sheep numbers have however been declining rapidly in Queensland since 1990 and increased predation from dingoes reinvading regions inside the dingo barrier fence DBF has been identified as a key factor (Allen & West 2013, 2015).

Central and western Queensland has been an important sheep, goat and cattle producing region since the 1850's (Allen 2011).

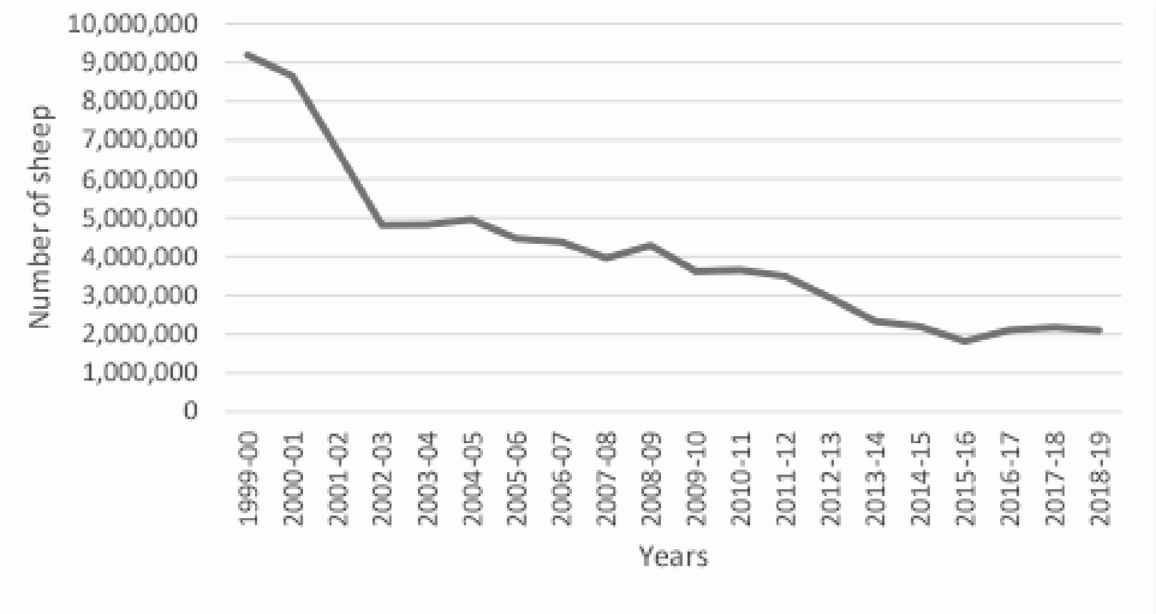

Figure 2.2 Total sheep numbers for Queensland between 1999–2018.
Source: (Chudleigh 2021).

Figure 2.3 Long term sheep numbers for Queensland 1885-2015. Source: (Chudleigh 2021).

Figure 2.2 shows a precipitous decline in the Queensland sheep herd since the year 2000 for which a partial attribution has been the increase in density and distribution of dingoes inside the DBF (Chudleigh 2021).

Figure (2.3) shows that the current Queensland sheep herd is the lowest since records commenced in 1885. A sharp decline in post 1965 sheep numbers can also be seen in figure (2.3) and is attributed firstly to changing economic conditions within the industry and secondly to predation from dingoes (Chudleigh et al. 2011). Following the demise of the wool reserve price scheme in 1991, a downturn in the wool industry and the financial burden of predator management saw many graziers inside the DBF switch from sheep to cattle (Allen & Sparkes 2001). High maintenance contiguous private netting fences around individual properties inside the DBF that once restricted dingo movements throughout the landscape were abandoned by many cattle producers (Allen & Sparkes 2001), along with broad scale reduction in wild dog control (Agriculture and Environment Commitee 2017). The Queensland government further attributed the success of Sodium fluoroacetate (1080) baiting which led to a complacency in fence maintenance, damage to the fence by floods and fire and the need to rebuild older sections of the fence as further reasons for increasing dingo predation (Department of Agriculture and Fisheries 2019). Degradation of the DBF was already flagged in the early 1970's and by 1982, check fences were being constructed to ameliorate permeability issues in the DBF (Biosecurity Queensland 2019). Finally, by 2015, the construction of cluster fences became a necessary strategy for any livestock producers in Queensland that wished to continue sheep production (Castle et al. 2021). Furthermore, the recent Agriculture and Environment Committee's inquiry into barrier fences in Queensland stated that the considerable population of dingoes existing inside the protected area made it hard to justify claims that a difference in dingo density actually existed on either side of the DBF

(Agriculture and Environment Commitee 2017) despite claims from a number of studies to the contrary (Letnic & Dworjanyn 2011; Gordon & Letnic 2016; Morris & Letnic 2017; Contos & Letnic 2019).

Numerous studies conducted either side of the DBF claim that dingo density inside the fence is so impoverished that sheep can be grazed with little threat from dingoes (Letnic & Dworjanyn 2011; Gordon & Letnic 2016; Contos & Letnic 2019; Feit et al. 2019), for which all of them cite the 52 year old anachronous study from McKnight (1969) which does not reflect the contemporary situation. Notwithstanding these claims, the reality is that in order to remain commercially viable, sheep producers have been forced to spend millions of dollars on the erection of dingo exclusion fencing or 'cluster fencing' around the perimeter of their properties (Smith et al. 2020), including properties inside the DBF where dingoes have been described as rare (Letnic & Dworjanyn 2011; Gordon, C.E. et al. 2017; Gordon, Christopher E et al. 2017; Morris & Letnic 2017), virtually absent (Feit et al. 2019) and 'functionally extinct' (Rees et al. 2017; Rees, Kingsford, et al. 2019; Rees, Rees, et al. 2019).

Whatever the functions of dingoes are, they are clearly not 'functionally extinct' enough to lose their function as an agent of rapid sheep decline (Allen & West 2013, 2015).

Dingo impacts on livestock

It has been suggested that dingoes are a naturalised invasive species in Australia (Brawata & Neeman 2011; Steindler et al. 2018) while others embrace the chimera that dingoes have lived in harmony with native Australian fauna for the last 3 500 years with minimal to no detrimental effect (Wallach et al. 2009). This debate rages and the taxonomic status of dingoes remains controversial and clouded through their hybridization with feral dogs (Crowther et al. 2014). This apparent 'dingo dichotomy' does not change the fact that mitochondrial DNA analysis shows that dingoes originated from a population of East Asian dogs (Savolainen et al. 2004) and thus are wild living descendants of domesticated dogs and so are by strict definition, feral animals (Allen & Fleming 2012). It is therefore hard to reconcile the utopian view that the ascendancy of an invasive mesopredator to the role of a keystone apex predator has not been problematic when it epitomizes the phenomena of shifting baselines syndrome (Soga & Gaston 2018).

Despite their reported function as apex predators, dingoes are also regarded by some as an introduced pest (Allen & Sparkes 2001; Allen & West 2013). This is reflected by numerous state Acts, such as the *Land Protection (Pest and Stock Route Management) Act 2002*, that declare dingoes as pests in agricultural areas and that landowners are obliged to control, (a euphemism for kill), them. Dingoes, foxes and feral cats, have had devastating effects on Australian livestock and native species through direct killing, the infliction of injuries and the spreading of zoonotic diseases (Jenkins et al. 2000; Allen & Fleming 2004; Allen & West 2013). All three have also been implicated in the precipitous extinction of native animals, and all three are subject to control measures designed to mitigate further impact (Dickman 1996). McLeod (2016) estimated the economic impact of dingo predation alone to Australia's agricultural sector was somewhere between 60 and 110 million dollars every year, while foxes inflicted 230 million in costs annually. Similarly, Legge et al. (2020) found that transmission of *Toxoplasma gondii* from feral cats to sheep cause spontaneous abortion rates that kill 62 300 lambs annually at an estimated cost of just under $10 million.

Figure 2.4 Injuries caused by dingoes to weaners on a cattle property outside the Tambo cluster fence, but inside the DBF where dingoes are described as ‘rare’ and ‘functionally extinct’ (Morris & Letnic 2017). Source: (Geoff Castle 2019).

In order to help mitigate these stock losses, the construction of cluster fences inside the DBF has been a necessary and expensive process for graziers who wished to reduce the pernicious dingo predation upon their sheep since 2015. For example, one of my study sites at Morven has a perimeter fence length of 424 kilometres which cost just under $3 million dollars to fence.

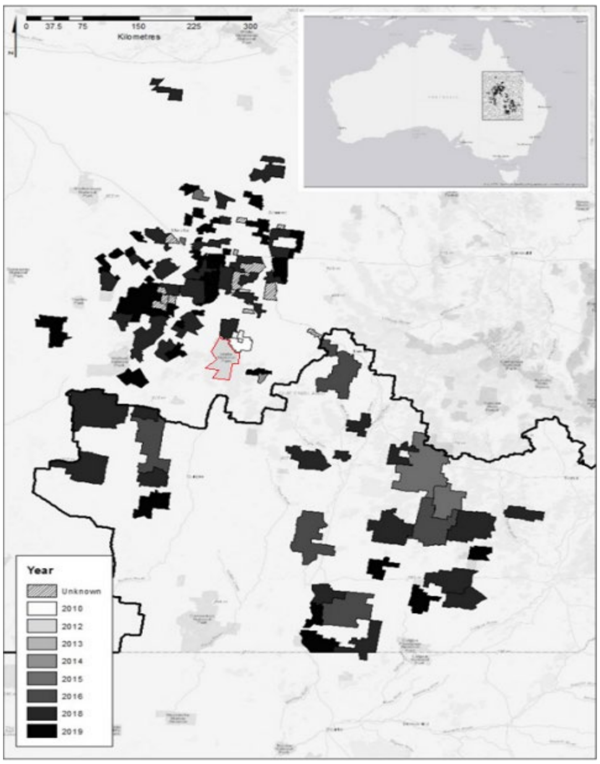

Figure 2.5 Map showing fund assisted Cluster fences highlighted as constructed inside the DBF (black line) since 2015 in response to increased wild canid predation rates. Source: (Smith et al. 2020).

Cluster fencing

Exclusion fencing has been used on a small scale in Australia to protect threatened endemic species from introduced carnivores such as dingoes, cats and foxes (Hayward & Kerley 2009). While rudimentary netting fences have been used in Australia to exclude dingoes from livestock properties for over 100 years (McKnight 1969), upgraded pest exclusion fencing called ‘çluster fencing’ has recently been deployed on large spatial scales to reduce the negative impacts of dingo predation on Queensland livestock properties, especially sheep grazing properties inside the DBF (Allen & West 2013; Smith et al. 2020; Castle et al. 2021). The erection of cluster fences began at Morven and Tambo in 2013 and were completed in 2015 (Smith et al. 2020). The Queensland Feral Pest Initiative has provided $19.7 million dollars in subsidies since 2015 to assist multiple private landholders with the construction of cluster fencing around the perimeter of their adjoining properties (Chudleigh 2021). By the end of 2019 there were approximately 105 cluster fenced areas in Queensland alone which enclose more than 66 000 km^2 of livestock grazing land (Smith et al. 2020). Cluster fences allow land managers to suppress dingo predation on stock to very low levels and better manage the total grazing pressure (TGP) of their properties though the control of native and exotic herbivores, such as *Macropus spp*., and feral pigs (Smith et al. 2020).

The construction of these ‘clusters’, which are essentially dingo-proof enclosures, has provided an unprecedented opportunity to suppress the apex predator and control their immigration over massive spatio-temporal scales, ie Tambo having an area of 2,265 km^2 and Morven 3,763 km^2. Cluster fences are built with the intention of eradicating dingoes from inside the broader cluster fenced areas and prohibiting their post-control reinvasion from the outside. According to Allen (2009), hundreds of dingoes from dozens of packs would be extant in cluster regions of this size based on dingo home range data collected prior to the erection of these fences. These estimates are similar to those reported in (Castle et al. 2021) who documented the removal of 906 dingoes from inside the Morven cluster and over 250 from inside the Tambo cluster during their study.

Clusters are typically encircled by 1.5 metre tall pre-fabricated ring-lock or hinge-joint wire mesh with a 300 mm ground skirt extended toward the ‘outside’ to prevent wild dogs burrowing under the fence. The lower 500 mm of the mesh consists of rectangles measuring 160 mm X 100 mm and the upper portion of the fence consists of 160 mm squares. Fences are built to a total height of 1800 mm by adding top strand(s) of barbed wire. The average cost of these fences is ~ $7000 per kilometer, half of which is government subsidized (Cockfield et al. 2018).

Figure 2.6 A typical section of dingo–proof exclusion fence (Source G. Castle 2021).

Although the fence is considered a highly effective barrier preventing post-control reinvasion, temporary damage induced by flooding or holes created by large herbivores can allow occasional, brief opportunities for dingoes to re-enter the cluster (Castle et al. 2021).

Dingo control

1080 baiting has been used in Australia since the 1950's and remains the preferred method for reducing depredation upon livestock by invasive mammalian predators such as dingoes, foxes and to a lesser extent feral cats over large scales (Allen & Sparkes 2001).

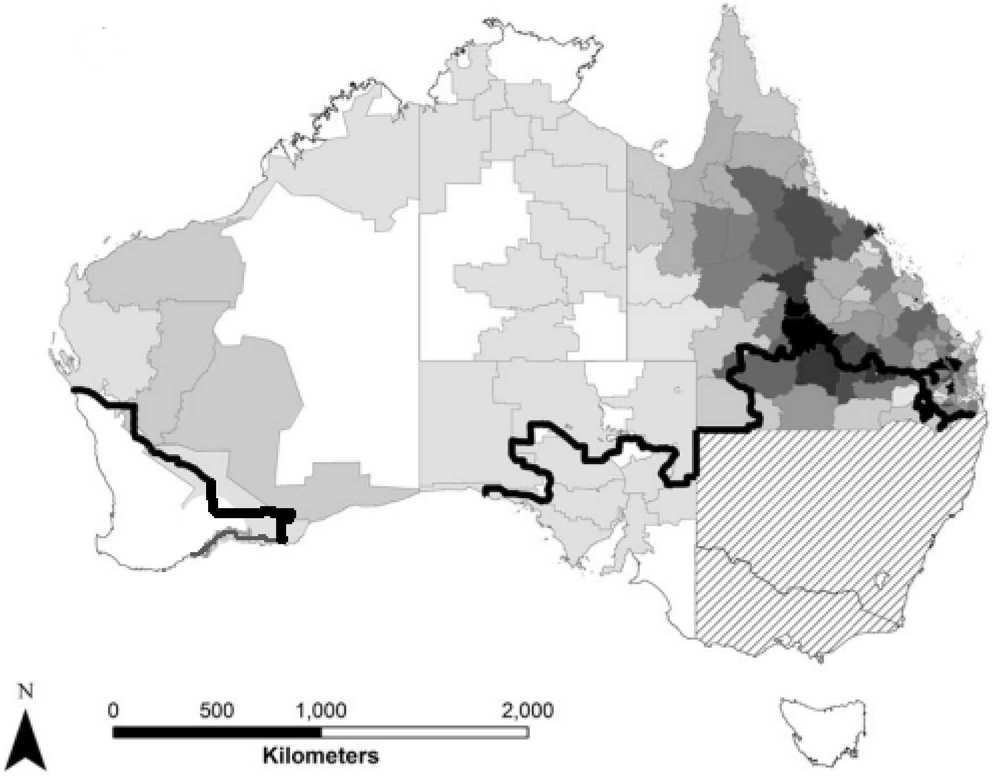

Figure 2.7 Map of Australia showing the location and intensity of lethal dingo control using 1080.
Hatched areas (no data), white areas (no lethal control), pale grey to black areas (increments of 0.5 baits/km2/year up to 4.5 baits/km2/year, then >4.5 baits/km2/year). (Source: (Allen et al. 2015).

Other methods used to mitigate dingo predation on livestock include exclusion fencing, guardian animals, shooting and trapping Figure 2.8).

Figure 2.8 Common strategies used by graziers to ameliorate dingo predation on livestock. A–exclusion fencing, B– guardian animals, C–poison baiting, D–trapping and E–Opportunistic shooting. (Photos source G. Castle 2021).

Trophic cascades

The TCH has been defined as indirect species interactions beginning with apex predators that filter downward through food webs in destabilised ecosystems (Ripple et al. 2016). Essentially, the hypothesis itself is based on how apex predators may structure entire ecosystems through their interactions with their prey (Ripple et al. 2016). It has been argued that predators at high trophic levels suppress the abundance of species at lower trophic levels, including mesopredators and herbivores (Hairston et al. 1960), and that a loss of this suppression induces 'mesopredator releases' leading to decreases in small prey abundance and potential changes in plant biomass (Ripple et al. 2016).

This suppression is thought to occur through top-down direct predatory interactions with herbivores and mesopredators (Kreplins et al. 2021) and non-consumptive effects, such as behavioural changes in response to predation risk that can lower the fitness of species at lower trophic levels (Brown et al. 1999). For example, Contos and Letnic (2019) argued that suppression of dingoes triggered a ≥ 4 link trophic cascades such that when dingo abundance decreased, fox abundance increased which then drove a decline in the abundance of the native prey of mesopredators such as dusky hopping mice (*Notomys fuscus*) and lizards *(Veranus gouldii).* Arthropod assemblages were hypothesized to increase through the loss of small insectivores which released arthropod communities from predation or, shifts in vegetation that improved the suitability of habitat for arthropods.

TCH predicts that the removal or loss of top-predators such as dingoes, from inside the cluster fences, may trigger trophic cascades through herbivorous *Macropus spp*. and vegetation (Morris & Letnic 2017), and also through foxes, cats and small native prey species (Letnic, Ritchie, et al. 2012). The fundamental tenet underlying this hypothesis is that trophic cascades must involve indirect effects such that the impact of one species on another species requires the presence of a third intermediary species (Wootton 1994). (See Fig 2.9)

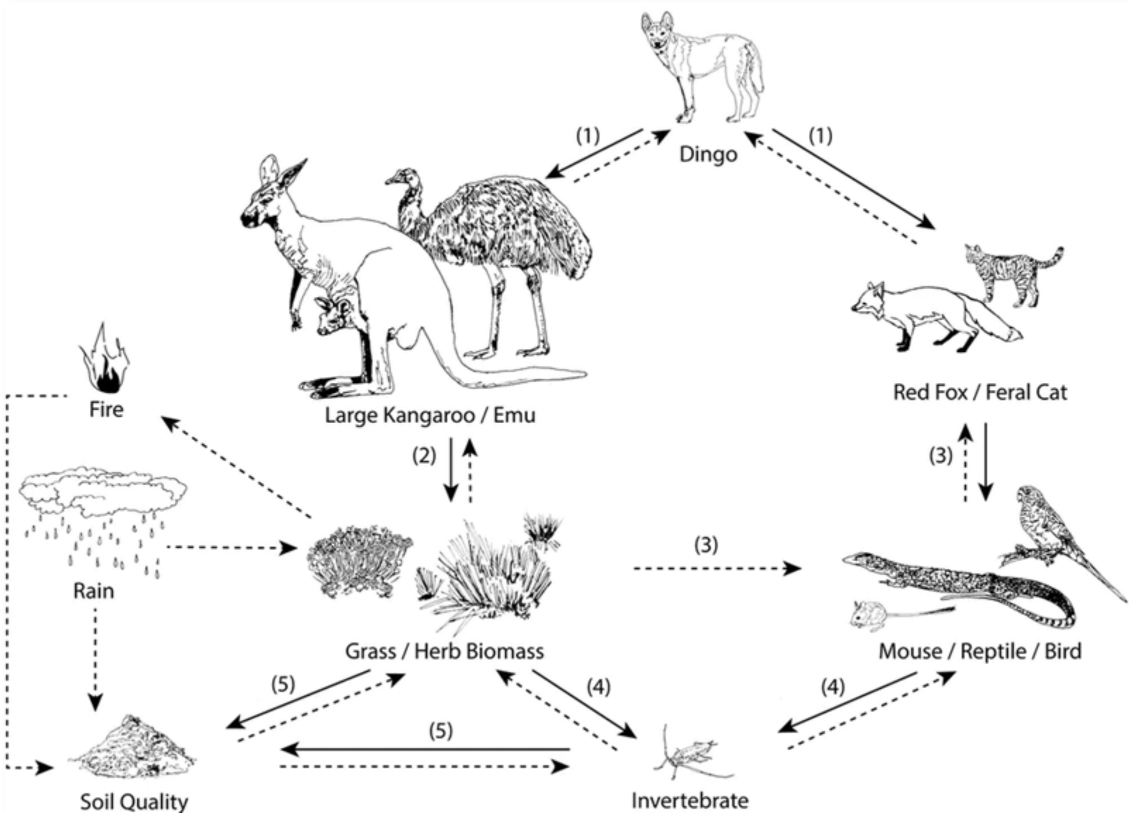

Figure 2.9 Interactions predicted by the TCH in Australia.
If dingoes suppress cats, foxes and large herbivores, populations of smaller native prey species, birds and plant biomass are predicted to increase. Invertebrates may also increase in response to increased vegetation (Source: (Newsome et al. 2015).

Mesopredator release

Mesopredator release has been broadly defined as an increase in the density and distribution of intermediate-sized predators following a measured decline in the density or distribution of apex predators (Brashares et al. 2010). Theory predicts that a loss of apex predators facilitates a trophic cascade by allowing mesopredator abundance to increase (Ripple et al. 2016), with a concomitant decline in the prey of the mesopredators (Crooks & Soulé 1999).

Wolves in North America have been compared to dingoes in Australia and the ecological role of both canids has been deemed analogous for their roles in mesopredator release (Morgan et al. 2017) and ecosystem restoration (Ritchie et al. 2012). The successful reintroduction of wolves into YNP has fuelled calls in Australia to cease lethal dingo control (Cupples et al. 2011; Colman et al. 2014) and actively reintroduce dingoes into areas where they have been previously extirpated (Dickman et al. 2009; Letnic, Greenville, et al. 2011; Ritchie et al. 2012; Rees, Kingsford, et al. 2019).

Ominous predictions of broad-scale ecosystem collapse from a release of mesopredators following lethal control of dingoes in Australia has become a pervasive theme in the literature (Johnson et al. 2007; Kennedy et al. 2012; Letnic, Ritchie, et al. 2012; Rees, Kingsford, et al. 2019). Numerous papers have argued that the persistence of small prey species is inextricably linked to the presence of dingoes (Glen et al. 2011) and that threatened species declines are strongly correlated with dingo absence (Johnson et al. 2007). However, long-term mensurative studies (Arthur et al. 2012) and experimental studies that suppressed dingoes in open systems, (Eldridge et al. 2002; Kennedy et al. 2012; Allen, Allen, et al. 2013; Allen, Allen, et al. 2014; Eldridge et al. 2016; Fancourt et al. 2019) found no evidence for dingo control-induced trophic cascades (DC-ITC) or inverse relationships between dingoes and mesopredators.

In the Australian context, it has been reported that lethal control of dingoes has resulted in increases in fox density (Letnic, Ritchie, et al. 2012; Rees, Kingsford, et al. 2019) and cats (Johnson et al. 2007; Kennedy et al. 2012). It has therefore been suggested that dingoes could act as biological control tools to regulate mesopredator populations of invasive foxes and cats (Schroeder et al. 2015; Rees, Kingsford, et al. 2019). Conversely, these findings are weakened by studies that did not support reported inverse relationships between foxes and dingoes (Glen & Dickman 2005; Mitchell & Banks 2005; Arthur et al. 2012) and studies supporting cats co-existing with dingoes rather than being suppressed by them (Colman et al. 2014; Fancourt et al. 2019; Moseby et al. 2019). Allen et al. (2018) argue the suppressive effects of apex predators are amplified in simpler systems and that mammal declines in arid regions are primarily influenced by the availability of food, and suitable habitat. Similarly, a long-term 28 year study by Arthur et al. (2012) supported the view that ground dwelling mammal abundance correlated more positively with vegetation structure changes than predator-prey interactions.

Section 3

Mesopredator Release Concerns

There is now a growing worldwide acceptance of using predator restoration as a tool to maintain functioning ecosystems through the suppression of mesopredators (Crooks & Soulé 1999; Prugh et al. 2009). Recent empirical studies conducted in Australia have suggested that dingo populations play a key role in suppressing invasive mesopredators (Schroeder et al. 2015). Some recent studies have correlated the removal of dingoes with increased cat and fox abundance (Dickman 1996) and concomitant reductions in native prey species abundance (Letnic & Dworjanyn 2011). Similarly, increased cat abundance was correlated with the loss of coyotes (*Canis latrans*) in California, resulting in increased cat predation on avian prey (Crooks & Soulé 1999). Trophic cascade theory predicts that the effects of dingo control scale with body size, so that CWR mammals <5.5 kg will decrease in abundance due to mesopredator release and larger herbivores >6kg will increase in abundance due to reduced predation when dingoes are absent (Colman et al. 2014; Leo et al. 2019). Therefore, the main concerns relate to potential negative effects on native species inside clusters after the removal of the dingo because numerous studies have asserted that even small reductions in dingo abundance produce disproportionate and cascading negative effects on ecosystems through the release of mesopredators and large herbivores. (Soulé et al. 1988; Cupples et al. 2011; Greenville et al. 2014). For example, a review of field studies by Ritchie and Johnson (2009) concluded that every unit of decreased top-predator abundance lead to a 400% unit increase in mesopredator abundance. It is a widely held view that these interactions are occurring between dingoes, cats and foxes in Australian ecosystems following the lethal control of dingoes by livestock producers (Brook et al. 2012; Colman et al. 2014; Leo et al. 2019). However, despite these findings, the implications of this research remain ambivalent (Allen et al. 2011b; Fleming et al. 2012; Allen, Fleming, et al. 2013; Allen et al. 2015) and robust discussions have ensued which have sometimes become heated and acrimonious debates centring on experimental design flaws and confounding factors (Allen et al. 2011b, 2011a; Letnic, Crowther, et al. 2011; Glen 2012).

Threatened Species Concerns

Thirty four Australian mammal species have gone extinct since European settlement, the primary causes being habitat loss and subsequent predation by introduced predators such as feral cats, foxes (Woinarski et al. 2019) and the dingo (Woinarski et al. 2015). So great is the predation pressure from these three introduced eutherian carnivores that an additional 32 predator-susceptible mammal species now only exist within 17 fenced mainland areas and 101 offshore islands where these three predators are absent (Legge et al. 2018). This fact, at least in the Australian context, diminishes the claim that reintroducing dingoes is essential to protect native species of conservation (Ritchie & Johnson 2009) due to their alleged ability to suppress foxes (Letnic, Greenville, et al. 2011) and cats (Kennedy et al. 2012).

Assessments by Smith et al. (2020) determined that multiple threatened species were extant within cluster-fenced areas (see Fig 2.5 and Table 2.1). Therefore, the construction of cluster fences, the concomitant removal of dingoes inside the fences and the purported mesopredator release of cats and foxes, has raised concerns for the potential unintended negative consequences that may occur for native species living within these cluster fenced areas. This is especially relevant to predator-sensitive species already threatened by anthropogenic activities including habitat loss, invasive species, livestock grazing and climate change (Evans et al. 2011; Kearney et al. 2019).

Table 2.1 List of threatened species present within these clusters.

CE) critically endangered, (E) endangered, (V) vulnerable. % is how of the clustered land the species is likely to occupy. Source: (Smith et al. 2020).
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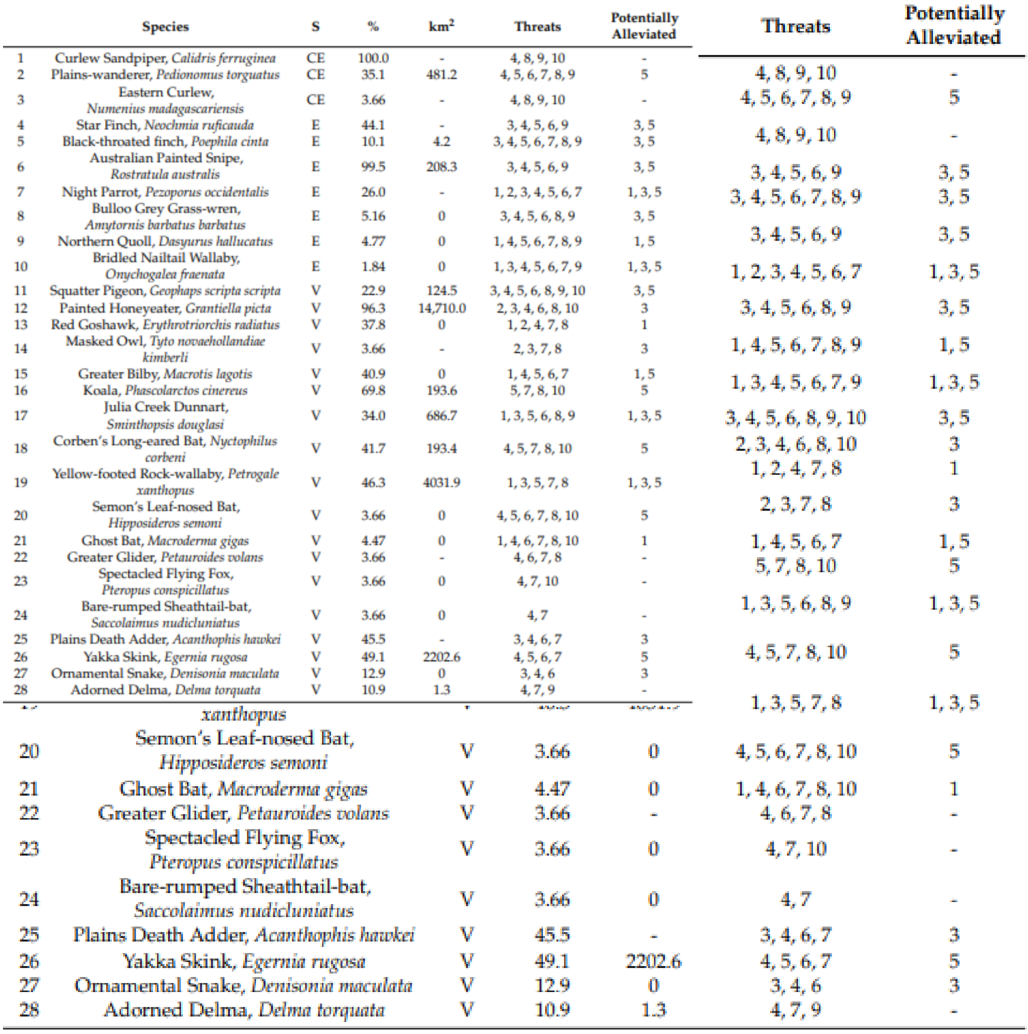

	Species	S	%	km^2	Threats	Potentially Alleviated
1	Curlew Sandpiper, *Calidris ferruginea*	CE	100.0	-	4, 8, 9, 10	-
2	Plains-wanderer, *Pedionomus torguatus*	CE	35.1	481.2	4, 5, 6, 7, 8, 9	5
3	Eastern Curlew, *Numenius madagascariensis*	CE	3.66	-	4, 8, 9, 10	-
4	Star Finch, *Neochmia ruficauda*	E	44.1	-	3, 4, 5, 6, 9	3, 5
5	Black-throated finch, *Poephila cinta*	E	10.1	4.2	3, 4, 5, 6, 7, 8, 9	3, 5
6	Australian Painted Snipe, *Rostratula australis*	E	99.5	208.3	3, 4, 5, 6, 9	3, 5
7	Night Parrot, *Pezoporus occidentalis*	E	26.0	-	1, 2, 3, 4, 5, 6, 7	1, 3, 5
8	Bulloo Grey Grass-wren, *Amytornis barbatus barbatus*	E	5.16	0	3, 4, 5, 6, 8, 9	3, 5
9	Northern Quoll, *Dasyurus hallucatus*	E	4.77	0	1, 4, 5, 6, 7, 8, 9	1, 5
10	Bridled Nailtail Wallaby, *Onychogalea fraenata*	E	1.84	0	1, 3, 4, 5, 6, 7, 9	1, 3, 5
11	Squatter Pigeon, *Geophaps scripta scripta*	V	22.9	124.5	3, 4, 5, 6, 8, 9, 10	3, 5
12	Painted Honeyeater, *Grantiella picta*	V	96.3	14,710.0	2, 3, 4, 6, 8, 10	3
13	Red Goshawk, *Erythrotriorchis radiatus*	V	37.8	0	1, 2, 4, 7, 8	1
14	Masked Owl, *Tyto novaehollandiae kimberli*	V	3.66	-	2, 3, 7, 8	3
15	Greater Bilby, *Macrotis lagotis*	V	40.9	0	1, 4, 5, 6, 7	1, 5
16	Koala, *Phascolarctos cinereus*	V	69.8	193.6	5, 7, 8, 10	5
17	Julia Creek Dunnart, *Sminthopsis douglasi*	V	34.0	686.7	1, 3, 5, 6, 8, 9	1, 3, 5
18	Corben's Long-eared Bat, *Nyctophilus corbeni*	V	41.7	193.4	4, 5, 7, 8, 10	5
19	Yellow-footed Rock-wallaby, *Petrogale xanthopus*	V	46.3	4031.9	1, 3, 5, 7, 8	1, 3, 5
20	Semon's Leaf-nosed Bat, *Hipposideros semoni*	V	3.66	0	4, 5, 6, 7, 8, 10	5
21	Ghost Bat, *Macroderma gigas*	V	4.47	0	1, 4, 6, 7, 8, 10	1
22	Greater Glider, *Petauroides volans*	V	3.66	-	4, 6, 7, 8	-
23	Spectacled Flying Fox, *Pteropus conspicillatus*	V	3.66	0	4, 7, 10	-
24	Bare-rumped Sheathtail-bat, *Saccolaimus nudicluniatus*	V	3.66	0	4, 7	-
25	Plains Death Adder, *Acanthophis hawkei*	V	45.5	-	3, 4, 6, 7	3
26	Yakka Skink, *Egernia rugosa*	V	49.1	2202.6	4, 5, 6, 7	5
27	Ornamental Snake, *Denisonia maculata*	V	12.9	0	3, 4, 6	3
28	Adorned Delma, *Delma torquata*	V	10.9	1.3	4, 7, 9	-

Threats	Potentially Alleviated
4, 8, 9, 10	-
4, 5, 6, 7, 8, 9	5
4, 8, 9, 10	-
3, 4, 5, 6, 9	3, 5
3, 4, 5, 6, 7, 8, 9	3, 5
3, 4, 5, 6, 9	3, 5
1, 2, 3, 4, 5, 6, 7	1, 3, 5
3, 4, 5, 6, 8, 9	3, 5
1, 4, 5, 6, 7, 8, 9	1, 5
1, 3, 4, 5, 6, 7, 9	1, 3, 5
3, 4, 5, 6, 8, 9, 10	3, 5
2, 3, 4, 6, 8, 10	3
1, 2, 4, 7, 8	1
2, 3, 7, 8	3
1, 4, 5, 6, 7	1, 5
5, 7, 8, 10	5
1, 3, 5, 6, 8, 9	1, 3, 5
4, 5, 7, 8, 10	5
1, 3, 5, 7, 8	1, 3, 5

	xanthopus					
20	Semon's Leaf-nosed Bat, *Hipposideros semoni*	V	3.66	0	4, 5, 6, 7, 8, 10	5
21	Ghost Bat, *Macroderma gigas*	V	4.47	0	1, 4, 6, 7, 8, 10	1
22	Greater Glider, *Petauroides volans*	V	3.66	-	4, 6, 7, 8	-
23	Spectacled Flying Fox, *Pteropus conspicillatus*	V	3.66	0	4, 7, 10	-
24	Bare-rumped Sheathtail-bat, *Saccolaimus nudicluniatus*	V	3.66	0	4, 7	-
25	Plains Death Adder, *Acanthophis hawkei*	V	45.5	-	3, 4, 6, 7	3
26	Yakka Skink, *Egernia rugosa*	V	49.1	2202.6	4, 5, 6, 7	5
27	Ornamental Snake, *Denisonia maculata*	V	12.9	0	3, 4, 6	3
28	Adorned Delma, *Delma torquata*	V	10.9	1.3	4, 7, 9	-

Furthermore, it has been suggested that native fauna struggling to adapt to the combined novel predation of three invasive eutherian predators may be locked into a slow population continental-scale death by attrition (Strauss et al. 2006).

Three invasive eutherian predators

Australian mainland ecosystems are unique, given that the three top mammalian carnivores, the dingo, the European red fox and the cat are all introduced eutherian mammals. All three predators have benefitted from the widespread establishment of artificial water points (Allen, Allen, et al. 2013) and increased prey following the introduction of the European rabbit *(Oryctolagus cuniculus)* (Corbett 2001), goats, sheep, cattle and pigs (Fleming et al. 2012). Introduced carnivores also prey upon many endemic species (Crisp et al. 2001) with 87% of Australia's 316 terrestrial mammals being endemic (Woinarski et al. 2015). Australia's high level of endemism is most likely a function of vicariance and isolated speciation (Crisp et al. 2001) resulting from its separation from Gondwana in the late-Eocene (~32 Ma) (Crisp et al. 2004) and the long period of relative isolation that ensued (Black et al. 2012). This unique mix of endemic marsupial prey and introduced eutherian carnivores raises concerns over the applicability of standard mesopredator release and trophic cascade theories, purported in previously published studies, compared to systems containing largely native predators and prey (Fancourt et al. 2019). It is possible that cat and fox populations may not be regulated by dingoes, and so implementing the restoration of dingoes may simply lead to higher predation of endemic species (Fleming et al. 2012) as dingo predation has been identified as a key threat to 94% of listed vulnerable Australian mammals, reptiles and birds in arid and semi-arid areas (Allen & Fleming 2012).

Australia's antecedent apex predators

It is clear from the fossil record that Australian native prey co-existed and co-evolved with a suite of marsupial carnivores for ~32 million years (Mya) since the separation of Australia from Antarctica in the mid-Cenozoic Era. The presence of all extant orders of Australian marsupials preserved in the fossil record of the late-Oligicene (~28−24 Mya) (Black et al. 2012), represents a long period of co-evolutionary history with thylacines (family Thylacinadae) spanning more than 24 million years. The thylacine (*Thylacinus cynocephalus*) and the Tasmanian devil (*Sarcophilus harrisii*) were the last surviving native apex mammalian predators to survive into the late Holocene (Feigin et al. 2018). *T. cynocephalus,* often presented as a single species, was in fact the last representative of the family (Thylacinadae) that consisted of twelve species from eight genera (Rovinsky et al. 2019). Thylacines first appear in the fossil record ~24 Mya in the late-Oligocene deposits of the Riversleigh region in Queensland where up to five species of thylacine are thought to have co-existed (Wroe 2003; Attard et al. 2014).

The concept of co-evolution is important because invasive predators are reported to exert at least twice the impact on native prey species than their native counterparts (Salo et al. 2007) and the attribution of their deleterious effect to prey naivety is now well documented in the literature (Blumstein et al. 2002; Banks & Dickman 2007; Moseby et al. 2015; Heise-Pavlov & Bradley 2021). By the mid to late-Holocene, ~4 thousand years ago (Kya), the Australian mainland Thylacine and the Tasmanian devil were about to face one of their greatest existential evolutionary challenges, the arrival of the dingo.

The arrival of the dingo

When viewed on geological timescales, dingoes are an extremely recent arrival into Australian ecosystems that did not co-evolve with the extant antecedent marsupial carnivores present on the continent upon their arrival. Multiple lines of evidence from numerous studies place the arrival of the dingo in Australia at ~3 500 years before present (BP) (Gollan 1984; Smith & Litchfield 2009; Ardalan et al. 2012; Letnic, Fillios, et al. 2012; Letnic et al. 2014; Woinarski et al. 2015; Balme et al. 2018). It is almost certain that the dingo was transported to Australia by humans travelling in boats (Fillios & Taçon 2016; Balme et al. 2018), suggesting the animals were tamed to a point where they possessed a tolerance for human presence (Shipman 2021), that may have stemmed from a historical commensal relationship with humans (Brüniche–Olsen et al. 2018). The dispersal of dingoes across mainland Australia occurred rapidly (Brüniche–Olsen et al. 2018), with continental-wide dispersal estimated to have taken ~500 years (Balme et al. 2018), the rapidity of which may have been facilitated by their commensal relationship with humans (White et al. 2018).

When the dingo arrived, the Thylacine, the Tasmanian devil and the Tasmanian native hen (*Tribonyx mortierii)* were widely distributed throughout mainland Australia and Tasmania, with the exception of arid regions (Brüniche–Olsen et al. 2018).

Numerous studies agree that the thylacines and devils became extinct, along with the Tasmanian native hen (Johnson & Wroe 2003), on the Australian mainland around 3000 years BP, (~500 years after the arrival of dingoes), (Brown 2006; Figueirido & Janis 2011; Hunter et al. 2015; Brüniche–Olsen et al. 2018) for which the dingo has been heavily implicated (Corbett 1995; Letnic, Fillios, et al. 2012).

The results of a more contemporary carbon dating study by White et al. (2018) support a synchronous extinction of mainland devils and thylacines occurring between 3 227−3 179 years BP. It is therefore likely that a 25 million year evolutionary lineage of mainland thylacines and devils ceased to exist within as little as 400−500 years of the arrival of the dingo. Further evidence that the dingo is implicated in the extinction of mainland thylacines, devils and the Tasmanian native hen, is their extinction on the mainland where dingoes were present and their persistence in Tasmania where dingoes were absent (Johnson & Wroe 2003). Late Holocene Australia now had a new default meso-come-apex predator, itself a beneficiary of mesopredator release (Prugh et al. 2009). When dingoes arrived in Australia they decoupled from their evolutionary history and left their predators behind and the corollary of this was finding novel, naïve organisms to exploit (Kolbert 2014).

Accidental or deliberate introductions of alien species are exceptional natural experiments for studying the role that shared evolutionary history plays in novel species interactions. The deliberate release of foxes and cats into the Australian landscape in the early to mid-19th century was perhaps the greatest spatio-temporal 'dingo' experiment ever conducted and the results are in. Cats historically spread throughout Australia following multiple coastal releases between 1824–1886 and fox distribution increased from 1871 following releases from Melbourne and south-east South Australia (Abbott et al. 2014). In less than 100 years, cats were ubiquitous across the Australian mainland (Abbott 2002; Arim et al. 2006), and foxes occupied most of the continent with the exception of the northern tropics north of 20 degrees S (Dickman 1996; Allen et al. 2015). The rapidity of these invasions was likely augmented by the release and rapid dispersal of rabbits in the 1860's and the provision of artificial watering points on pastoral properties. (Allen & West 2013).

A key weakness with the argument that dingoes suppresses invasive mesopredators is highlighted perhaps by the fact that established dingo populations, having had a ~3 500 year head start to adapt to the Australian environment, failed to prevent small numbers of foxes and cats establishing across most of the Australian continent during their initial invasion in the 19th century (Fancourt et al. 2019). Whilst dingoes were opportunistically shot, trapped and poisoned after first settlement, it is unlikely that the scale of this persecution had a bearing on the overall outcome of the dispersal of foxes and cats. The dingo currently occupies ~ 85% of the Australian mainland (Allen & Leung 2014).

Figure 2.100 A–dingo distribution in Australia 2012, B– cat distribution C– fox distribution. Source: (Fleming et al. 2014) A and C, (Allen et al. 2015) B.

CHAPTER 3: STUCK IN THE MUD: A CRITICAL REVIEW OF THE PERSISTENT FAILURE OF ‘THE SCIENCE’ TO PROVIDE RELIABLE INFORMATION ON DINGO-MESOPREDATOR RELATIONSHIPS.

Abstract

Apex predators are believed to play a critical role in maintaining the integrity and function of ecological systems. Removal of apex predators is further believed to produce subsequent increases in mesopredator populations, which is then expected to have cascading, negative effects on smaller native prey species. Evidence for these processes in terrestrial systems has been mixed and equivocal, largely due to the systemic and continued use of weak-inference, correlative study designs to investigate this issue. This has prompted pleas, over many years, for researchers to use experimental study designs capable of elucidating these important ecological issues. Here we assess the progress towards this goal by reviewing the experimental designs of 37 empirical studies examining relationships between dingoes and mesopredators in Australian ecosystems since 2011, when a similar review was undertaken. We found that 84% (31 out of 37) studies were still missing essential experimental design features (such as controls, replication or randomisation) for assessing causal relationships, demonstrating that the strength or reliability of ‘the science’ on this subject remains weak and equivocal. We encourage researchers to use inferentially strong experimental designs in applied dingo-mesopredator studies and caution that persistent failure to improve in this area will potentially waste more time and money and add to the growing body of weak research obfuscating this ecological debate.

Introduction

Apex predators have been identified as a positive, stabilising force that maintain the structure and biodiversity of ecological communities (Estes et al. 2011; Ripple et al. 2014). However, data is lacking for most species in terrestrial ecosystems and information supporting this view comes from inferentially weak studies containing numerous methodological design faults (Allen et al. 2011b; Allen, Fleming, et al. 2013). In contrast, there is now a large body of seminal evidence demonstrating that apex predators are not the overarching force they were once thought to be (Wang & Fisher 2012; Allen, Allen, et al. 2013; Allen, Allen, et al. 2014; Fancourt et al. 2019; Stobo-Wilson, Stokeld, Einoder, Davies, Fisher, Hill, Mahney, Murphy, Scroggie, et al. 2020; Stobo-Wilson, Stokeld, Einoder, Davies, Fisher, Hill, Mahney, Murphy, Stevens, et al. 2020; Castle et al. 2021; Kreplins et al. 2021; Castle et al. 2022). This is especially true in the Australian context where some believe that Australian dingoes exhibit metaphysical earth-saving powers, including providing continental-scale refuges from feral cats (Brook et al. 2012) and/or fox predation (Colman et al. 2015), changing soil chemistry by elevating soil nutrients (Morris & Letnic 2017) preventing shrub encroachment (Gordon, C.E. et al. 2017), preserving avian predators (Rees, Rees, et al. 2019) and even shifting entire epigeic arthropod assemblages (Contos & Letnic 2019). Furthermore, Wallach (2011) maintained that the positive effects of dingoes outweighed the effects of rainfall in the desert and Hunter and Letnic (2022) concluded that dingoes influence mesopredators to a greater degree than the thousands of tonnes of 1080 baits distributed annually to control them.

Despite such ongoing conclusions from numerous short-term quasi and pseudo-experimental studies, almost all available long-term correlative studies and manipulative experiments of stronger inferential ability, unanimously find that dingoes do not suppress mesopredators or initiate associated trophic cascades (Allen, Allen, et al. 2013; Allen, Allen, et al. 2014; Castle et al. 2021; Castle et al. 2022). Thus, the most reliable studies are quite clear on the issue, but debate still remains given that all studies are considered inferentially equal. At the centre of this debate are the experimental designs and methods used in various studies. A decade old review by Allen et al. (2011b), found predator sampling methods around these studies to be deficient, and a follow-up review in 2013 determined that most experimental designs were incapable of evaluating predator responses to lethal dingo control (Allen, Fleming, et al. 2013). A further re-evaluation of three unique case studies showed that these studies were also unable to answer the question (Allen, Lundie-Jenkins, et al. 2014). These reviews cast doubt on the reliability of reliable evidence for dingo suppression of mesopredators, prompting pleas for researchers to use stronger experimental designs capable of elucidating dingoes' causal roles (Newsome et al. 2015; Allen et al. 2017a).

Scientific knowledge, and the transferability of that knowledge, advances most quickly when study designs contain the elements that allow researchers to make stronger inferences. The essential ingredients of robust scientific experiments include a measured control, treatment randomisation, treatment replication and relevant data analysis (Hone 2007). When one or more of these elements are missing, such studies become more observational and correlative and their findings are limited to weaker, correlative inferences that simply do not have the ability to answer cause-and-effect questions, no matter how much data manipulation and analysis and modelling is undertaken (Hone 2007). Other study features are also vital in order to have a 'good' experimental design capable of making strong inferences. Foremost is that the treatment effect is actually measured and not just 'assumed', as has been the case with most experiments conducted either side of the DBF. Measuring the treatment effect is typically achieved by conducting surveys before and after the treatment in both treated and non-treated areas (Underwood 1997). Sampling effort is critical and should be conducted on a sufficiently large spatial and temporal scales with repeated observations, in all seasons and over multiple years in order to obtain sufficient data to analyse. A strong experimental design is constrained without appropriate sampling effort just as a large sampling effort is constrained without a strong experimental design. The most valuable studies are those with a large dataset derived from an inferentially strong experimental design (Hone 2007). Knowing where to find such studies is also very important for those seeking the most reliable information.

Here I reviewed the methods of dingo-mesopredator interaction studies published between 2011 and 2022 to determine if the quality of ecological studies is improving. This review essentially picks up where (Allen, Fleming, et al. 2013) left off. I classified the design strengths of 37 published experiments and assessed the reliability of their reported inferences based on their experimental design, sampling effort, study duration and potential confounding factors. I also assessed the relationship between design strength and their institutional rank and journal impact factor to determine if journal or institutional ranks were useful guides for finding the best studies. My objectives were to (1) see if the quality of literature is getting any stronger, (2) to see if institutional rank and journal impact factor was a potential guide for identifying the studies with the greatest inferential strength, and (3) to identify where improvements can be made to advance the science on this issue.

Methods

Experimental Design Limitations

This critical review focuses on dingo-mesopredator interaction studies and is based on a search for all empirical studies conducted in Australia between 2011 and 2022. My search period commences in 2011 because this is when a similar review was completed (Allen, Fleming, et al. 2013), with the present review essentially following on from this one by assessing studies published since that time. I searched for all studies that surveyed predators using passive tracking stations (i.e. sand plots), camera traps and spotlighting surveys given that these are the primary field techniques used for assessing Australian predator populations. I also obtained a small number of studies that surveyed predators using GPS collars. At least one of these techniques were used by each of the studies I reviewed.

I searched four international databases (CSIRO Publishing, Web of Science, EBSCOhost Megafile Ultimate and Science Direct) which were accessed between (6 and10 March 2021), and searched using the following terms:

For CSIRO Publishing:

Dingo OR wild dog AND fox OR cat AND mesopredator
An advanced search of papers published in natural environment journals produced 946 results.

For Web of Science:

Dingo OR wild dog AND fox OR cat AND mesopredator
A basic search of papers published produced 1109 results.

For EBSCOhost Megafile Ultimate:

Dingo OR wild dog AND fox OR cat AND mesopredator
A search of Biological and Physical Science Journals produced 162 results

For Science Direct:

Dingo OR wild dog AND fox OR cat AND mesopredator
An advanced search of papers produced 784 results

A total of 3 001 abstracts were read to determine whether they fitted within the scope of this review. After removing duplicates, studies focussing on predator-habitat relationships (e.g. (Arthur et al. 2003; Leo et al. 2019), predator-prey relationships or trophic cascades (Morris & Letnic 2017; Letnic et al. 2018; Contos & Letnic 2019) or predator diet studies (McDonald et al. 2018) were excluded because they did not report empirical data on dingo-mesopredator relationships. If insufficient content was reported in the abstract, the methods and results section of each report was then read to investigate further. Ultimately, 37 reports examining dingo-mesopredator interactions were selected for review.

Each study was then classified into 16 categories representing the inferential capacity or strength of their experimental designs as defined in Hone (2007) (see Table 3.1). According to Hone (2007), the three essential elements of the inferentially strongest studies (i.e. 'classical experiments' are the presence of both treatments and experimental controls, treatment replication and treatment randomisation, with the threshold separating causal studies from correlative studies having a ranking of 3 or less (see Table 3.1). Studies ranked 4 or more lack at least one of these essential elements and are therefore limited to providing only observational or correlative data (Festing 2003) inferior to, or less reliable than, those data obtained from stronger experimental designs (Hone 2007).

Table 3.1: Description of experimental designs as per Table 1.2 in (Hone, 2007).
Classification ranges from (1 highest inference classical experiment) to (16 lowest inference simple observations).

Rank	Classification	Experimental control used	Treatment randomisation used	Treatment replication used	Analysis conducted
1	Classical experiment	✓	✓	✓	✓
2	Data set awaiting analysis	✓	✓	✓	
3	Un-replicated experiment	✓	✓		✓
4	Un-replicated, unanalysed experiment	✓	✓		
5	Quasi-experiment type l	✓		✓	✓
6	Quasi-experiment type ll	✓		✓	

Rank	Classification	Experimental control used	Treatment randomisation used	Treatment replication used	Analysis conducted
7	Quasi-experiment type lll	✓			✓
8	Quasi-experiment type lV	✓			
9	Pseudo-experiment type l		✓	✓	✓
10	Pseudo-experiment type ll		✓	✓	
11	Pseudo-experiment type lll		✓		✓
12	Pseudo-experiment type lV		✓		
13	Pseudo-experiment type V			✓	✓
14	Pseudo-experiment type Vl			✓	
15	Pseudo-experiment type Vll				✓
16	Simple observations				

I recorded the lead university of each study by identifying the first Australian university reported in the list of author affiliations, except for one study (Forsyth et al. 2019) which was not associated with any university. The 2022 university rankings in ‘environmental science’ were then obtained from Elsevier’s Scopus database (SCImago 2022). The purpose of assessing this information was to explore any relationship between the ranking of the lead institution with the inferential strength or quality of the work they produced on this subject. The most recent journal impact factor for every study I reviewed was also obtained from SCImago (SCImago 2021) so that potential correlations between the Hone rank of each study and journals citation rates could be evaluated. Specifically I aimed to determine if journals with higher impact factors correlated with the quality of the study experimental design as ranked by Hone.

In addition to assessing the inferential strength of each study and their institutional rank and impact factor, I then recorded the stated spatio-temporal scales of each study and their reported predator sampling strategy and effort. I wanted to assess (1) when and how long each study was conducted, (2) the spatial scale the study was conducted over, (3) if and/or how frequently predators were repeatedly sampled, (4) which techniques were used to sample predators and how these techniques were applied, (5) and the resulting amount of data collected in each study or their available sample sizes (e.g. number of sand plot nights or camera trap nights of data). Sample sizes were not reported in many cases, and where this occurred I estimated approximate sample sizes based on the stated descriptions of the methods. The purpose of assessing this information was to identify the volume of data present in each study. Finally, I summarised the resulting strengths and weaknesses of each study and identified other methodological issues that may also weaken the reliability of the reported data, such as seasonal or habitat confounding, or the presence of unmeasured treatment effects (Table 3.2; see also (Allen et al. 2011b).

Results

Table 3.2: An overview of the experimental design strengths, predator sampling methods, and other characteristics of 36 empirical studies of dingoes and mesopredators, 2012 to 2022. See Allen et al. (2013) for studies conducted prior to 2012, and see Allen et al. (2011) for additional explanation of methodological weaknesses described below.

#	Reference	Study topic	Methodological strengths	Methodological weaknesses	Study scale, sampling strategy and effort	Experimental design, and level of inference	MRH support	Journal impact factor	University rank
1	(Allen, Allen, et al. 2013) Sand plots, poison baiting	Relationships between predators exposed to lethal control	• Manipulative experiment (baiting) • Large spatial scale • Treatments and controls • Measured control • Random allocation of treatments • Time series data • BACI design	• Non-independence of treatments at 3 of 9 study sites • Non-independence of treatments over time at all sites (predator migration was possible) • Treatment size, intensity and duration varied between sites • Only one survey conducted before commencement of treatments at some sites • Replication used (but not analysed)	• 9 large study sites 45 600 km^2 • 2–5 year study period • Each site comprised of paired treated (baited) and non-treated (unbaited) treatment areas • 92–166 road-based sand plots spaced 1 km apart per study site • 6–23 repeated surveys every few months per study site • Predator activity calculated as the mean number of tracks per plot per night (mean of daily means) • 35,399 sand plot-nights of data	Unreplicated experiment (although could be a classical experiment if re-analysed) 3(1)	NS	3.172	1
2	(Allen, Allen, et al. 2014) - Sand plots, poison baiting	Responses of predators and prey to predator control	• Manipulative experiment (baiting) • Large spatial scale • Treatments and controls • Measured control • Random allocation of treatments • Time series data • BACI design	• Non-independence of treatments at 3 of 9 study sites • Non-independence of treatments over time at all sites (predator migration was possible) • Treatment size, intensity and duration varied between sites • Only one survey conducted before commencement of treatments at some sites • Replication used (but not analysed)	• 9 large study sites • 2–5 year study period • Each site comprised of paired treated (baited) and non-treated (unbaited) treatment areas • 92–166 road-based sand plots spaced 1 km apart per study site • 6–23 repeated surveys every few months per study site • Predator activity calculated as the mean number of tracks per plot per night (mean of daily means) • 35,399 sand plot-nights of data	Unreplicated experiment (although could be re-analysed as a classical experiment) 3(1)	NS	3.172	1
3	(Bird et al. 2018) Sand plots, fire	Species' association with fire history	• Snapshot study • Stratified random sampling	• No treatments or controls, randomisation or replication • Used a categorical measure of predator activity over continuous measures • Used a categorical measure of fire/habitat over continuous measures	• 1 large study site • 2 year study period • 76 x 1 ha sand plots spaced at least 1 km apart, within 2 km of a vehicle track, on sandy soils only, and sampled only in the winter months sometime between July 2014 and July 2016 • Predator activity categorised as absent, rare, moderate, or common based on the 'freshness' and number of observed tracks • 1 single survey at each study site • 76 sand plot-nights of data	Pseudo-experiment type VII 15	S	5.99	33
4	(Brook et al. 2012) Camera traps, baiting	Relationship between dingoes and feral cats	• Large spatial scale • Spatial replication	• Unmeasured control • Non-independence of treatments at some sites • Non-random allocation of treatments • Treatment size, intensity and duration varied between sites • Results confounded by historical and current land use, camera type, sampling effort	• 9 large study sites • 3 year study period • 20-40 baited camera traps per study site, deployed in pairs (1 on-road and 1 off-road) and spaced at 2–5 km intervals for a single 5-8 day survey period at each site • 6 of 9 study sites surveyed once only between March and November	Quasi-experiment type I 5	S	6.528	14

				and schedule, survey duration, season, and lure combinations	• 3 of 9 study sites surveyed three times over several months (but the data were pooled) • 5,308 camera trap-nights of data				
5	(Castle et al. 2021) Sand plots, poison baiting	Responses of predators to dingo removal	• Manipulative experiment (dingo eradication) • Large spatial scale • Treatments and controls • Measured control • Random allocation of treatments • Treatment independence • Time series data	• Treatment efficacy varied between study sites • Replication used (but not analysed)	• 2 large study sites • 5 year study period • Each site comprised of paired 'inside fence' and 'outside fence' areas • 94–122 road-based sand plots spaced 1 km apart per study site • 14 repeated surveys every 4 months per study site • Six x 10 km spotlight surveys inside and outside of each cluster repeated 3 times per year is 720 km x 5 years = 3600 km of vehicle tracks spotlighted • Predator activity calculated as the mean number of tracks per plot per night (mean of daily means) • 8,484 sand plot nights of data	Unreplicated experiment (although could be re-analysed as a classical experiment) 3(1)	NS	4.379	25
6	(Castle et al. 2022) Sand plots, poison baiting	Responses of prey to dingo removal	• Manipulative experiment (dingo eradication) • Large spatial scale • Treatments and controls • Measured control • Random allocation of treatments • Treatment independence • Time series data	• Treatment efficacy varied between study sites • Replication used (but not analysed)	• 2 large study sites • 5 year study period • Each site comprised of paired 'inside fence' and 'outside fence' areas • 94–122 road-based sand plots spaced 1 km apart per study site • 14 repeated surveys every 4 months per study site • Predator activity calculated as the mean number of tracks per plot per night (mean of daily means) • 120 km of spotlight transects (6 x 10 km transects per treatment) at each site, surveyed three times each year • 8,484 sand plot nights of data • 3,360 km of vehicle track spotlighted	Unreplicated experiment (although could be re-analysed as a classical experiment) 3(1)	NS	2.618	25
7	(Colman et al. 2015) (but see Catling and Burt 1994, 1997; and Catling et al. 1997) Sand plots	Relationships between predators and prey	• Mensurative study • Large spatial scale • Spatial replication	• No treatments or controls • Non-independence between some sites, and between repeat surveys at some sites • Results confounded by seasonal and habitat differences in predator activity	• 44 small study sites • 10 year study period • 20–35 road-based sand plots, spaced 200 m apart, along transects 4–7 km long, at 13 sites, surveyed twice sometime between October 1989 and April 1992 (Catling and Burt 1994) • 284 road-based sand plots, spaced 200 m apart, along a series of short transects, at 10 sites, surveyed once sometime	Pseudo-experiment type V 13	S	5.349	35

					between January 1995 and June 1995 (Catling et al 1997) • 10–35 road-based sand plots (443 in total), spaced 200 m apart, along transects 2–7 km long, at 21 sites, surveyed twice sometime between October 1987 and May 1994 (Catling and Burt 1997) • Surveys occurred sometime in “late summer / autumn and again in late winter / spring” or “autumn and spring” • Sites spaced at least 3 km apart • 5,574 sand plot nights of data (2,035 from Catling and Burt 1994, 822 from Catling et al. 1997, and 2,717 from Catling and Burt 1997)				
8	(Colman et al. 2014) Sand plots, poison baiting	Relationships between predators exposed to lethal control	• Treatments and controls • Treatment replication	• Unmeasured control • Non-independence between some study sites • Non-independence between treatments at some study sites • Non-random allocation of treatments • Invalid comparison of indices between species • Used a binary measure of predator activity over continuous measures • Results confounded by season, sampling schedule and timing of baiting	• 7 small study sites • 18 month study period • 40 road-based sand plots spaced 500 m apart per study site • 1 single survey at each study site • Predator activity calculated as “the percentage of plots on which the tracks were detected during the three-night tracking session” • 840 sand plot nights of data	Quasi-experiment type I 5	S	4.324	35
9	(Fancourt et al. 2019) Camera traps	Relationship between dingoes and feral cats	• Spatial replication • Measured fine-scale spatial relationships between predators	• No experimental treatments or controls • Land use varied between study sites	• 2 small study sites • 3 month study period • 90 camera traps used per site • Each site divided into 30 x 4 km^2 grid cells, with 3 cameras (1 on-road and 2 off-road) used in each grid cell • 2 repeated surveys (of at least 21 days duration) spaced ~1 month apart • ~7,500 camera trap-nights of data	Pseudo-experiment type V 13	NS	6.528	32
10	(Feit et al. 2019) Spotlighting, cross-fence study	Relationships between predators and prey	• Treatments and controls, spatial replication • Time series data	• Non-random allocation of treatments • Treatment replication confounded by land use	• 4 small study sites • 6 year study period • 1 spotlight transect per site, each ~30 km long • 18 repeated surveys spaced at ~4 month intervals	Quasi-experiment type I 5	S	4.217	2

				• Non-independence of treatments over time (predator migration was possible) • Invalidly pooled data across different species and land uses • Measurement of control was possible, but not undertaken • Results confounded by historical and current land use	• ~120 km of vehicle track spotlighted (~9,720 km over the study period)			
11	(Forsyth et al. 2019) Camera traps, density estimation	Evaluation of methods for estimating predator densities and interactions	• Multiple density estimation procedures tested	• No treatments or controls • No randomisation • No replication	• 1 very small study site (<1 km^2) • 64 day study period • 100 baited camera traps • 2 cameras (facing different directions) placed at 50 locations within a single grid • 3,200 camera trap-nights of data	Pseudo-experiment type VII 15	S	2.469	Government Departmentt
12	(Geary et al. 2018) Camera traps, fire	Species' association with fire history	• Stratified random sampling	• No treatments or controls • No replication • Non-independence between survey plots (predator migration was possible) • Results confounded by seasonal differences in predator activity	• 1 large study site • 6 month study period (April to August) • 21 'landscape sites' or survey plots, 12.56 km^2 in size and spaced 2 km apart • 5 baited cameras per survey plot (105 in total), spaced >200 m apart, off-road and away from fire scar edges • 1/3 of cameras were deployed in April, 1/3 deployed in May-June, and 1/3 deployed in July for a minimum of 33 days per deployment • Dingo occupancy information supplemented with two scat surveys spaced 3 months apart at each camera location • ~4,000 camera trap-nights of data for predators (or 8,369 trap nights of data if small mammal camera traps are included)	Pseudo-experiment type VII 15	S	6.528	19
13	(Gordon et al. 2015) Spotlighting, sand plots	Relationships between predators and prey	• Time series data • Large spatial scale	• Non-independence of study sites over time (predator migration was possible) • No treatments or controls • No replication • Unmeasured control • Used categorical measures of predator activity over continuous measures	• 3 large study sites • 7 year study period • 1 spotlight transect per site, each 120 km, 136 km, and 241 km long • 4 spotlight surveys conducted in 2007 and again in 2012, 2013, and 2014 • 497 km of vehicle track spotlighted • 47 locations (total across all three sites) surveyed with a single sand plot, 40 m long, at the base of a sand dune, for 2-3 consecutive nights, once only	Pseudo-experiment type III 11	S	5.349	35

				• Results confounded by seasonal differences in predator activity	sometime between May and October 2012 • In one analysis, predator activity calculated as the proportion of nights that predators were detected • 18 of the 47 locations included an additional sand plot, 40 m long, at the top of a sand dune, sampled once only sometime between July and August 2012 • In another analysis (with data from only 2 sites), predator activity was calculated as “the total activity between dune top and bottom areas per sampling night” • <160 sand plot nights of data				
14	(Gordon, C.E. et al. 2017) Sand plots, cross-fence study	Relationships between dingoes, prey species, and vegetation change	• Treatment and control • Large spatial scale	• Non-random allocation of treatments • Unmeasured control • No replication • Used a categorical measure of predator activity over continuous measures • Results confounded by historical land use, sampling effort and schedule, and season	• 1 large study site • 1 year study period • 91 locations surveyed with a single sand plot, 40 m long, for 2-3 consecutive nights, once only in either May, July, August, or October 2012 or March 2013 • Predator activity calculated as the proportion of nights that predators were detected • <273 sand plot nights of data	Quasi-experiment type III 7	S	5.091	35
15	(Gordon, Christopher E et al. 2017) Spotlighting, cross-fence study	Relationships between predators and quail	• Large spatial scale • Treatments and controls, spatial replication • Time series data	• Basic methodological details unreported • Non-independence of treatments over time (predator migration was possible) • Non-random allocation of treatments • Unequal sampling effort between treatments • Unmeasured control • Results confounded by seasonal and habitat effects, and sampling schedule • Predator scat data pooled across all treatments • Spotlighting surveys and scat surveys spatially separated	• 1 large study site • 2 year study period Temporal study • Number and length of spotlight transects unreported • Livestock properties sampled on 9 occasions between May 2012 and June 2014, and conservation reserves sampled on 6 occasions between August 2012 and June 2014 • Unreported sampling effort in temporal study (but probably <500 km of vehicle track spotlighted) Spatial study • 14 transects located in livestock areas (192 km in total) • 6 transects located in conservation reserves (72 km in total)	Quasi-experiment type III (temporal study) 7 Quasi-experiment type I (spatial study) 5	S	3.549	2

					• Of these 20 transects, 8 were located inside the fence and 12 were located outside the fence • Transects surveyed once only sometime between May and November 2012 • 264 km of vehicle track spotlighted in spatial study				
16	(Greenville et al. 2014) Camera traps	Relationships between predators, prey and rainfall	• Time series data	• No treatments or controls • No replication • Results confounded by seasonal and species differences in activity	• 1 small study site • 2 year study period • 25 camera traps, spaced 1–10 km apart, along vehicle tracks in dune swales • Camera traps deployed continuously during the study period • Data pooled across seasons and years into three periods (bust, boom, decline) of variable length • Rodent data pooled across four different species • 10,260 camera trap-nights of data	Pseudo-experiment type VII 15	S	3.225	8
17	(Hernandez-Santin et al. 2016) Camera traps	Interactions between dingoes, cats and quolls	• Time series data • Replication attempted	• Non-independence of study sites over time (predator migration was possible) • Control present, but not used • Replication present, but not possible with the design used • Results confounded by seasonal differences in species activity	• 2 large study sites • 2.5 year study period • 7 x 2–4 week sampling periods between March 2013 and July 2015 • 5 transects (each 2.5 km long) per study site • Each transect comprised of 10 baited (with sardines), road-based camera traps, spaced 250 m apart • 2,761 camera trap-nights of data	Pseudo-experiment type V (although could be re-analysed as a quasi-experiment type I) 13(5)	S	5.99	1
18	(Hunter & Letnic 2022) Sand plots	Relationships between dingoes and foxes	• Treatments and controls • Treatment replication	• Unmeasured control • Non-independence between some study sites • Non-independence between treatments at some study sites • Non-random allocation of treatments • Results confounded by year, season, sampling schedule, timing of baiting, and data transformation	• 27 small study sites • 4 year study period • 10–28 road-based sand plots spaced 500–750 m apart per study site • 1 single survey at each study site • Predator activity calculated as "the number of sand plots with tracks [divided by] the number nights", and them transformed by dividing all values by the largest value "so that values fell within the range of 0 to 1" • 2,747 sand plot nights of data	Quasi-experiment type I 5	S	3.903	2
19	(Kreplins et al. 2021)	Relationships between dingoes and	• Treatments and controls • Time series data	• Location of treatments and controls were alternated back	• 2 study sites • 16 month study period	Quasi-experiment type III 7	NS	2.618	27

	Camera traps, baiting study	mesopredators		and forth during the study period • Longer term treatment effect obscured by study design (i.e. ‘unbaited’ areas had a long history of baiting, and were baited a few months earlier) • Different camera brands were used	• Baited camera traps were placed at 1 km intervals along 3–4 road-based transects each 20-30 km long in each treatment, and remained in place during the entire study period • 92 camera traps were used at one site, and 90 were used at the other site • 93,002 camera-trap nights of data				
20	(Leo et al. 2019) Sand plots, baiting	Relationships between predators and prey	• Treatments and controls • Spatial replication	• Non-independence of study sites over time (predator migration was possible) • Non-random allocation of treatments • Unmeasured control • Results confounded by seasonal differences in species activity	• 7 large study sites • 2 year study period • Each site comprised of paired treated (baited) and non-treated (unbaited) sub-sites • Each site was sampled once only (over a two week period) in the dry season (April to November) sometime between April 2012 and November 2014 (although supplementary material says surveys were conducted between May 2013 and May 2015) • 24 road-based sand plots spaced 1 km apart at each sub-site (i.e. 48 sand plots per site, or 336 sand plots in total) • Predator activity was calculated as the ‘percentage of plots on which we detected tracks during the three-night tracking session’ • 1,008 sand plot nights of data	Quasi-experiment type l 5	S	3.903	2
21	(Letnic & Dworjanyn 2011) Spotlighting, cross-fence study	Relationships between dingoes, foxes and hopping-mice	• Treatments and controls • Replication attempted • Two measures of predator abundance used	• Non-random allocation of treatments • Non-independence of “replicate” spotlighting transects • Unmeasured control • Results confounded by seasonal differences in predator activity	• 1 large study site • 18 month study period • Site divided into ‘inside fence’ and ‘outside fence’ treatment areas Abundance assessment • 3 spotlighting transects, each 10–20 km long, established on each side of the fence (and considered as replicates) • Site surveyed on only 2 occasions (September 2007 and March 2009) • ~90 km of vehicle track spotlighted Foraging plot assessment • Predator activity surveyed on a single 30 x 30 [m] track-plot surrounding 96 rodent foraging trays (48 inside, and 48 outside the fence), spaced at least 500 m apart	Quasi-experiment type I 5	S	5.992	8

				• Surveys conducted over 2 nights during a full moon, and for another 2 nights at 96 different locations during a waning moon a few days later • Predator activity calculated as "the number of nights predator tracks were detected divided by the number of mornings each site was assessed for tracks" • 384 sand plot nights of data				
22	(Letnic, Greenville, et al. 2011) Sand plots	Relationships between dingoes and foxes	• Spatial replication	• Basic methodological details unreported • No treatments or controls • Results confounded by land use, seasonal, and habitat factors	• 26 small study sites • < 1 year (104 days). • Study period unreported • 25–40 sand plots per site, spaced at 1 km intervals, and checked for 3 consecutive days • Surveys conducted once only • Predator activity calculated as "the number of nights a plot was visited by each species of predator divided by the number of nights that the plot was considered valid" • <3,120 sand plot nights of data	Pseudo-experiment type I 9	S	7.144	35
23	(McHugh et al. 2019) Camera traps	Relationships between predators and prey	• Mensurative study • Spatial replication	• No treatments or controls • Results confounded by land use, seasonal, and habitat factors	• 9 small study sites • 1 year study period • 20–40 road-based and baited camera traps per site (298 in total), spaced 500 m apart • 2 x 21-day survey periods per site • Surveys conducted sometime between May 2016 and August 2016, and again between October 2016 and January 2017 • 12,516 camera trap nights of data	Pseudo-experiment type I 9	S	2.912	31
24	(McHugh et al. 2020) Camera study, fire	Predator and prey responses to fire	• Treatments and controls • Spatial replication • Time series data • BACI design	• Non-random allocation of treatments • Sites burned in different seasons and years • Results confounded by seasonal differences in predator activity	• 2 very small study sites • 2 year study period • Sites divided into paired burnt and unburnt treatments areas • 10 camera traps per treatment, spaced a few hundred m apart • Camera traps repeatedly deployed for 3 x 14 day periods before, 3 x 14 day periods immediately after, and 3 x 14 day periods 3 months after fire at each site (9 x 14 day periods in total) • 5,040 camera trap nights of data	Quasi-experiment type I 5	N/A	2.241	31

25	(Morris & Letnic 2017) Spotlighting, cross-fence study	Relationships between dingoes, herbivores, vegetation and soil	• Treatments and controls • Time series data	• Non-random allocation of treatments • No replication • Unmeasured control	• 1 large study site • 4 year study period • Treatments allocated for inside/outside and reserve/pastoral areas • A single spotlighting transect per treatment, ~30 km long • 14 repeated surveys conducted every ~4 months between May 2012 and June 2016 • ~120 km of vehicle track spotlighted each survey (or ~1,500 km of vehicle track spotlighted over 14 surveys)	Quasi-experiment type III 7	S	5.349	2
26	(Moseby et al. 2019) Sand plots, dingo addition	Effect of dingoes on mammals	• Manipulative experiment (dingo addition) • Treatment and control • Time series data • BACI design	• No replication • Small spatial scale • Results obscured and influenced by incorporation of unrelated data from other studies	• 1 small study site • 4.5 year study period • Site divided into ‘inside’ and ‘outside’ treatment areas • 77 x 200 m sand plot transects sampled over two consecutive nights • 13 repeated surveys between February 2008 and July 2012 • Species activity calculated as “the number of nights a plot was visited by each species divided by the number of nights that the plot was considered valid” • 2,002 sand plot nights of data	Unreplicated experiment 3	S	4.217	2
27	(Moseby et al. 2012) Sand plots, collars, dingo addition	Interactions between dingoes, mesopredators, and prey	• Manipulative experiment (dingo addition) • Treatments and controls • Time series data • BACI design • Two measures of activity used	• No replication • Small spatial scale • Used binary measure of activity over continuous measure	• 1 small study site • 2 year study period • Site divided into ‘inside’ and ‘outside’ treatment areas • 77 x 200 m sand plot transects sampled over two consecutive nights • 7 repeated surveys between February 2008 and February 2010 • Species activity calculated as percentage of sand plots visited over the two nights of counting • 1,078 sand plot nights of data	Unreplicated experiment 3	S	1.6	11
28	(Raiter et al. 2018) Camera traps, sand plots	Effects of roads and vegetation on predator activity	• Mensurative study • Two factors assessed (roads and habitat) • Spatial replication	• Data pooled across study/survey periods • Invalid assumptions about predator activity • No control used.	• 1 large study site • 1 year study period • 16 x 3 km transects beginning at a road and extending perpendicular away from the road, spaced at least 7 km apart Camera trapping	Pseudo-experiment type V 13	N/A	5.99	10

					• 5 camera trap sites (80 in total) established along each transect at set distances away from the road • 40 camera traps used at any one time, rotated amongst camera traps sites over 4 monitoring periods, for an average of 174 nights each • 13,950 camera trap-nights of data Spoor counts • Tracks and scats counted along entire transects on 3 occasions in January, March and July 2014 • 48 sand plot nights of data				
29	(Rees, Kingsford, et al. 2019) Sand plots, cross fence study	Relationships between predators and prey	• Treatments and controls • Site and treatment independence • Spatial replication	• Non-random allocation of treatments • Unmeasured control • Unbalanced sampling per site, treatment, and survey • Results confounded by sampling effort and schedule, and seasonal effects	• 2 large study sites • 2 year study period • Each site divided into 'inside' and 'outside' treatment areas, inclusive of mixed land use histories in both treatments • Road-based sand plots spaced 1 km apart and sampled for 3 consecutive nights per survey • One site sampled once only in February 2013 (17 sand plots) • The other site sampled twice in November 2014 (118 sand plots) and February 2015 (100 sand plots) • Carrion sampling with 2 x 10–15 km roadkill transects in March 2013 at one site, and 4 x 35–76 km transects in September 2012 at the second site • Bird sampling occurred once only at 200 locations, comprised of a 500 m strip, over four surveys conducted in March 2014, July 2014, March 2015, and April 2015 • Species activity calculated as "the mean number of tracks per plot, per night" • 235 sand plot nights of data	Quasi-experiment type I 5	S	5.992	2
30	(Rees, Rees, et al. 2019) Spotlighting,	Relationship between dingoes and barn owls	• Treatments and controls • Time series data • Spatial replication	• Non-random allocation of treatments • Non-independence of treatments (owls free to	• 7 small study sites • 4 year study period • Spotlighting transects 15–45 km long at each site	Quasi-experiment type I 5	S	3.549	2

	cross fence study			forage/migrate across both sides of the fence over the study period) • Spatial and temporal mismatch between dingo sampling and owl diet sampling	• 2–12 repeated surveys per site • <315 km of vehicle track spotlighted			
31	(Schroeder et al. 2015) GPS tracking study	Fine-scale interactions between dingoes, foxes and feral cats	• Multiple individuals monitored in detail • Examines both spatial and temporal activity of predators	• Small spatial scale • Low sample size of some animals, and short duration • Artificially constructed predator assemblage • Pre/post (BACI) data available for 4 cats, but unreported	• 1 small study site • 2 year study period • GPS tracking of 2 dingoes, 5 foxes, and 10 cats • GPS points continuously recorded every 2 hours • 3–16 days of dingo interaction data for each fox, and 3–180 days of dingo interaction data for each cat • Number of GPS points analysed unreported	Pseudo-experiment type V 13	S	2.511	11
32	(Stobo-Wilson, Stokeld, Einoder, Davies, Fisher, Hill, Mahney, Murphy, Scroggie, et al. 2020) Camera traps	Ecological processes influencing mammal abundance	• Large spatial scale • Spatial replication • Multiple methods of small mammal sampling	• No treatments or controls • Results confounded by seasonal differences in predator activity	• 1 very large study area • 3 year study period • 312 camera trap sites, with a mean of 2.5 km between sites • 5 baited camera traps at each site • Each site surveyed once only for 26–80 days (mean 50 days) • Survey effort unreported, but probably ~70,000 camera trap nights of data	Pseudo-experiment type V 13	NS	5.99	34
33	(Stobo-Wilson, Stokeld, Einoder, Davies, Fisher, Hill, Mahney, Murphy, Stevens, et al. 2020) Camera trap study	Relationship between dingoes and feral cats	• Large spatial scale • Spatial replication	• No treatments or controls • Data potentially confounded by seasonal differences in predator activity	• 1 very large study area • 3 year study period • 376 camera trap sites, with a mean of 2.5 km between sites • 5 baited camera traps at each site • Each site surveyed once only for 26–80 days (mean 50 days) • 83,357 camera trap nights of data	Pseudo-experiment type V 13	NS	5.139	34
34	(Wang & Fisher 2012) Camera traps	Relationships between dingoes and feral cats	• Randomised, complete and representative sampling of the study site • Mensurative study	• No treatment or controls • No replication • Data from multiple camera trap types pooled together (though interspersed throughout the study site)	• 1 small study site • 1 year study period • Camera traps placed on roads nearest to 41 randomly generated locations across the site, and spaced at least 500 m apart	Pseudo-experiment type VII 15	NS	2.511	1

				• Results confounded by seasonal differences in predator activity	• Each location was surveyed for 38–185 nights (mean = 96 nights) sometime between August 2009 and August 2010 • 4,045 camera trap nights of data			
35	(Wooster et al. 2021) Camera traps, scat indices	Monitoring fox behaviour at key resource points used by dingoes to see if foxes are more cautious in areas of high dingo activity.	• Time series data	• No treatments or controls, randomisation or replication • Sample sizes (number of scats collected) unreported • Data pooled across camera trap types, resource point types, and years	• 1 large study site • 3 year study period • Scats collected at a total of 50 resource points (within 20 m radius around 21 water points, 4 cattle carcasses, and 25 rabbit warrens) • Scats collected sometime in the winter of 2016, 2017 and/or 2018 • 10 resource points sampled in 2016, 37 in 2017, and 20 in 2018 (some points sampled once, and others up to three times) • 67 resource point counts of data • 1–3 camera traps deployed at each location during the winter survey periods • 1,366 camera trap nights of data	Pseudo-experiment type VII 15	N/A	2.671	5
36	(Wysong, Hradsky, et al. 2020) GPS tracking study	Relationships between dingoes and cats	• Multiple individuals monitored in detail • Examines both spatial and temporal activity of predators	• Short duration, or exclusion of substantial amounts of data • Pre/post (BACI) data available, but unreported	• 1 large study site • 1 year study period • GPS tracking of 17 dingoes and 29 cats • GPS points continuously recorded every 2 hours for dingoes and every 4 hours for cats • Data analysis focussed on the 2 x 70 day periods prior to annual cat control programs in July 2013 and July 2014 • 16,458 GPS points analysed	Pseudo-experiment type V 13	NS	2.511	10
37	(Wysong, Iacona, et al. 2020) Camera traps, baiting study	Relationship between sampling strategy and predator occupancy	• Before/after baiting data • Complete and representative sampling of the study site	• No experimental control, randomisation, or replication • Short duration	• 1 large study site • 2 month study period • 80 camera traps spaced at least 1.5 km apart • 20 camera traps allocated to each of four treatments (on-road–lure, on-road–no lure, off-road–lure, off-road–no lure) • 3,683 camera trap-nights of data	Pseudo-experiment type VII 15	S	3.6	10

I found that the majority of dingo-mesopredator studies conducted over the last decade continued to use correlative study designs and therefore have weak inferential power (Figure 3.1). Twenty four out of 37 studies (65%) supported the MRH yet all but two of them were low-inference studies with no capacity to reliably describe such causal processes. Thirty one of the 37 (84%), had a weak-inference study design and possessed no capacity to assess causal relationships between dingoes and mesopredators and I found no improvement in the inferential strength of experimental designs between 1993 and 2022 ($r = 0.12$, df 75, $p = 0.28$).Viewed alongside the results of Allen, Fleming, et al. (2013), which found 36 of 39 (92%) of studies published prior to 2012 to have similarly weak study designs. Only 9 studies published since 1993 reached the required threshold (i.e. had a design ranking of 3 or under) to assess causal relationships between dingoes and mesopredators and only one published study met the criteria for a classical experimental design Allen (2012); see (Figure 3.1).

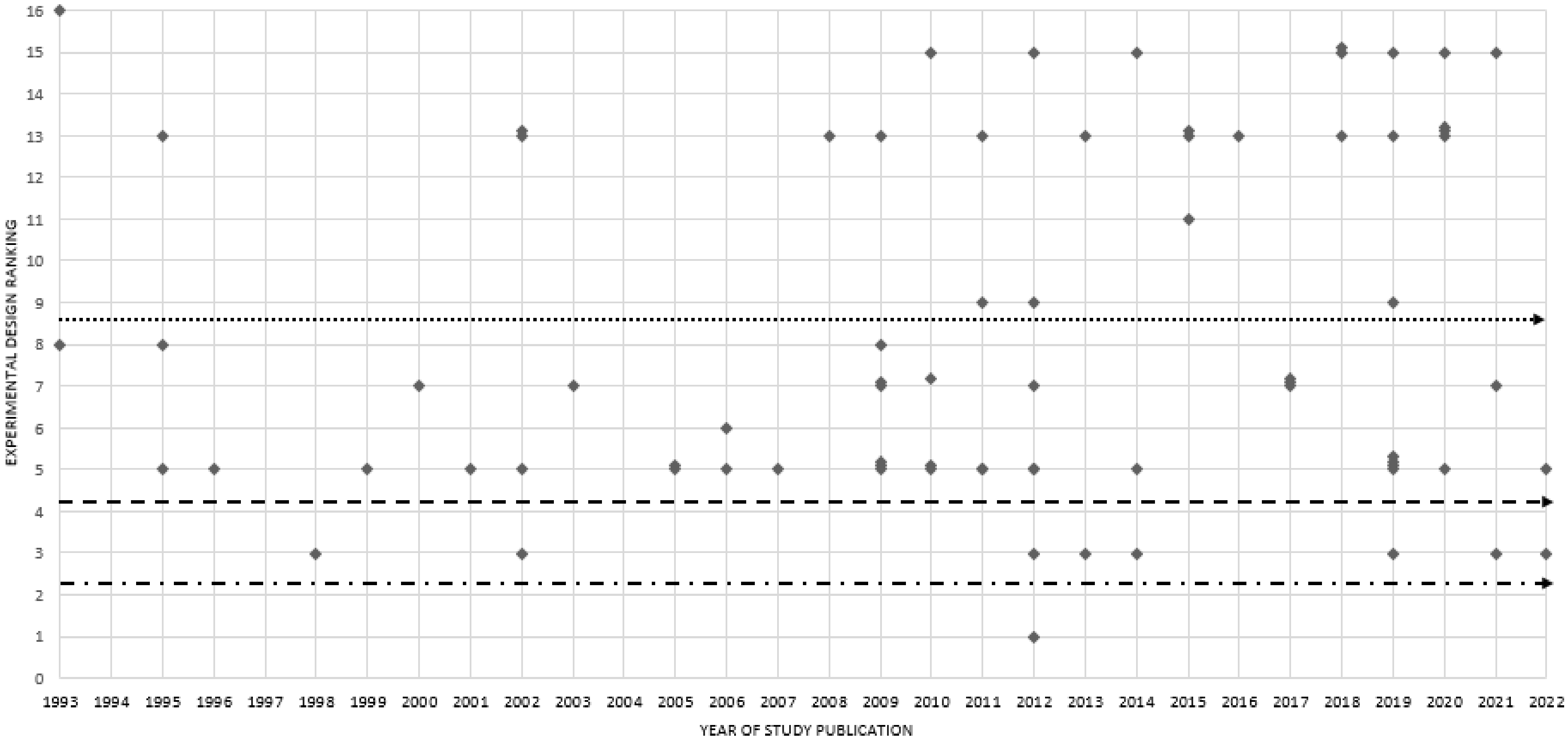

Figure 3.11 Showing combination of the 76 studies reviewed by Allen et al. 2013b and Castle et al. 2022.
Inferential power of studies according to Hone 2007. Multiple studies conducted with the same classification number in the same year are differentiated using a single unit decimal places which enables differentiation of overlapping circles. Studies below the dotted line (top) used a control. Studies below the dashed line (middle) used a control and randomisation. Studies below the dashed and dotted line (bottom) used a control, randomisation and replication.

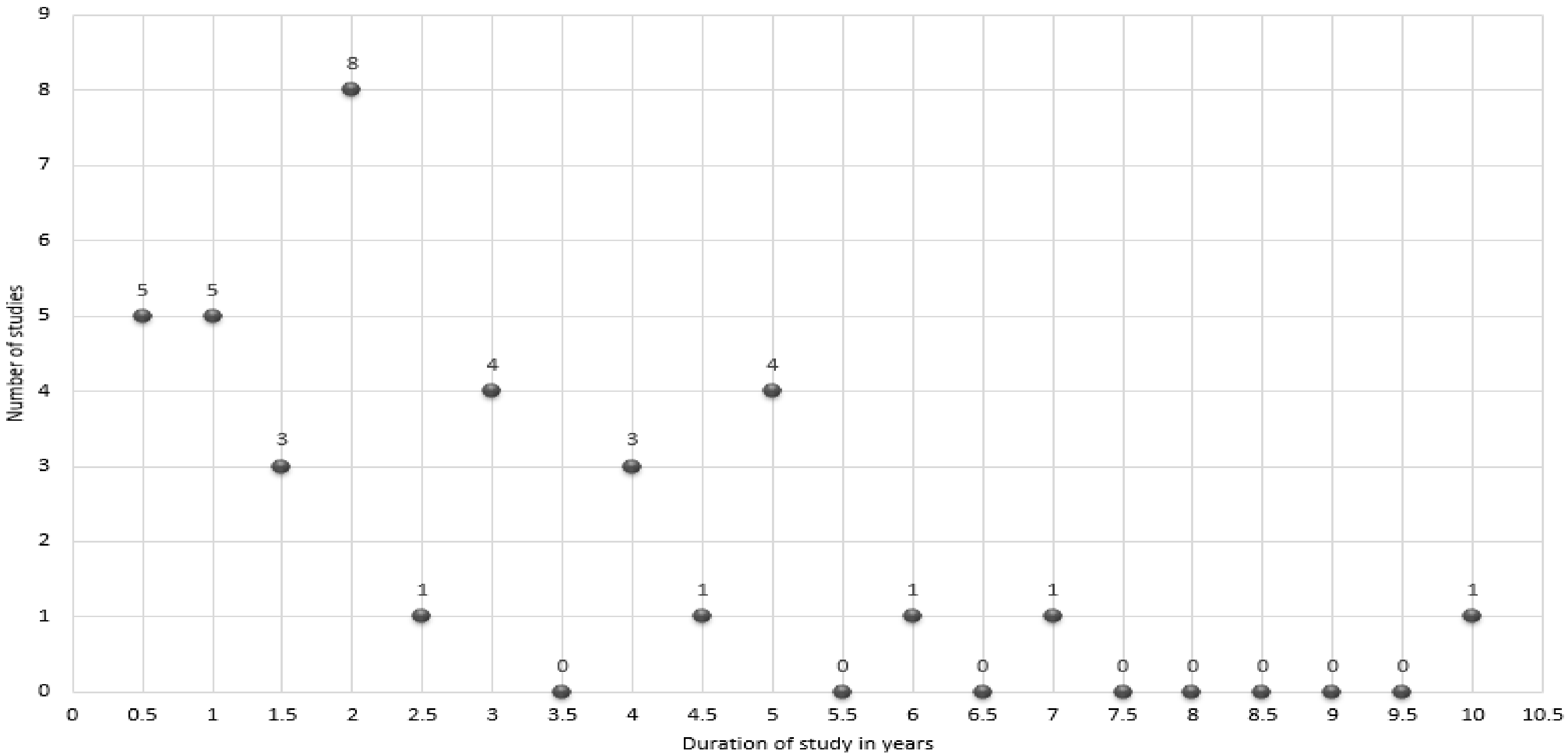

Figure 3.2 Duration of the study period for 37 studies investigating the relationship between dingoes and mesopredators between (February 2011 and May 2022). The data labels denote the number of studies pertaining to each time period.

Most of the studies were conducted over a short timeframe. Ten out of 37 (27%) of the studies were conducted within one year or less, 21 out of 37 (57%) of studies were conducted in two years or less and 26 out of 37 (70%) were conducted in three years or less (Figure 3.2). All of the studies under three years duration had very weak experimental designs, and studies with the strongest inference were typically four to seven years in duration. Studies with study periods exceeding seven years had weaker experimental designs. Moreover, many of these ‘longer term studies’ were not the result of repeated sampling at a given study site(s) during the study period, but were instead the result of combining data from two disjunct studies conducted at different places at different times, giving the misleading appearance of a long term study (Moseby et al. 2019). The mean duration of the six studies that met the threshold for causal studies (ranking 3) was 4.4 years.

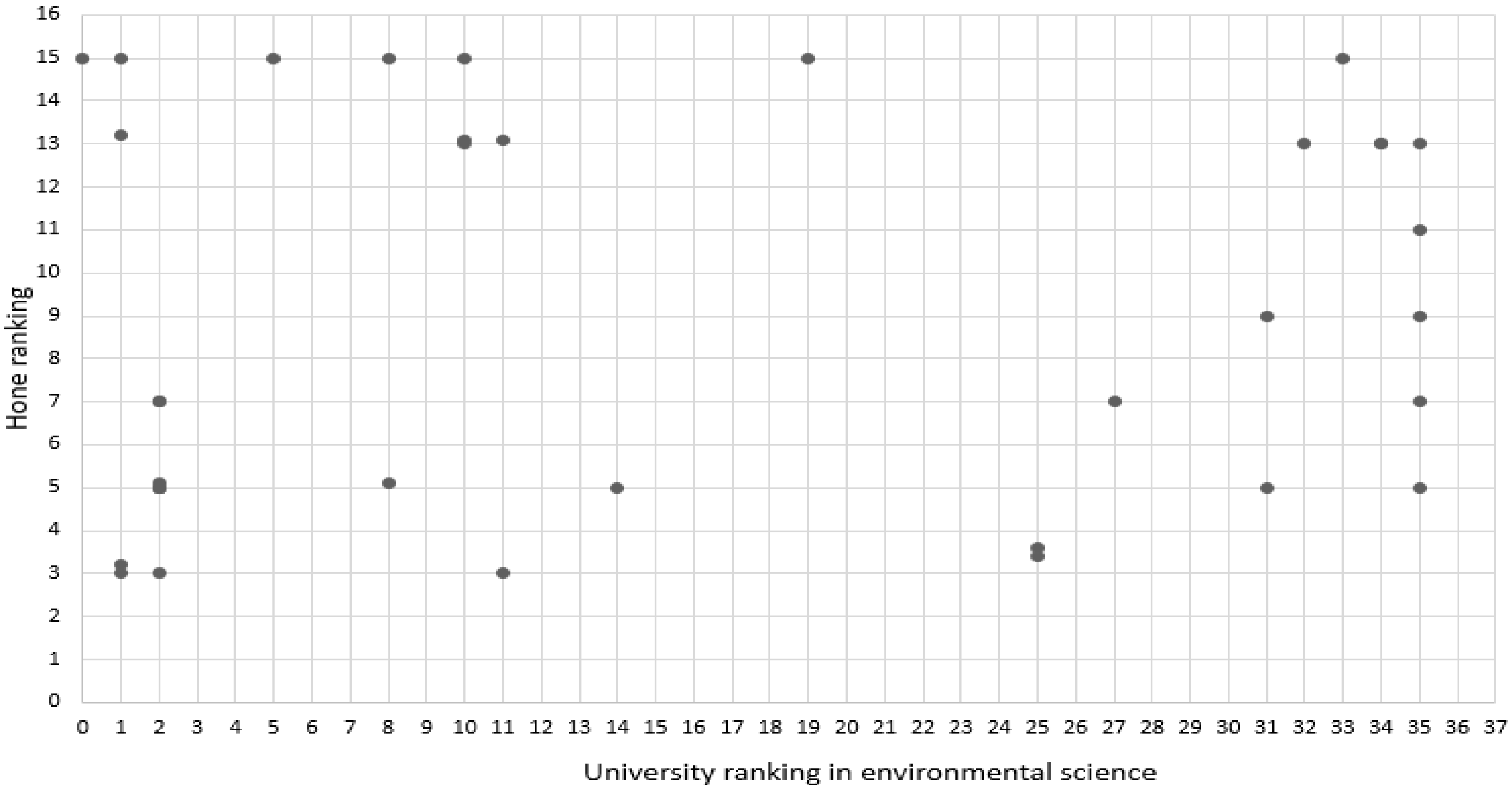

Figure 3.3 Relationship between the strength of inference according to Hone and university ranking in environmental science for 37 studies investigating the relationship between dingoes and mesopredators between (February 2011 and May 2022).

I found no relationship (Figure 3.3) between the inferential strength of the study and the university's rank in environmental science ($r = 0.20$, df 35, $p = 0.24$). The highest university rank was the University of Queensland (UQ) with a ranking of 1, and the lowest was the University of Western Sydney with a ranking of 35. Higher ranking universities published both weak and strong experimental studies just as lower ranking universities have published both weak and strong experimental studies (Figure 3.3).

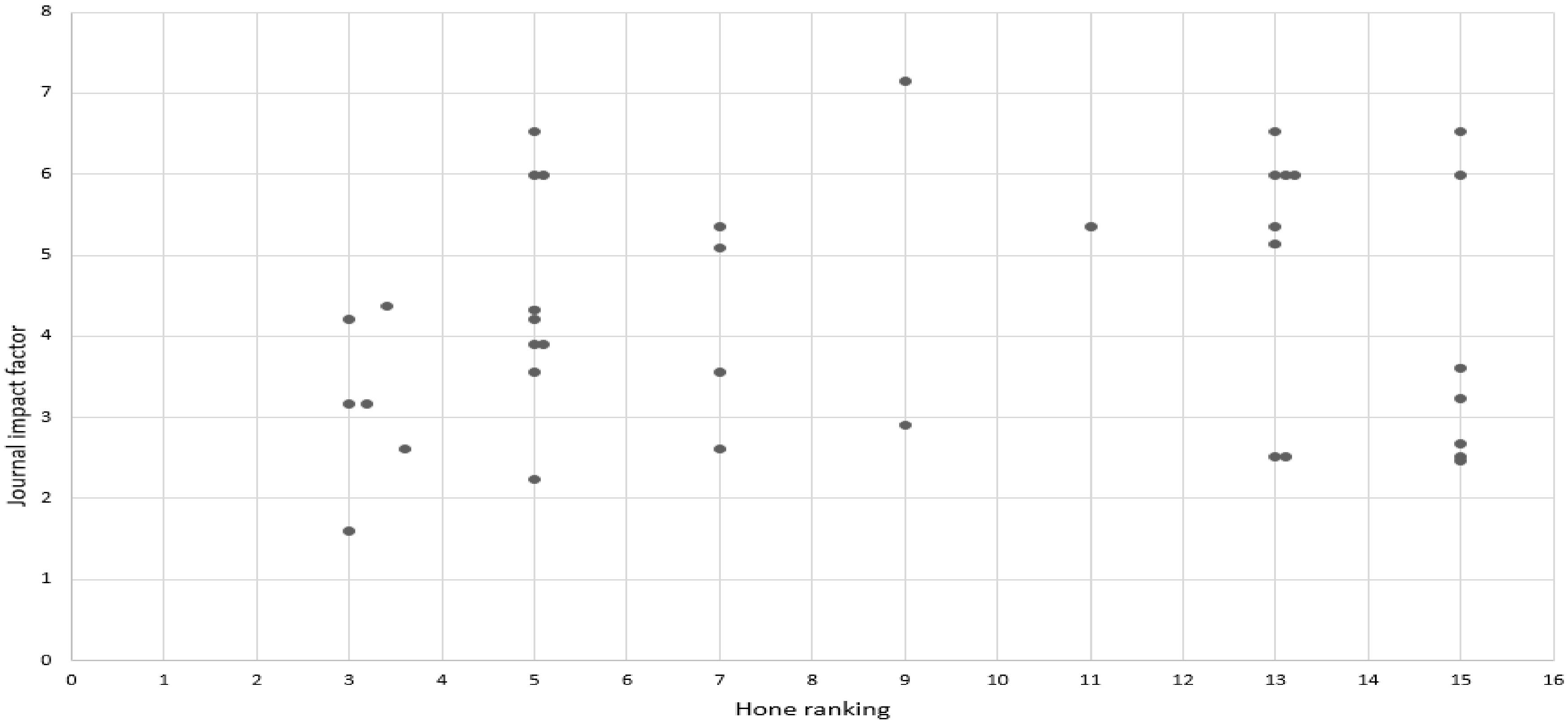

Figure 3.4 Relationship between the strength of inference according to Hone and journal impact factor for 37 studies investigating the relationship between dingoes and mesopredators between (February 2011 and May 2022).

I found no relationship between the inferential strength of the study and the impact factor (Figure 3.4) of the journal it was published in (r = 0.19, df 36, p = 0.26). The highest journal impact factor within the 37 studies was 7.144 published in the journal *Global Ecology and Biogeography* by (Letnic, Greenville, et al. 2011) and the lowest impact factor was 1.6 for a study published in the *International Journal of Ecology* by (Moseby et al. 2012). Higher ranking journals have published both weak and strong experimental studies just as lower ranking journals have published weak and strong experimental studies (Figure 3.4). The strongest experimental studies were published in journals with impact factors between 1.6 and 4.379 (Table 3.2).

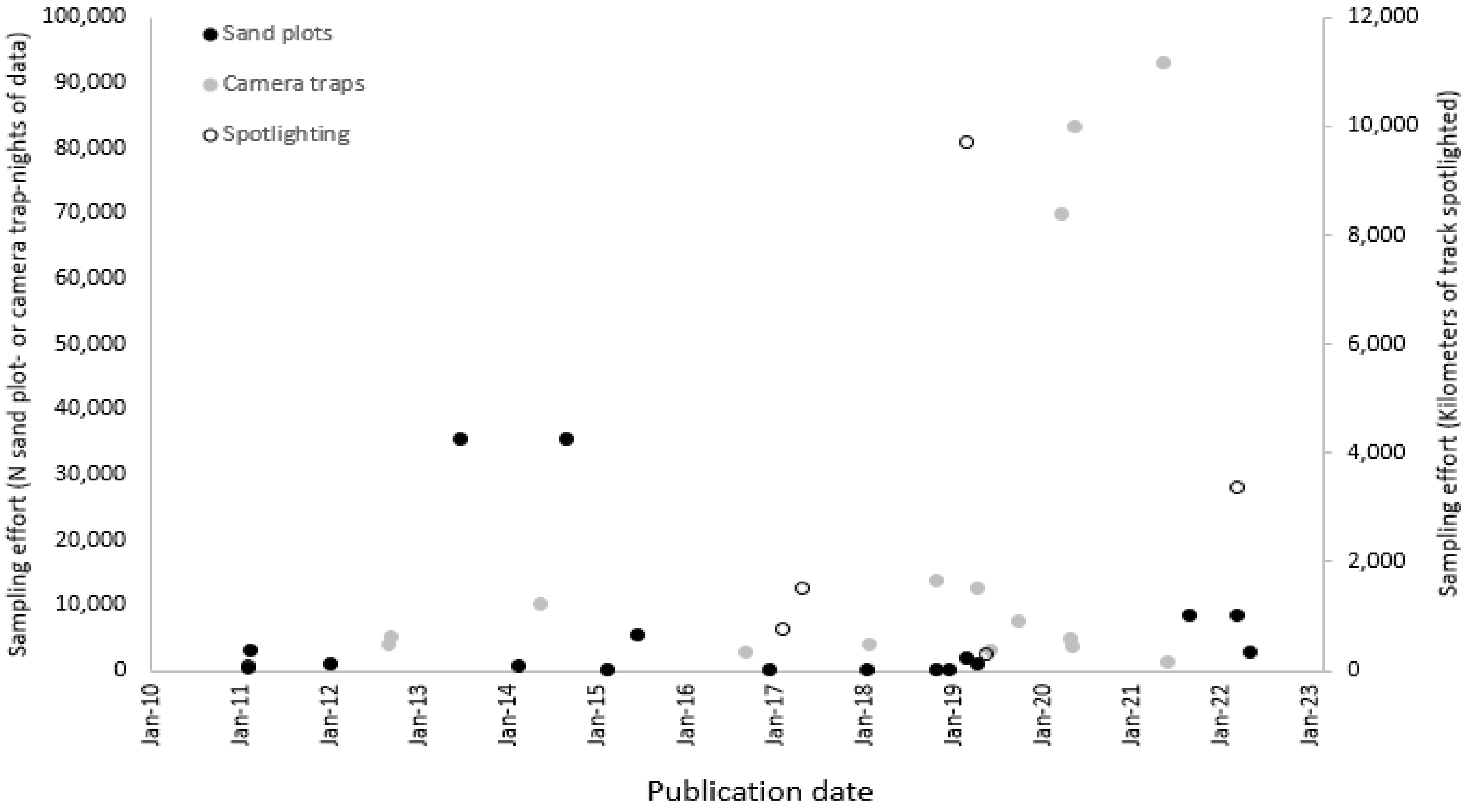

Figure 3.5 Temporal trends in sampling effort or amount of available data contained in the 37 studies investigating the relationship between dingoes and mesopredators between (February 2011and May 2022).

The amount of sampling effort and data reported in each study was highly variable. Only 4 of the 17 (24%) studies using PTI reported using over 6 000 sand plot-nights of data (Allen, Allen, et al. 2013; Allen, Allen, et al. 2014; Castle et al. 2021; Castle et al. 2022) and only 4 of the 19 (21%) camera studies reported more than 14 000 nights of data (Stobo-Wilson, Stokeld, Einoder, Davies, Fisher, Hill, Mahney, Murphy, Scroggie, et al. 2020; Stobo-Wilson, Stokeld, Einoder, Davies, Fisher, Hill, Mahney, Murphy, Stevens, et al. 2020; Wysong, Iacona, et al. 2020; Kreplins et al. 2021). All six of the studies that met the threshold for causal inference were sand plot studies, one of which (Castle et al. 2021), also reported using spotlighting data. Most studies reported relatively low sample sizes, or contained relatively small volumes of data (Figure 3.5). Five studies reported exceptionally large volumes of data (Allen, Allen, et al. 2013; Allen, Allen, et al. 2014; Feit et al. 2019; Stobo-Wilson, Stokeld, Einoder, Davies, Fisher, Hill, Mahney, Murphy, Scroggie, et al. 2020; Kreplins et al. 2021), though only two of these also used strong experimental designs (Allen, Allen, et al. 2013; Allen, Allen, et al. 2014).

Discussion

The ability of apex predators to supress mesopredators is considered to be an important factor for determining the structure and function of ecosystems (Estes et al. 2011). But supporting data for these roles is deficient for almost all species, and dingoes are reported to be one of the only two species (the other is grey wolves, *Canis lupus*), for which sufficient supporting data is available (Ripple et al. 2014). However, literature on dingo-mesopredator relationships has been the subject of much debate, primarily centred on the reliability of the experimental designs and sampling methods used in the various original studies (Allen et al. 2011b) and what kind of inferences those methods allow. It is almost certain that correlative studies have no power whatsoever to determine causal factors

(Platt 1964; Shadish et al. 2002; Hone 2007) and that studies with more data should contain a greater amount useful information than studies that contain less. For many years researchers have been calling for the publication of studies with inferentially strong experimental designs and large volumes of data to better elucidate dingoes' ecological roles and cut through some of the unnecessary acrimonious debate (Glen et al. 2007; Newsome et al. 2015). I therefore reviewed the experimental designs, sampling strategies and sampling methods reported in empirical dingo-mesopredator studies published over the last decade to determine the inferential strength of the available literature on this issue and identify the robust studies capable of addressing these important ecological issues. I found that the vast majority of studies remain correlative and of relatively short duration (Table 3.2, Figure 3.2). Moreover, the strength of these studies is not improving over time and is unrelated to the academic ranking of the institution that produced the work or the impact factor of the journal that published it (Figure 3.4). Only six studies published since 2012 use methods that reach the threshold for providing information on causal relationships between dingoes and mesopredators, all others are correlative, and only two of these six studies obtained relatively large volumes of data (Table 3.2; Figure 3.5). No classical experiments were performed but four of the six unreplicated experiments were implemented in a way that could potentially enable re-analysis as classical experiments (Allen, Allen, et al. 2013; Allen, Allen, et al. 2014; Castle et al. 2021; Castle et al. 2022). In other words, most studies investigating dingo-mesopredator relationships did not collect enough data, nor did they have sufficient strength in their experimental design to reliably quantify these relationships even if they did.

The quality of studies performed over the last three decades can be clearly seen in Figures 3.1. When I included the results from Allen, Fleming, et al. (2013), I found that of 76 published studies investigating dingo-mesopredator relationships, only 9 (12%) of those studies were capable of making justifiable causal statements concerning the ecological role of dingoes. The science of dingo control-induced mesopredator release is not getting any better after nearly 30 years of research, but instead appears 'stuck in the mud'.

One might expect that the quality or rank of the journal might be a useful guide for identifying the best studies, but this is not the case. I found that journals with higher impact factors do not necessarily publish higher quality research. The use of quantitative citation rate analysis does not facilitate quality assessments of a published study (Kurmis 2003) and my results further support this view. While it is a truism that journal impact factor is a function of citation rates, citation rates are not a function of journal impact factor (Seglen 1997). For example, the study by Geary et al. (2018) was published in the *Journal of Applied Ecology* which has an impressive journal impact factor of 6.5. However, this camera study had an inferential ranking of 15, which means it had no experimental control, no randomisation and no replication. Furthermore, the study was conducted over a very short timescale (5 months from April-August), there was non-independence between their survey plots and their results were potentially confounded by seasonal differences in predator activity as well. Several other studies were also published in high ranking journals despite exhibiting many of these same methodological weaknesses. In contrast, (Castle et al. 2021) conducted a predator-removal experiment in a closed system that was published in the journal *Food Webs,* which has a journal impact factor of 2.6. Their experiment had an inferential ranking of 3, which means it only lacked replication. Information contained within their study, however, suggests that stronger-inference analysis may even be possible if the data were reanalysed in a different way. Furthermore, the experiment was conducted over 5 years with data collected repeatedly every 4 months (in all seasons) and the treatments were independent and actually measured. They were applied on a large spatial scale (over 6 000 km^2), and ultimately collected over 8 000 sand plot nights of data and almost 8 000 km of spotlight survey data. Many such contrasts between individual studies might be made, but the key learning from these observations is that individual studies can be vastly different in their inferential strength and the amount of data they provide; not all published reports are equal.

One might also expect that the reputation or status of the university that produced the work might also be a useful guide for identifying the best studies, but this was also not the case. The university rankings for environmental science varied from 1 (University of Queensland) to 35 (University of Western Sydney) but higher ranking universities were not associated with better quality publications (Figure 3.3). For example, over the last decade, the University of Southern Queensland (ranked 25) published 2 of the 6 studies that actually met the Hone ranking threshold of 3 which allows causal inferences (Castle et al. 2021; Castle et al. 2022) whereas the University of New South Wales, (ranked 2) published 1 study with a threshold of 3 (Moseby et al. 2019), 5 quasi-experiment type I studies and two quasi-experiment type III studies (see Table 3.2). Finally, the duration of the study is also an unreliable indicator of data obtained given that the 7 year study by Gordon et al. (2015) used less than 160 sand plots to formulate their conclusions whereas the 5 year study by Allen, Allen, et al. (2013) reported data from 35 399 sand plots to formulate theirs.

It should be obvious that the most robust studies are those with the strongest inferential ability and the greatest amount of data. Studies that lack the key elements of experimental design, have a paucity of data and are/or are confounded by multiple alternative hypothesis can infer very little. For example, Wooster et al. (2021) obtained 53.33 minutes of footage during three, 1–3 week sampling sessions over three years to record fox behaviour, and from these data concluded that foxes at the study site display confident body language because socially stable dingo packs (which were not measured), but rather assumed, are more predictable and less frightening (than socially unstable dingo packs which were also not measured). Their experiment had no experimental control, randomisation or replication, and very little data (1 366 camera trap-nights of data). Hence, the causes underlying the observed fox behaviour are unmeasured, unknown, unfathomable and a matter of pure speculation.

In contrast, Allen, Allen, et al. (2013) conducted a predator removal experiment over 5 years at 9 large study sites, spanning 5 ecosystem types and totalling over 45 000 km^2. Sampling was undertaken on a repeated, systematic basis each year over all seasons, yielding 35 399 sand plot nights of data. Their study is one of the six that contained all of the essential elements of a classical experiment and had an inferential ranking of 3.

Only six studies (Moseby et al. 2012; Allen, Allen, et al. 2013; Allen, Allen, et al. 2014; Moseby et al. 2019; Castle et al. 2021; Castle et al. 2022) conducted over the last decade that met the threshold which empowers a study to move beyond mere observational, correlative findings to those inferring causality (Table 3.2; Figure 3.1). All six studies added or removed dingoes to or from a treatment area and recorded the responses of mesopredators. Allen, Allen, et al. (2013) demonstrated no release of mesopredators and concluded that dingo removal in open systems that permit migration does not generate a mesopredator release because contemporary dingo control practices do not remove dingoes for sufficient periods of time to initiate trophic cascades. Castle et al. (2021) demonstrated that complete eradication of dingoes inside closed systems where migration is prevented likewise fail to produce a mesopredator release or trophic cascade response. Moseby et al. (2012) demonstrated that mesopredators released into fenced enclosures containing dingoes are swiftly killed but not consumed by dingoes, concluding that interference competition is the primary mechanism underpinning anecdotal and correlative reports that dingoes suppress mesopredators. Though the results of these strong-inference studies may at first appear contradictory, given that negative dingo-mesopredator interactions obviously occur at small scales (i.e. when individual predators come in contact with each other), they have never been experimentally observed at population-level scales or beyond (Allen, Fleming, et al. 2013).

Some of the studies were written in a way that made it difficult to extract the methodological information needed to confidently determine the reliability of the study. I found ambiguous descriptions of basic methodological details such as how many sand plots were used, when they were used, and where they were deployed (Letnic, Greenville, et al. 2011; Colman et al. 2015; Gordon et al. 2015; Gordon, Christopher E et al. 2017). Other studies (Schroeder et al. 2015; Wysong, Hradsky, et al. 2020), left fundamental data unreported (Table 3.2),and the results from a micro-scale study by Moseby et al. (2019) were obscured and heavily influenced by unrelated data sourced from a separate mensurative study in order to build complex models of hypothesised interactions, rather than report on observed interactions. Based on the information I could extract from the text of each study, I attempted to classify the strength of their experimental designs as they related to exploring dingo-mesopredator interactions. However, individual studies may have weaker or stronger designs than what I have reported depending on how the available data are organised for analysis. In other words, some studies may have been perfectly executed for their intended purposes, but, for the purpose of investigating dingo-mesopredator relationships, all save six of them were correlative at best.

Seven such studies (19%) reviewed here were conducted on either side of the DBF and their experimental control was predicated on the assumption that the density of dingoes inside the fence has been reduced by lethal control to a point where they have become ‘functionally extinct’ (Gordon & Letnic 2016; Contos & Letnic 2019). None of these studies actually measured whether or not the dingoes in their study area were affected in any way by the control programs that targeted them, but merely assumed that they had been affected because they were targeted. Dingo control programs are widely known to reduce dingo populations anywhere from 0–100% (Allen, Engeman, et al. 2014) and often even increase dingo populations (Allen, Allen, et al. 2014) meaning that such assumptions are entirely unsupported without actual measurement of dingo population change. Claims that dingoes inside the fence are functionally extinct is also incongruous with the fact that these functionally extinct dingoes still exert sufficient function to decimate sheep and goat grazing industries across hundreds of thousands of square kilometres. The claim is also dubious given that sheep producers inside the DBF in western Queensland are forced to erect cluster fencing around their properties in order to save their remaining flocks from being eradicated by those same functionally extinct dingoes (Chudleigh et al. 2011). These facts do not support the assertion that dingoes inside the dingo barrier fence are functionally extinct, and correlative studies can provide no support to alter this view. Indeed the caveats of some of the authors align with this conclusion. One of these studies by Feit et al. (2019) conceded that their study only yielded correlative evidence because they did not manipulate dingo abundance and instead relied upon an assumed difference in dingo density across the fence. Rees, Kingsford, et al. (2019) further acknowledged the most parsimonious observation that 150 years of intensive sheep, goat and kangaroo grazing pressure (and not dingo absence) may explain the loss of groundcover inside the DBF, diminishing their conclusion that dingo removal indirectly reduced groundcover and granivorous bird abundance through a complex series of unmeasured and cascading ecological events. These admissions highlight exactly why correlative studies provide no reliable data on dingoes' ecological roles.

Correlative surveys are certainly useful for formulating hypotheses about potential causal processes for DC–ITC, but they are unable to demonstrate those causal processes, (Caughley 1977; Underwood 1997; Shadish et al. 2002; Hone 2007; Fox et al. 2015) regardless of continued cries that they represent 'strong evidence' (Gordon, Christopher E et al. 2017; Geary et al. 2018; Leo et al. 2019). One of the simplest things researchers could do to substantially improve their inferences would be to randomly select their treatment areas, along with undertaking repeated sampling to actually measure the effect of their treatment. This will require moving away from the stock-standard snapshot comparisons (Table 3.2) of baited and unbaited areas characteristic of many studies, towards the implementation of dingo addition or removal experiments in randomly selected treatment areas. Had this been done it would have more than doubled the number of studies capable of causal inference. Spatial scales displayed enormous variation with some studies being conducted inside a 1 km^2 area e.g. (Forsyth et al. 2019) while others sampled in combined treatment areas exceeding 45 000 km^2 (Allen, Allen, et al. 2013). It is evident from the data in table 3.2 that some studies used 35 399 sand plots nights of data and some used 48, some used 93 000 camera nights and some used 1 300, some studies drove over 9 000 kilometres conducting spotlight surveys and some drove only 90 kilometres. There is no magic number that represents a sufficient sample size, and we might expect sample sizes to remain variable. But it should be obvious that greater amounts of data are likely to provide a lot more information than smaller amounts, especially when those data are collected within a strong experimental design. Apparently, there has been no consensus reached among Australian environmental scientists with regard to sampling effort. Standardising survey effort may assist with comparing “apples with apples” when comparing the findings of similar groups of studies

Conclusion

I conclude that the growing body of evidence claiming that dingoes suppress mesopredators and initiate trophic cascades is based almost entirely on a growing body of low-inference studies with no capacity to reliably describe such processes, and claiming otherwise is overt science denialism (Allen et al. 2017a). The failure of the science to improve over time is also disheartening, in that it represents much wasted time and effort for no advancement in knowledge. I warn that continued failure to improve the inferential strength of dingo-mesopredator experiments will maintain this trend. I support the views expressed by (Glen et al. 2007; Allen et al. 2017b; Engeman et al. 2017; Haswell et al. 2017; Newsome et al. 2017) that predator manipulation experiments conducted on large spatio-temporal scales are the most effective way to progress the science on the ecological role of the dingo, and we strongly discourage land managers and policy makers from basing their decisions on the collective results of the many weak and correlative studies available. Management decisions based on such unreliable information may inevitably lead to poor ecological outcomes (Allen et al. 2011a), and possible extinctions. Readers may be justifiably pessimistic about the future of dingo science given that similar conclusion were postulated by (Allen, Fleming, et al. 2013) a decade ago, and there has been little improvement in the reliability of work on this subject since that time. Despite twenty four out of 37 studies (65%) critiqued in this review supporting positive dingo management as a conservation tool, IUCN guidelines indicate that proposed dingo reintroductions should not proceed. Until researchers in this field commit to improving the inferential strength of their experimental designs and avoid the methodological pitfalls that continue to confound their findings, the scientific knowledge of dingo ecology and management will remain unreservedly ‘stuck in the mud.’

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CHAPTER 4: TERRESTRIAL MESOPREDATORS DID NOT INCREASE AFTER TOP-PREDATOR REMOVAL IN A LARGE-SCALE EXPERIMENTAL TEST OF MESOPREDATOR RELEASE THEORY.

Chapter 4 is the first of two published papers reporting on the predator data obtained from my field experiment.

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Terrestrial mesopredators did not increase after top-predator removal in a large-scale experimental test of mesopredator release theory

Geoff Castle, Deane Smith, Lee R. Allen & Benjamin L. Allen

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Abstract

Removal or loss of top-predators has been predicted to cause cascading negative effects for ecosystems, including mesopredator release. However, reliable evidence for these processes in terrestrial systems has been mixed and equivocal due, in large part, to the systemic and continued use of low-inference study designs to investigate this issue. Even previous large-scale manipulative experiments of strong inferential value have been limited by experimental design features (i.e. failure to prevent migration between treatments) that constrain possible inferences about the presence or absence of mesopredator release effects. Here, we build on these previous strong-inference experiments and report the outcomes of additional large-scale manipulative experiments to eradicate Australian dingoes from two fenced areas where dingo migration was restricted and where theory would predict an increase in extant European red foxes, feral cats and goannas. We demonstrate the removal and suppression of dingoes to undetectable levels over 4–5 years with no corresponding increases in mesopredator relative abundances, which remained low and stable throughout the experiment at both sites. We further demonstrate widespread absence of negative relationships between predators, indicating that the mechanism underpinning predicted mesopredator releases was not present. Our results are consistent with all previous large-scale manipulative experiments and long-term mensurative studies which collectively demonstrate that (1) dingoes do not suppress red foxes, feral cats or goannas at the population level, (2) repeated, temporary suppression of dingoes in open systems does not create mesopredator release effects, and (3) removal and sustained suppression of dingoes to undetectable levels in closed systems does not create mesopredator release effects either. Our experiments add to similar reports from North America, Asia, Europe and southern Africa which indicate that not only is there a widespread absence of reliable evidence for these processes, but there is also a large and continually growing body of experimental evidence of absence for these processes in many terrestrial systems. We conclude that although sympatric predators may interact negatively with each other on smaller spatiotemporal scales, that these negative interactions do not always scale-up to the population level, nor are they always strong enough to create mesopredator suppression or release effects.

Introduction

Global biodiversity loss is accelerating and the rate of species extinctions now exceeds the background rate by 2–3 orders of magnitude[1]. Up to 80% of the world's largest terrestrial predator populations are in decline as a result of habitat loss and fragmentation, human conflict (especially livestock-related conflict), and reductions in prey populations[2]. Because many predators fulfil important ecological functions, such as regulation of herbivory[3,4], the loss or removal of top-predator populations can be particularly concerning for some ecosystems[5,6]. One major concern is the potential for subsequent increases in the abundance and impacts of mesopredators that are reported to have devastating consumptive and non-consumptive effects on multiple species[7,8,9], especially endangered prey species[10]. Mesopredators are expected to be suppressed by larger-sized top-predators, so losing or removing top-predators is expected to produce a 'mesopredator release' with undesirable cascading effects on prey fauna at lower trophic levels. Understanding the ecological outcomes of top-predator removal is important for improving predation management practices and stemming biodiversity declines[11,12].

Dingoes (*Canis familiaris;* a canid) are Australia's largest terrestrial predator, and one of the two top-predator species in the world (the other is grey wolves, *Canis lupus*) whose ecological roles have been most thoroughly explored[2]. At an average adult body weight of 15.7 kg[13], dingoes are believed to suppress extant populations of European red foxes (*Vulpes vulpes;* ~ 7 kg; another canid) and feral cats (*Felis catus;* ~ 3 kg; a small felid) (e.g.[8,11,14,15,16,17]. All three sympatric species co-occur across most of the continent and have done so since foxes were introduced in ~ 1878 and cats between 1824 and 1886[18]. Dingoes did not evolve in Australia and arrived less than 3,500 years ago[19], but are nevertheless considered a naturalised native species[20,21]. All three species are generalist predators with overlapping dietary niches which include livestock and threatened native fauna. All three predators are also subject to broad-scale lethal control programs in many places to reduce these impacts[22,23]—control programs which simultaneously target all three predators. However, some have raised concern that controlling or reducing dingoes in this context could have the net effect of releasing or increasing foxes and/or cats that will then go on to exacerbate declines in native fauna populations (e.g.[24,25,26,27,28]). Goannas (varanidae) are similar-sized, native, reptilian mesopredators with generalist diets that might also be released following mammal predator removal[29,30].

Dingoes are supposed to supress mesopredator abundance through two mechanisms. First, being larger and more dominant in agonistic interactions, dingoes are expected to directly kill mesopredators. Evidence for dingoes killing foxes, cats, and goannas has been largely inferred from the presence of their remains in dingo scat and stomach samples[31,32,33,34], but has also been directly observed in some cases[35]. Second, their broadly overlapping distributions and diet suggests that dingoes may suppress mesopredators through indirect competition for shared prey resources[10,11,33], though others have pointed out that this simply means all three predators eat the same things and threaten the same species[36]. While these two types of negative interactions undoubtedly occur at fine spatial and temporal scales, reliable evidence for population-level effects at larger spatial and temporal scales has been mixed and equivocal[37,38]. In areas of eastern and northern Australia where bottom-up factors like rainfall and climate are more stable, long-term studies have not found negative relationships between populations of dingoes and mesopredators[39,40,41]. Thus, negative relationships between dingoes and mesopredators are expected to be strongest and most apparent in arid and semi-arid areas of Australia where the climate is unpredictable and competition for unreliable prey resources is strongest[10]. Frequent drought conditions produce frequent prey shortages which should enhance the suppressive effects of dingoes on mesopredators in these areas[42,43].

Many studies have investigated these processes (at least 22 literature reviews are listed in[44]). However, after approximately five decades of dingo research there is still no reliable evidence for dingo control-induced mesopredator release due, in large part, to the systemic and continued use of low-inference study designs to investigate the subject[12,37,45,46]. This conclusion is debated by some authors[47,48,49,50,51]. However, what is *not* debated is the fact that almost all the evidence 'for' the occurrence of dingo control-induced mesopredator release comes from snap-shot, single-survey or correlative studies, whereas almost all the evidence 'against' it comes from large-scale and long-term manipulative experiments of greater inferential value[37,45,52]. Correlative studies are certainly useful for formulating hypotheses about potential causal processes, but they have no power whatsoever for demonstrating causal processes—this is indisputable[53,54,55,56,57,58,59,60,61,62]. Thus, not only is there a demonstrable absence of reliable evidence for dingo control-induced mesopredator release, there is also demonstrable evidence of absence for it as well.

For example, Allen and colleagues[63,64] (but see also[65,66]) experimentally demonstrated that contemporary dingo removal practices (i.e. repeated, temporary reductions in dingo abundance) at multiple sites across Australia did not produce mesopredator releases of foxes, cats or goannas, and cessation of dingo removal practices (i.e. passive increases in dingo abundance) did not produce decreases in fox, cat or goanna abundances either. Theirs was an applied study in open systems to investigate whether or not contemporary predation management practices produced the mesopredator releases feared by some people. They demonstrated that mesopredator releases did not occur because dingo populations quickly recovered following each removal event, so the 'trophic cascade' never got a chance to begin. Johnson[50] (see also response by[67]) quite rightly observed that the unmanaged immigration or post-control recovery of dingo populations in those experiments meant that they were not a strict test of mesopredator release theory, recommending that future inferences about the absence of mesopredator release could be improved by experimentally controlling for dingo migration. Newsome et al.[68] reinforced this view, affirming that uncertainty about dingo effects on mesopredators could be resolved if experiments were conducted in closed or fenced ecosystems where dingo numbers can be sufficiently and sustainably reduced and the ecological outcomes observed. Allen and colleagues' experiments[63,64] were the second-largest predator manipulation experiments in the world, and the largest and strongest-inference experiments ever conducted on the subject in Australia. But addressing the migration issues raised by Johnson[50] and Newsome et al.[68] required fortifying the levels of inference even further by conducting similar experiments in closed, fenced systems where dingo populations can be manipulated more effectively.

Implementation of such predator manipulation experiments had already begun, and are described here for two fenced sites (Morven and Tambo) used for extensive livestock production in a semi-arid area of Australia. Our goal was to eradicate dingo populations inside the two fenced areas and give foxes, cats and goannas a chance of being freed from any suppressive effects that dingoes might impose on them. At each site we compared the fenced treatment areas to adjacent, paired nil-treatment areas outside the fences, and simultaneously monitored populations of dingoes, foxes, cats and goannas over 4–5 successive years. We repeatedly sampled predator populations through spotlighting (density estimates) and passive tracking indices (PTI; relative abundance estimates). In this context, mesopredator release theory predicts that foxes, cats and/or goannas would increase inside the fences—relative to outside the fences—in response to the demonstrated removal of dingoes inside the fences. We therefore predicted that:

1. Dingo PTI would be, on average, lower inside the fences than outside;

2. Mesopredator PTI would be, on average, higher inside the fences than outside;

3. Dingo control would supress or remove dingoes inside the fenced areas, but not outside;

4. Mesopredator PTI trends would increase inside the fenced areas relative to the paired outside nil-treatment areas over time; and

5. Negative relationships would be apparent between dingoes and mesopredators.

Our experiments and analyses closely follow the 'classical experiment' approach most recently applied by Allen et al.[63,64] and recommeded by Glen et al.[69], Johnson et al.[50] and Newsome et al.[68]; although in the present case, our treatment areas were also fenced with dingo-proof fencing to prevent migration of dingoes back into controlled areas post-control, thereby facilitating their sustained removal inside the fences. We assess overall mean PTI differences between treatments (inside vs. outside); evaluate the success of dingo removal efforts inside the fences (i.e. demonstrate a treatment effect); assess the responses of mesopredator PTI to dingo removal over time, after accounting for normal seasonal variation in predator activity (i.e. determine if mesopredator releases occurred); and evaluate the relationships between dingoes and mesopredators (i.e. verify the presence of the proposed mechanism). Finally, we summarise the status of manipulative experimental research on dingo-control induced mesopredator release and offer some guidance for future studies investigating the ecological outcomes of top-predator removal or introduction.

Results

Spotlighting efforts produced insufficient data on predator populations for any meaningful analyses (Table 1; see also[70]), so we focussed all our analyses on data obtained from passive tracking indices.

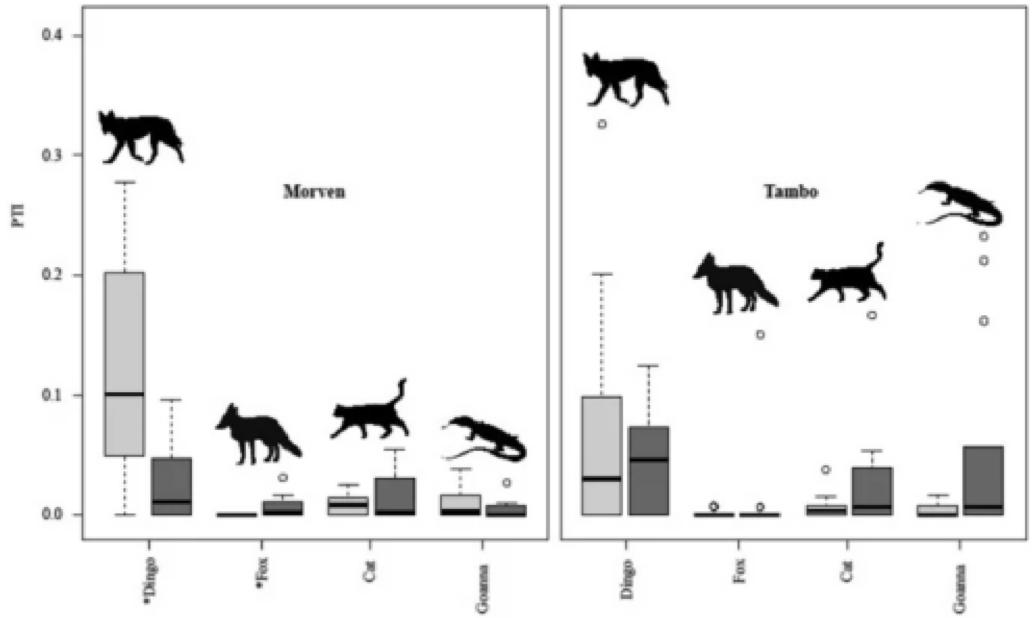
Table 1 Total number of dingoes, foxes, feral cats and goannas observed during the entire study period.

Overall patterns in relative abundance

Dingoes, foxes, cats and goannas were present both inside and outside the fences at both sites; each were detected on sand plots in both treatments at both sites, although foxes outside the fence at Morven were only detected during spotlighting (Table 1). Welch's T-tests indicated that overall mean dingo PTI was lower inside the fence at Morven ($t = -3.579$, $df = 17$, $p = 0.002$) where fox PTI was higher ($t = 2.721$, $df = 13$, $p = 0.018$). Cat PTI appeared higher inside the fence at Tambo ($t = 1.997$, df 22, $p = 0.059$). We found no other differences in overall mean PTI for any predator species at either site (Table 2, Fig. 1). Thus, the greater overall relative abundance of foxes inside the fence at Morven and cats inside the fence at Tambo were the only instances (of six possible site x mesopredator combinations) where a sympatric mesopredator was detected more frequently inside the fence at either site.

Table 2 Overall mean predator PTI values inside and outside fenced areas at Morven and Tambo.

Figure 1



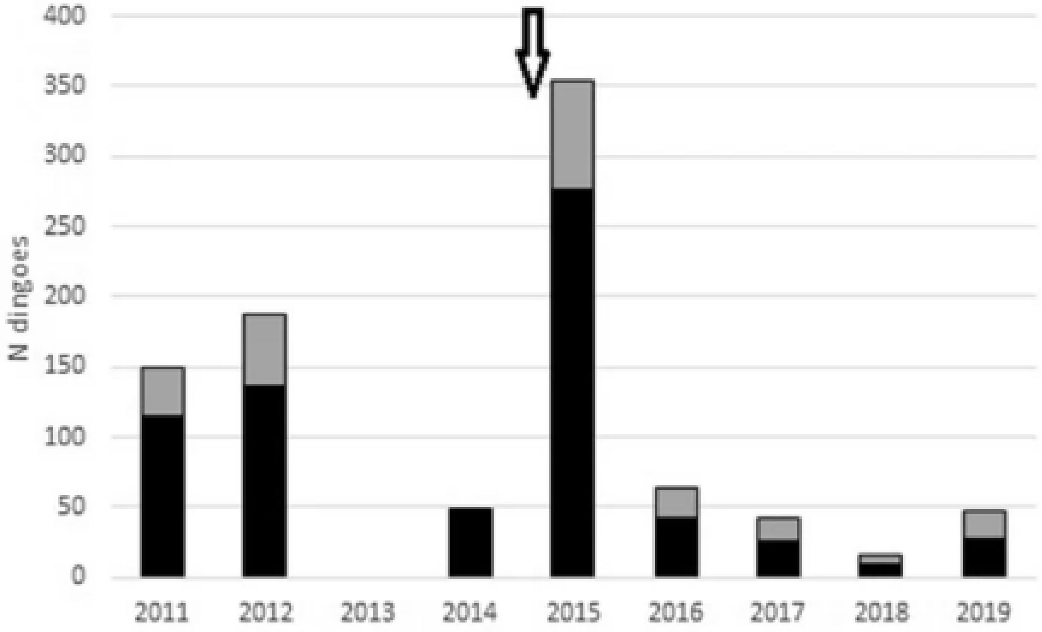
Overall mean PTI values for dingoes and sympatric mesopredators at Morven and Tambo. PTI values are from all surveys outside (light grey) and inside (dark grey) fenced areas. *Denotes demonstrable differences, see Table 2 for details.

Evidence of a treatment effect

We could not quantify all forms of dingo control undertaken at each site (i.e. repeated poison baiting, trapping, and shooting) to confirm exactly how many predators were removed and precisely when they were removed, but we were able to ascertain some accurate information on dingo control effort.

Livestock producers at Morven reported that all livestock properties engaged dingo trappers on at least one occasion each year, and many of them engaged trappers on multiple occasions each year. Self-reported trapping records from Morven indicated that at least 906 dingoes were trapped and removed from inside the fenced area between 2011 and 2019, of which 226 (25%) were pups or juveniles (Fig. 2). However, the dingo exclusion fence was still under construction in the early part of this period, and the fence was not completely sealed until January 2015. A rapid and substantial increase in control effort followed the completion of the fence, and livestock producers reported the subsequent removal of 354 dingoes in the first year after fence completion. In addition to this trapping effort, all properties inside the fence at Morven distributed poisoned baits twice each year, except for one property which baited five times each year. Like baiting, trapping at Tambo was less intensive, and yielded only 250 dingoes between 2016 and 2019. Trappers did not report trapping or shooting any foxes, cats or goannas during the study at either site.

Figure 2

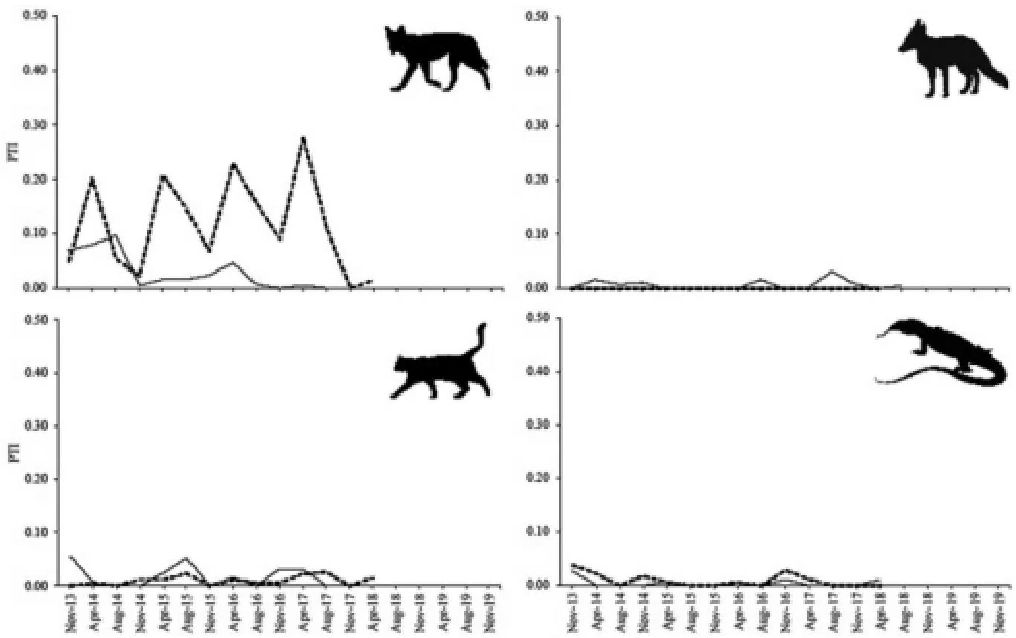


Dingo removal effort at Morven. The number of landholder-reported adult (black) and pups/juvenile (grey) dingoes trapped and removed from inside the fenced treatment area at Morven, 2011 to 2019. Dingo control effort varied over time, but was most intensive and fairly consistent between 2015 and 2019. The arrow denotes the approximate date when the fence was completely closed.

These dingo control efforts are reflected in the PTI trends which suggest a marked decline of dingoes inside the Morven fence between 2015 and 2016, with sustained suppression of dingoes at undetectable levels thereafter (Fig. 3). Outside the fence at Morven, dingo PTI increased over time while fluctuating with seasonal peaks in autumn (mating season) and troughs in spring (whelping season)—a predictable and normal seasonal activity pattern widely expressed by dingo populations across the continent[21,22]. Dingo PTI at Tambo likewise fluctuated seasonally both inside and outside the fence (Fig. 4), although dingo control efforts at this site were apparently not as effective at supressing dingoes (Fig. 4). At Tambo, dingo PTI steadily declined over time both inside and outside the fence. After accounting for seasonal influences on our data and assessing differences in dingo PTI trends between inside or fenced and outside or unfenced areas (Table 3, Fig. 5), we found that dingoes were indeed reduced and sustainably supressed inside our treatment area at Morven (autumn data

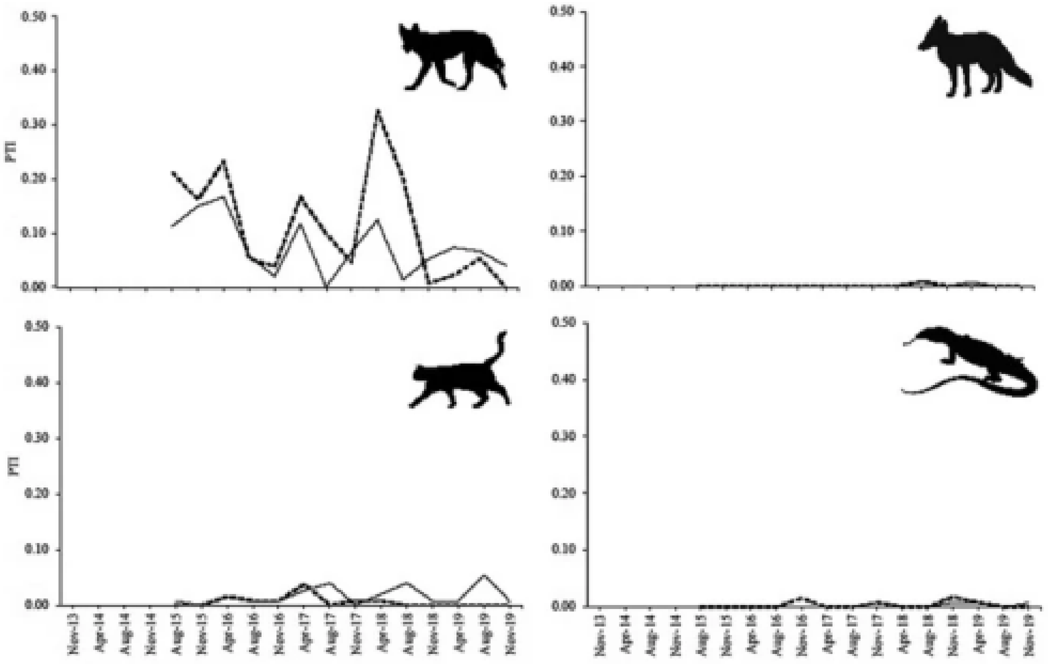
$R^2 = 0.86$, $p = 0.072$; spring data $R^2 = 0.99$, $p = 0.004$; combined data $R^2 = 0.36$, $p = 0.040$). This did not occur at Tambo, where dingoes declined slower inside the fence then they did on the outside (spring data $R^2 = 0.82$, $p = 0.034$).

Figure 3



PTI trends of dingoes, foxes, cats, and goannas at Morven, 2013–2018.

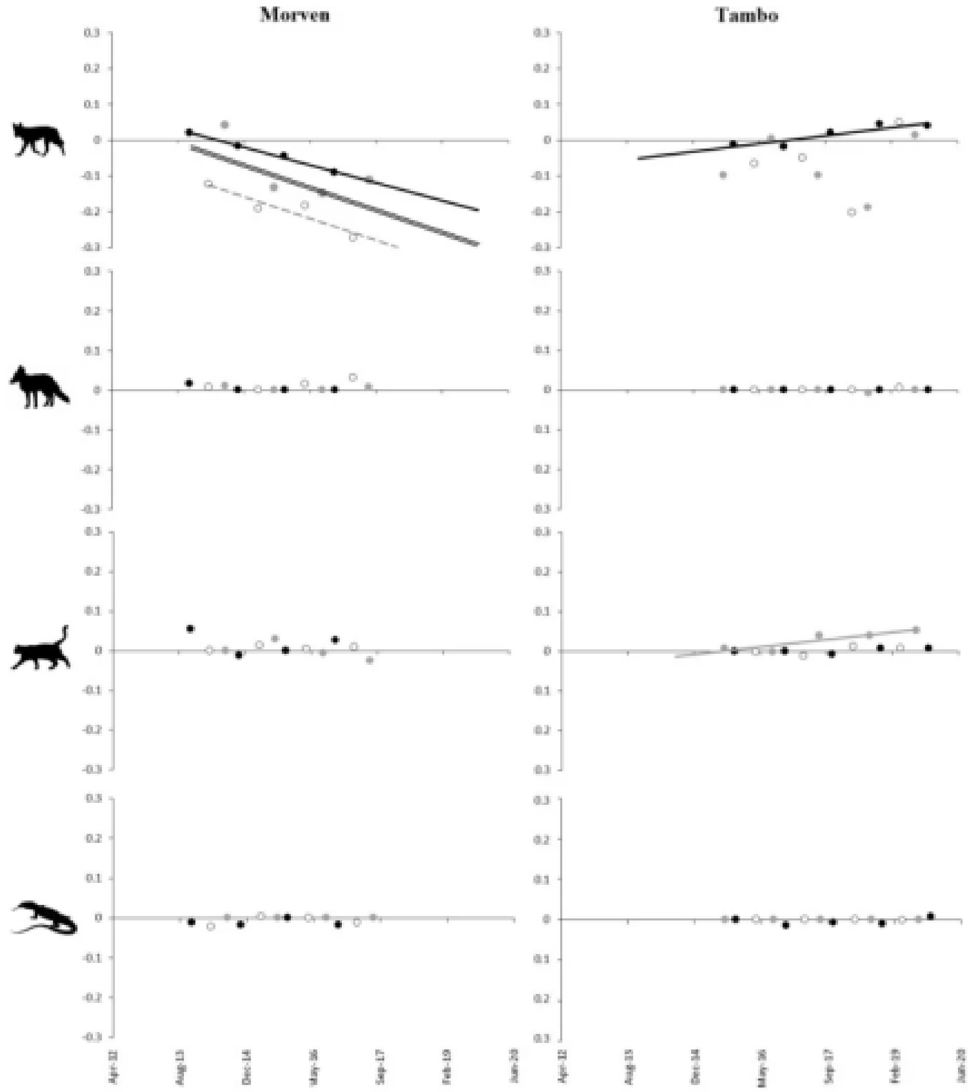
Figure 4



PTI trends of dingoes, foxes, cats, and goannas at Tambo, 2015–2019.

Table 3 Temporal trends in dingo, fox, cat and goanna PTI treatment differences at Morven and Tambo.

Figure 5



Temporal trends in dingo, fox, cat and goanna PTI treatment differences at Morven and Tambo. Black marks and black lines = November (spring) surveys, hollow marks and dashed line = April (autumn) surveys, and grey marks and grey line = August (winter) surveys. Black double-line = all seasons combined. Ascending slopes denote increases inside the fence relative to outside, whereas descending slopes denote decreases inside the fence relative to outside. See Table 3 for further details.

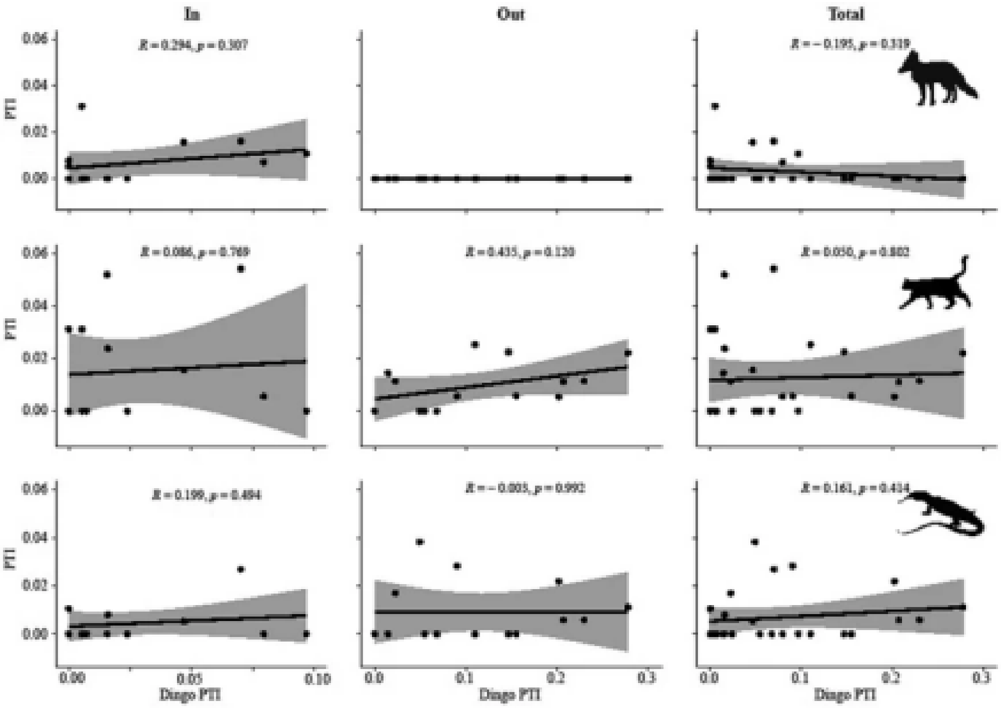
Evidence of mesopredator release

We found no evidence of fox, cat, or goanna PTI increases inside fenced areas where dingoes had declined (Figs. 3 and 4)—a result reinforced by the almost complete absence of any PTI divergence between treatments for any mesopredator (Fig. 5). Fox, cat and goanna PTI trends were essentially identical inside and outside dingo-fenced areas at both sites (Figs. 3, 4, 5). Each of these mesopredator species were present inside the fence at the beginning of the study at both Morven and Tambo, but by the end of the study 4–5 years later each had failed to increase inside the fence (relative to outside) despite dingo control efforts demonstrably eliminating and supressing dingo populations, at least at Morven. The only possible exception to this was cats at Tambo. At this site, analyses of data from the winter surveys suggested that cat activity peaks in winter increased over time, but this trend was not detectable when using the autumn or spring data, or all the data combined (Table 3, Fig. 5).

Relationships between dingoes and mesopredators

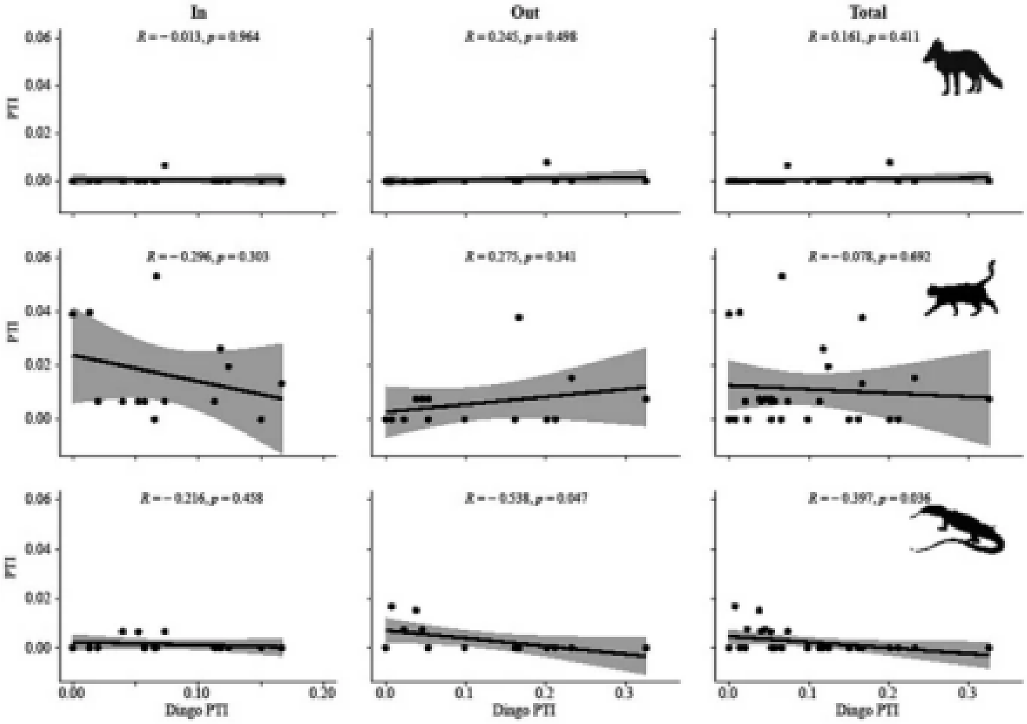
We found no relationships—negative or positive—between dingoes and either foxes or cats at Morven, whether inside the fence, outside the fence, or pooling the data and ignoring the fence altogether (Fig. 6). We likewise found no relationships—negative or positive—between dingoes and either foxes or cats at Tambo, whether inside the fence, outside the fence, or pooling the data and ignoring the fence altogether (Fig. 7). We did detect a positive relationship between cats and goannas inside the fence at Morven ($r = 0.566$, $p = 0.035$) and a positive relationship between foxes and goannas inside the fence at Tambo ($r = 0.536$, $p = 0.048$). But the only negative relationship we detected was between dingoes and goannas outside the fence at Tambo ($r = -0.538$, $p = 0.047$), which was also detectable when data was pooled and fences were ignored ($r = -0.397$, $p = 0.036$). All other pairwise relationships between dingoes, foxes, cats and goannas indicated that predator relative abundances fluctuated independently of each other (Figs. 6 and 7). Fox, cat and goanna PTI remained relatively low and stable regardless of whether or not dingo PTI was low or high. In other words, mesopredator population trends fluctuated independently of dingo population trends over time both inside and outside the fences.

Figure 6



Relationships between dingo PTI and fox, cat and goanna PTI at Morven. Shading denotes 95% confidence intervals. Pairwise correlations (r) and p values also shown. Note that the scales are inconsistent between panels and have been adjusted to allow closer inspection of the data.

Figure 7



Relationships between dingo PTI and fox, cat and goanna PTI at Tambo. Shading denotes 95% confidence intervals. Pairwise correlations (r) and p values also shown. Note that the scales are inconsistent between panels and have been adjusted to allow closer inspection of the data.

Discussion

Mesopredator release theory predicts that the removal or loss of top-predators will cause numerical increases in mesopredators[7,8], but we found no evidence for these processes in our experiments. Neither goannas, cats, nor foxes increased inside the fence at Morven despite the sustained removal and suppression of dingoes there (Figs. 3 and 5). Initial lethal control efforts (Fig. 2) demonstrably depopulated the area inside the fence of dingoes (Figs. 3 and 5) and ongoing control efforts held them at near-undetectable levels over subsequent years while their relative abundance increased outside the fence (Fig. 3). Yet despite the sustained removal of dingoes throughout the fenced area, the extant mesopredator populations inside the fenced area at the beginning of the study failed to increase over time. Similarly, neither goannas nor foxes increased inside the fenced area at Tambo despite substantial declines (about a 60% reduction) of dingoes inside the fence at that site (Fig. 4). However, we could not attribute this decline solely to dingo control efforts because dingo PTI trends declined slower inside the fence than they did on the outside, implying a relative increase of dingoes inside the fence at Tambo (Fig. 5). Cats also failed to increase inside the fence at Tambo, although there was some suggestion that their winter-time activity peaks increased over time (Table 3, Fig. 5). Regardless, this possible increase in cat activity cannot be considered evidence of dingo control-induced mesopredator release given that dingoes at Tambo also increased inside the fence relative to outside (Fig. 5; i.e. a positive relationship between dingoes and cats). Results from both sites therefore provide no evidence of mesopredator release following dingo control and removal.

Overall PTI differences between treatments

After pooling data from all 14 surveys together to assess overall treatment differences in mean PTI, we found few differences for any predator except for foxes and dingoes at Morven, and cats at Tambo (Table 2, Fig. 1). At Morven, dingoes were lower inside the fence and foxes were higher (Fig. 1, Table 2). We expected overall mean dingo PTI to be lower given the intensive dingo control efforts inside the fence there. Dingo PTI at Morven ranged between 0.07 and 0.10 (i.e. one dingo track observed every 7–10 sand plots, on average) in the first year of the study, but was zero (not a single dingo track observed) throughout the entire last year of the study (Fig. 3). Though the difference in overall mean fox PTI might at first be considered a tantalising suggestion of a possible mesopredator release, this was instead an artefact of our sampling given foxes were not recorded on sand plots outside the fence on any occasion at Morven (Table 2). In other words, the Welch's two-tailed T-test was not functioning as a test for differences between PTI means in this case, but rather as a one-tailed T-test for a difference between a mean and zero. This test result essentially indicates that there were more than zero foxes inside the fence at Morven, which we had already known at the beginning of the study (Fig. 3) and is not particularly noteworthy. Moreover, and despite being a common way of searching for and claiming evidence of mesopredator releases (for examples, see[24,26,71,72,73]), such simplistic and correlative comparisons of overall mean PTI between treated and untreated areas cannot and do not elucidate any causal processes and hence cannot be used to make inferences about dingo control-induced mesopredator release[45] (but see also[53,54,55,56,57,58,59,60,61,62]).

The lower mean PTI of dingoes inside the fence at Morven (Fig. 1) coupled with demonstration of a treatment effect (Table 3, Fig. 5) confirms our Prediction 1 that the relative abundance of dingoes would be lower in places with intensive and sustained dingo control effort. However, the almost complete absence of higher mesopredator mean PTI values inside the fenced areas at each site did not accord with our Prediction 2 that mesopredator abundances would be higher in places where top-predators are reduced or absent.

Evidence of a treatment effect, dingo control effectiveness

There are a few possible ways of gauging the effectiveness of dingo control from the data in our study, or confirming a treatment effect. For this study we define effectiveness as the complete eradication or near-eradication of dingoes, or some sort of demonstrable reduction in dingo PTI. Like others we might consider an overall mean dingo PTI difference between treatments as evidence of a treatment effect (cited above), but alone, that would be a very weak approach. A far stronger approach is to assess divergence of PTI trends over time after accounting for normal seasonal influences on PTI variation[67,74]. Using only differences in mean PTI between treatments, we might conclude that dingo control was effective at Morven but not at Tambo (Fig. 1, Table 2). But closer inspection of Fig. 3 concurs and indicates that dingoes were declining inside the fence at the same time they were increasing outside the fence at Morven. Statistical support for this result was apparent using autumn data, spring data, and all data combined (Table 3, Fig. 5). Hence, the hundreds of dingoes removed from inside the fence at Morven by intensive and sustained baiting, trapping and shooting (Fig. 2) did indeed cause a demonstrable reduction in dingoes there, confirming a treatment effect. This does not often occur outside fences[75,76], but can occur in such open systems when control is particularly intensive[22,77].

Dingo control effectiveness at Tambo was not as pronounced given the lower spatial and temporal intensity of dingo control effort there, including the presence of livestock producers inside the fence that did not undertake any dingo control.

Although dingo PTI at Tambo declined by 41–73% inside the fence over the study period (depending on which season was used to measure the decline; Fig. 3), this decline occurred more slowly than it did outside the fence (Fig. 5). This implies a net increase or 'release' of dingoes inside relative to outside, and means that no treatment effect could be confirmed at Tambo. We suspect that the dingo control efforts occurring on both sides of the fence at Tambo were sufficient to reduce dingoes to some degree, but that control efforts inside the fence were clearly not intensive enough to generate demonstrable suppression of dingoes beyond the background levels observed outside the fence, as observed in other studies[78].

These results partially support our Prediction 3, demonstrating that dingo control can effectively reduce dingoes to functionally extinct or undetectable levels inside fences when control efforts are intensive, but not when control efforts are relaxed. Given that Morven was the only site where we demonstrated a treatment effect (Fig. 5), theory would predict that mesopredator releases would be more apparent at Morven than Tambo (discussed below).

The declines and suppression of dingoes at Morven and Tambo also highlight the value of the exclusion fencing erected at our sites (see also[78,79,80,81]). Multiple previous studies have demonstrated that even though dingo populations can be temporarily supressed by substantial amounts up to 100% in open or unfenced systems[22,63,77], they typically recover to pre-control levels within a few months or by the next annual breeding season due to immigration by dispersing dingoes looking for a new home range[82,83]. That dingo populations at Morven were knocked down and then held down inside the fence while dingo populations were increasing outside the fence (Fig. 3) is a powerful demonstration of the utility of cluster fences at excluding dingoes, much like other types of fences exclude other species[79]. This is an important feature of our results because some authors have asserted that even small reductions in dingo abundance produce disproportionate and cascading negative effects on ecosystems through mesopredator release effects. For example, a review of field studies by Ritchie and Johnson[8] concluded that every unit of decreased top-predator abundance leads to a fourfold increase in mesopredator abundance. The repeated temporary reductions of dingo abundance of 50–70% reported in Allen et al.[63] were insufficient to generate such predicted mesopredator releases[50], however, so the threshold level of dingo reductions required are clearly far higher than previously thought (see[10]). Yet Newsome et al.[68] go further and assert that before dingo control-induced mesopredator releases can be confidently demonstrated not to occur, experiments seeking to empirically test mesopredator release theory must use fenced areas where dingoes might be sustainably supressed to extremely low or undetectable levels. The experimental conditions and results from Morven meet these study conditions and produce the best opportunity yet to experimentally test the theory that contemporary dingo removal produces mesopredator releases.

Evidence for mesopredator release

We found no evidence of mesopredator releases following demonstrated dingo removal and suppression. Like the results from all previous manipulative experiments in open systems[63,64,65,66,84,85], not only was the overall mean PTI of mesopredators typically no different between treatments at both sites (Table 2, Fig. 1), but mesopredator PTI trends also fluctuated independently of dingo PTI at both sites over time (Figs. 3 and 4). Divergence analyses further failed to yield any evidence of mesopredator release of foxes, cats or goannas (Fig. 5) despite demonstrably reducing dingoes (Table 3) and holding them at undetectable levels at Morven (Fig. 3). The substantial declines of dingoes at Tambo, though not completely attributable to dingo control, likewise failed to generate mesopredator releases (Fig. 5). These results do not accord with our Prediction 4 that mesopredators would increase following a decrease of dingoes.

Foxes, cats and goannas were present inside the fence at both sites at the beginning of the study (Table 1), so the absence of mesopredator releases cannot be attributable to their physical absence. Goannas and cats, and to a lesser extent foxes, are also not impeded by the exclusion fencing used at our sites, so the absence of mesopredator releases cannot be attributable to disruption of mesopredator immigration opportunities potentially caused by the fencing. Dingoes were demonstrably reduced to undetectable levels inside the fence at Morven and evidently could not recover (Fig. 3) either through immigration or compensatory breeding given their ongoing removal (see also[83]), so the absence of any mesopredator releases at that site cannot be attributable to the absence of a treatment effect. Dingo populations inside the fence were reduced and held at undetectable levels while their relative abundance demonstrably increased year-on-year outside the fence, so the absence of mesopredator releases cannot be attributable to an insufficiently long study period needed to observe population-level predator abundance changes, which we were able to observe. The increasing dingo population outside the fence at Morven also suggests that environmental conditions in the region were able to support predator increases, at least until the final year of the study, so the absence of any mesopredator releases cannot be confidently attributable to unsatisfactory environmental conditions either (likewise found by[39,40]). And even if environmental conditions were considered poor, the number of available prey per capita of mesopredators should have increased given the removal of dingoes which share the same prey resources, producing conditions meant to exacerbate mesopredator releases[10,11,33]. Dozens of studies (listed in[38,86]) have also reported road-based passive tracking indices to be a reliable means for detecting mesopredator releases, so the absence of mesopredator releases cannot be attributable to an inability of our survey techniques to detect such changes[51,87,88]. Given that our experiment was executed in a way and at a time and place where mesopredator releases should have been detected if they occurred, we can think of no reason for the consistent absence of any detectable mesopredator releases other than a true absence of any population-level suppressive effects of dingoes on mesopredators.

Relationships between dingoes and mesopredators

Evidence for inverse relationships between dingoes and mesopredators is absent in most studies (for examples, see[38,41,85,89]), although enough studies (reviewed in[10,11,68,69,90]) and passionate advocacy by authors (for examples, see[14,16,91,92]) have reported inverse relationships to create the romantic religious belief among many people that dingoes supress mesopredators. Unfortunately however, all studies reporting inverse relationships are correlative (akin to our analyses in Table 2 and Fig. 1) and therefore have no power to identify any causal processes, including dingo control[37,45], so these beliefs are not grounded in strong evidence. Despite a great deal of discussion and excitement on the subject, at the time of writing there is still not a single available study that shows a demonstrable increase of foxes or cats in response to demonstrable decrease in dingoes, or vice versa—studies with both a treatment and an experimental control site where predator numbers have been measured both before and after the treatment or over time, and where the predicted treatment effects and mesopredator responses have been measured and demonstrated. Thus no experimental evidence for dingo control-induced mesopredator releases presently exists in either open systems[63,64,65,66,84] or closed systems (as reported here), but for completeness we nevertheless assessed pairwise relationships between dingoes and mesopredators to search for the presence of the proposed ecological mechanism and help understand why the predicted mesopredators releases are not occurring.

Similar to most other studies we likewise found very little evidence of negative relationships between dingoes and mesopredators at either site (Figs. 6 and 7). Of the four relationships (out of a possible 36 pairwise combinations) we did detect, two were positive, two were negative, and none were between dingoes and foxes or cats. These results were consistent inside fenced areas, outside fenced areas, and after pooling data together from both inside and outside fenced areas at both Morven and Tambo, revealing that our Prediction 5 was also not supported by our data. This absence of any reliable evidence for negative relationships between dingoes and mesopredators[37,38] may be the underlying reason behind the failure of dingo control to produce any mesopredator releases. Despite observations that dingoes share the same prey resources as mesopredators[31,33,34] and dingoes occasionally kill mesopredators in agonistic interactions[35], there is now a large and continually growing body of robust experimental evidence that these interactions do not scale-up to population level effects of dingoes on mesopredators in open or closed systems.

Our experiments focussed on the numerical responses of mesopredators to the removal of dingoes, and we did not directly assess the non-consumptive effects of dingoes on mesopredators. Some propose that a landscape of fear also exists between predators sufficient to drive trophic cascades even in the absence of demonstrable numerical effects[93,94], or what Haswell et al.[95] describe as a 'behaviourally-mediated trophic cascade'. For example, Colman et al.[96] and Brook et al.[24] both assert that fox and cat activity should increase even if their populations are not affected numerically. Our data were not intended to measure any psychological fear effects dingoes may have on mesopredators, but even if these fear effects do occur, they did not manifest themselves as mesopredator activity increases within five years after the fencing and subsequent removal of dingoes (Figs. 3, 4, 5; see also[97]). This suggests that dingoes do not create such fear effects at the population-level, or, that dingoes create such profound and lasting fear effects that they can exclude and supress mesopredator activity long after complete dingo removal. We believe this latter conclusion is unsupportable given that foxes and cats colonised Australia in the presence of dingoes[18] and all three species presently coexist across most of the continent[28]. That dingoes and goannas have coexisted for thousands of years and all the dingoes in Australia could not stop foxes or cats from spreading across the continent following their introduction supports the experimental results of the present study and others that dingoes do not exhibit strong mesopredator-suppressive qualities. Unfortunately, they all appear to coexist rather well, as they do on the continents where they evolved together before they were each brought to Australia[20,98]. We believe that the most parsimonious explanation for these observations and our experimental results is that dingoes do not suppress mesopredators at the population or community level, but additional data beyond our experiments is required to better explore potential non-consumptive effects of dingoes on mesopredators and what these might mean for fauna at lower trophic levels[85,99].

Based on previous experience we anticipate that some might question the reliability of our experimental results on grounds that: (1) passive tracking indices are unsuitable for monitoring changes in the relative abundance of dingoes, foxes, cats or goannas; that (2) count data like ours must be somehow transformed before it can be properly analysed; that (3) our analytical procedures are uninformative and we should have instead used occupancy modelling, quantile regressions, or some other form of modelling; that (4) we should have setup our analyses of the available experimental treatments and controls in some other way; or that (5) such applied, experimental tests of mesopredator release theory are somehow invalid because dingo control practices are known to also kill foxes and sometimes cats (but not goannas). These and other issues have been raised almost every time the published results of a study do not support the fashionable, religious belief that contemporary dingo control practices cause mesopredator releases (for examples, see[46,48,49,50,100,101]). As has been already discussed at length in many previous reports, however, to such criticisms we would simply respond by restating that: (1) passive tracking indices are a sensitive, robust, and valid survey technique for simultaneously monitoring relative abundances of dingoes, foxes, cats, goannas and many other terrestrial species; that (2) the arising count data do not necessarily require transformation and can be analysed in a variety of reliable ways that do not oblige researchers to use quantile regressions, occupancy models, or one particular analytical technique over another; that (3) experimental design features like large scales, treatment independence, randomisation, the presence of paired experimental controls, measurement and demonstration of a treatment effect, and stratified random sampling over multiple seasons and years, each add inferential value that cannot be matched by alternative correlative study designs that do not include these features; and (4) the reality that foxes and sometimes cats are also killed during dingo control programs has not constrained a great many other studies from claiming that dingo control causes widespread mesopredator releases despite this issue (for examples, see[24,26,71,96,102,103,104,105,106]). We do not elaborate on these issues here because they have already been discussed at length in many previous reports (for examples, see[12,20,56,64,67,74,86,87,88,107,108,109,110]). We encourage interested readers to first familiarise themselves with these reports before judging the results of our manipulative experiments to be unreliable.

Conclusions

Australia holds the embarrassing title for the country with (by far) the most mammal extinctions in modern history, and many more threatened fauna species are predicted to become extinct over the next few decades[111,112]. There are a variety of interacting reasons for this, but one of the primary causes of mammal decline in Australia is the pervasive impacts of feral cats and European red foxes[28,113,114]. Because dingoes also threaten many mammal species and have been associated with mammal extinctions, declines, and failed reintroduction attempts in the recent past[36,115,116], the positive indirect effects that dingoes are supposed to create by suppressing mesopredators are thought to be greater than their negative direct effects[10]. This has prompted advocacy for cessation of dingo control on grounds that doing so will supress mesopredators and stem mammal declines[14,16,91,92]. However, our large-scale and long-term manipulative experiments reveal that this view is unsupported, which has important consequences for predation management policy and practice across Australia.

Our results add to the large and growing body of long-term mensurative studies[39,40,41] and experimental evidence that contemporary dingo control practices—including repeated temporary suppression of dingoes[63,64,65,66,84,85] and also complete suppression of dingoes within fenced areas (this study)—do not produce mesopredator releases of foxes, cats or goannas. Moreover, the widespread and common absence of demonstrable negative relationships between dingoes and mesopredators at the population level (reviewed in[37,38,52]; see also[41]) further indicate that dingo control-induced mesopredator releases are unlikely to be found elsewhere. This implies that cessation of dingo control is not going to help combat the serious threat from foxes and feral cats, or that advocating for use of dingoes as some sort of biocontrol tool against cats and foxes is also misguided. We do not discount the possibility that mesopredators might be released following dingo control in some future study, or that foxes and cats may change their behaviour in the presence of dingoes without being affected numerically, but we expect such a result would be 'the exception' and not 'the rule' given the demonstrably widespread absence of evidence and evidence of absence for dingo control-induced mesopredator releases.

These results from Australia add to the growing body of evidence from other countries that mesopredator suppression or release processes are not ubiquitous. Work from Europe[117,118], Africa[119,120,121,122,123], Asia[124,125,126], North America[9,127], and South America[128,129] also continue to report an absence of strong top-predator effects on mesopredators, with bottom-up effects appearing to be more strongly associated with mesopredator population changes. Yellowstone National Park in North America appears to be the location where these effects are most apparent, for wolves, with limited evidence for these processes available for almost all other large carnivores ([2]; see also[12]). We share the view of many[3,68,69,74,107] that large-scale and long-term manipulative experiments are the best way of elucidating top-predators ecological roles and strongly discourage describing correlative studies as strong evidence for top-down effects. We also encourage future studies to assess prey population responses to predator manipulations as a means of bypassing the more academic predator-predator interactions and focussing on the applied issues most pertinent to conservation of threatened species.

Methods

Study sites

Our study was conducted at two sites near Morven (26.30S, 146.90E) and Tambo (25.20S, 146.10E) in south-central Queensland, Australia (for a map of the study sites, see[80]). Both sites are within the semi-arid Mulga Lands Bioregion which is dominated by relatively flat, undulating plains and low, timbered ranges. Mulga (*Acacia aneura*), gidgee (*Acacia cambagei*), poplar box (*Eucalyptus populnea*), coolabah (*Eucalyptus coolabah*), and silver-leaf ironbark (*Eucalyptus melanophloia*) co-dominate the taller vegetation strata at both sites. Mitchell grass (*Astrebla* spp.) is the dominate ground vegetation, interspersed with a variety of other grasses and burrs. The long-term median annual rainfall for Morven and Tambo is 510.0 mm and 518.3 mm, respectively (www.bom.gov.au), and the primary land use activities occurring at both sites are predominately sheep, goat, and some cattle grazing. At Morven, temperatures range between 46.8 °C in summer and – 9.4 °C in winter. Temperatures at Tambo range between 44.5 °C in summer and –5.6 °C in winter. Permanent natural and anthropogenic watering points exist throughout both sites. Both sites are typical and representative of the broader region of south-central Queensland where cluster fences are widespread[80].

Dingo exclusion fencing and lethal control

Dingo exclusion fencing was erected at each site, which consisted of a group of cooperating livestock producers that collectively erected a fence around the perimeter of their adjacent livestock properties, known locally as cluster fences (for further details, see[80,81]). The exact height and style of the fencing varied slightly from property to property, but fences were typically 1.5 m high wire mesh fences with a strained 300 mm apron and an additional one or two barbed wires on top, making the fence 1.8 m high in total. The lower 500 mm of the mesh usually consists of rectangles measuring 160 mm × 100 mm and the upper portion of the mesh consists of 160 mm squares. The fenced area at Morven is 3763 km^2 in size with a perimeter of 424 km which was completed in January 2015. The fenced area at Tambo is 2265 km^2 in size with a perimeter of 330 km which was completed in June 2015. These two cluster fences represent two of the largest cluster fences in the region[80], and each enclose up to 50 individual livestock properties. Thus, their sizes are as large as or larger than all other cluster fences in western Queensland. Dingo home range and movement data collected from the sites prior to the fences being installed[130] suggest that fenced areas of this size should contain hundreds of dingoes from dozens of packs.

Many properties on the inside of each cluster fence erected additional dingo exclusion fences of the same style around their individual property boundaries subsequent to the completion of the broader cluster fence, so that the entire area inside the cluster fences were also bisected with additional exclusion fences. Fences were erected at each site with the intention of subsequently eradicating dingoes from inside the broader cluster fenced areas and prohibiting their post-control immigration or reinvasion from the outside. These fences are also likely to provide some resistance to fox immigration, but are not expected to inhibit movement by cats or goannas in any way. Such fences do not perfectly exclude 100% of dingoes all the time (e.g. flooding or kangaroo pressure can sometimes produce temporary holes in fences which do allow some dingoes inside on occasion), but they are expected to facilitate their near-eradication, or at least enable dingoes to be removed and suppressed to functionally extinct or near-undetectable levels sufficient to raise sheep and goats with negligible predation impacts[81]. Fences at Morven were judiciously inspected and maintained on a regular basis (at least monthly) throughout the study period, with holes typically repaired within a day or two of discovery. Fences at Tambo were inspected and maintained on an irregular basis, with holes left unrepaired for several weeks following discovery in some cases.

Dingoes were controlled inside the fences by a comprehensive and intensive variety of lethal means. Repeated poison baiting with sodium fluouroacetate or ‘1080’ occurred repeatedly around April and October each year; April baiting is intended to target adult dingoes before they breed in autumn, and October baiting is intended to target pups and juveniles before they disperse in spring and summer[131]. All properties in the Morven cluster baited twice each year regardless of how many dingoes were observed or removed, except for one property which baited five times each year. Most of the properties in the Tambo cluster baited likewise, although a small number of cattle-producing properties did not participate in baiting at any time, potentially harbouring dingoes and providing a source of dispersing dingoes inside the Tambo fence.

Professional dingo trappers were employed on a repeated basis throughout the study both before and after fences were completed, along with several non-professional trappers (i.e. livestock workers). Trapping effort varied spatially and temporally inside the two fences, but was particularly intensive in the few years following the completion of the fences. Trapping effort was directed at those places and times where there was evidence of dingoes persisting. Trapping regularly occurred on all properties within the Morven cluster. Most properties in the Tambo cluster also participated in trapping, although the same cattle-producing properties that did not use poison baits likewise did not participate in trapping at any time.

Coordinated and opportunistic aerial and ground shooting activities were also undertaken at both sites, and all three forms of lethal dingo control (baiting, trapping, and shooting) were maintained at relatively high intensity throughout the entire study period. This was particularly true at Morven where there was high degree of cooperation between livestock producers within the cluster fence. However, cooperation between sheep farmers and cattle farmers at the cluster level at Tambo waned subsequent to the erection of individual fences within the cluster, producing a mosaic of smaller fenced areas where dingoes were controlled to a lesser or greater extent. Opportunistic shooting occurred inside all fenced areas at both sites.

Though experiencing short periods of high intensity control, dingoes outside the fences at both sites were generally subjected to only opportunistic shooting or sporadic trapping and baiting efforts which typically have little effect on dingo abundance over time[63].

Experimental design

Each site consisted of one treatment area (inside the cluster fence) where dingoes were intensively controlled and targeted for eradication, and one paired and adjacent nil-treatment area or 'experimental control' area of similar size (outside the cluster fence) where dingoes were only exposed to sporadic and opportunistic forms of lethal control, which is common across the broader region[63]. Experimental sites were randomly selected from the scores of other cluster fences where we could have undertaken our experiments (see[80]); and although the location of fences (or treatments) were preselected by livestock producers, allocation of treatments was essentially randomised with respect to our experimental purposes; general habitat features and historical land use etc. was relatively consistent between treatments. This experimental design was replicated at two independent sites, producing what Hone[56] defines as a 'classical experiment' when results are analysed together, or an 'unreplicated experiment' when results are treated separately for each site. These types of experimental design yield the highest levels of inference possible for these types of studies[69,74], but could have been improved by the inclusion of additional sites and/or additional treatments at each site. Predator population sampling was conducted in April, August and November during each year of the study beginning in November 2013 at Morven and August 2015 at Tambo. Surveys were concluded in April 2018 at Morven and November 2019 at Tambo, yielding 14 surveys at each site over 4–5 years.

Predator density estimation (spotlighting)

Spotlighting transects were established in each treatment at each site to estimate temporal changes in predator density. Six transects inside and six transects outside the cluster fence were established at each site. Each transect was 10 km long and was located along unsealed roads or property tracks to enable consistent vehicle speeds. Spotlighting was conducted from a four-wheel-drive utility vehicle travelling at 15 km/h with a spotter standing in the back with a 100-W handheld spotlight. The spotlight was constantly moved in an approximately 160 degree arc in front of the vehicle as it moved along the road. Each predator observation recorded during the counts included details of the species, group size, and distance (m) perpendicular from the transect centre line, following typical distance sampling methods[132,133].

We anticipated using multiple detection function models to calculate predator density estimates: a uniform key function, plus either a cosine or simple polynomial series expansion; a half-normal key function, plus either a cosine or a Hermite polynomial series expansion; and a hazard-rate key function, plus a cosine series expansion. Akaike's Information Criterion (AIC) were to assist with selecting the most parsimonious model. Where sample sizes were too sparse (< 60 animals) to calculate specific detection functions for each transect, global detection functions were to be modelled for each site (inside vs. outside) from all transects. Density estimates were to be calculated for each species at each survey period.

Relative abundance of predators (passive tracking indices)

Passive tracking transects (or 'sand plots') were established in each treatment at each site to estimate temporal changes in indices of relative abundance (PTI) of predators similar to that reported in Allen et al.[63]. This approach is endorsed by Nimmo and colleagues[51] and has been used widely by many others to investigate this subject[25,26,65]. PTI surveys are robust to the types of temporal and spatial correlations that can affect data derived from alternative techniques because the index makes no assumptions about the number of individual animals responsible for leaving footprints on the same or adjacent sandplots, and can therefore produce valid and reliable estimates of relative abundance when applied correctly[54,86,87,134]. PTI surveys were conducted in the week preceding spotlighting efforts (described above). Sand plots were spaced on transects at 1 km intervals along unsealed roads or vehicle tracks. Care was taken to establish each transect in a mix of habitat types that were similar between treatments at each site, before randomly selecting the location of the first sand plot. Predator tracks or footprints were counted at the same time each day over three consecutive days during each survey, and sand plots were raked and smoothed clear after counting predator tracks or footprints each day. Sand plots obscured by wind, rain or other factors on a given day were removed from all analyses. Tracks were counted for each individual predator that traversed each sand plot (i.e. a continuous measure), and no attempt was made to attribute individual footprints to a specific individual predator[134]. A total of 58 and 64 sand plots were placed outside and inside the cluster fence at Morven, respectively. A total of 44 and 50 sand plots were placed outside and inside the fence at Tambo, respectively. This effort produced a total of 4538 plot nights of data for Morven and 3946 plot-nights of data for Tambo.

Predator PTI was calculated as the number of tracks per plot per night, or the mean of daily means[87,134], which was calculated separately for each predator, treatment, site, and survey. Welch's two-tailed T-tests were used to explore overall mean differences in predator PTI between treatments. We then assessed correlations between dingoes and foxes, cats and goannas over time, separately for each treatment and site, and used linear regression to evaluate temporal divergence of trends in predator PTI differences between treatments (i.e. inside PTI minus outside PTI) separately for each season, and all seasons combined. Accounting for season is necessary given that normal seasonal variation in predator activity is known to otherwise confound inferences and interpretations about predator PTI and relative abundance trends[86]. Severe drought at Morven in the final year of the study caused abrupt population crashes of predators and most other fauna at that time (G. Castle, unpublished data; see also Figs. 3 and 4), so we removed the surveys from this period when assessing population divergences between treatments at that site (Table 3, Fig. 5). All analyses were performed in R[135].

Ethics approval and consent to participate

Ethical approvals to undertake the project were provided by the Queensland Department of Agriculture and Fisheries' Animal Ethics Committee (Approval Numbers: CA 2016/10/1010, CA 2013/10/728, and CA 2018/10/1232) and the University of Southern Queensland's Animal Ethics Committee (Approval Number: 16REA016). All procedures described in this report were performed in accordance with these approvals. The study complies with all relevant institutional and national guidelines.

ARRIVE guidelines

We confirm that our experiment is reported in accordance with ARRIVE guidelines (https://arriveguidelines.org).

Data availability

The datasets supporting the conclusions of this article are included within the article.

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Author information

Authors and Affiliations

Institute for Life Sciences and the Environment, University of Southern Queensland, Toowoomba, QLD, 4350, Australia
Geoff Castle, Deane Smith & Benjamin L. Allen

NSW Department of Primary Industries, Vertebrate Pest Research Unit, Armidale, NSW, 2351, Australia
Deane Smith

Department of Agriculture and Fisheries, Queensland Government, Toowoomba, QLD, 4350, Australia
Lee R. Allen

Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth, 6034, South Africa
Benjamin L. Allen

Contributions

L.A. conceptualised, designed and implemented the study, and collected the data in the early stages of the project. G.C. collected the data in the latter stages of the study. B.A. and D.S. analysed the data. All authors read, contributed to, and approved the final manuscript.

Corresponding author

Correspondence to Benjamin L. Allen.

Ethics declarations

Competing interests

The authors declare no competing interests.

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CHAPTER 5: TOP-PREDATOR REMOVAL DOES NOT CAUSE TROPHIC CASCADES IN AUSTRALIAN RANGELAND ECOSYSTEMS

Chapter 5 is the second of my published papers which reported on the prey data collected and analysed in my field experiment.

CHAPTER 6: DISCUSSION AND CONCLUSION

Key results

I conducted applied predator-removal experiments and demonstrated a measured treatment effect that ongoing lethal control inside cluster fenced areas can effectively reduce and maintain the dingo population to numbers approaching zero.

The Trophic Cascade Hypothesis predicts that this removal or loss of top-predators i.e. (dingoes), from inside the clusters, will indirectly reduce levels of plant biomass (Beschta & Ripple 2009; Ripple et al. 2016; Gordon, C.E. et al. 2017) and small native prey species due to the release of mesopredators and large herbivores (Wallach & O'Neill 2009; Letnic et al. 2018). But I found no evidence that the removal and continued suppression of the dingo inside the clusters resulted in a release of large herbivores (Macropus *spp*.), reductions in groundcover, or statistically significant reductions in small CWR mammal abundance after 4.5 years of observations.

Although many correlative studies have claimed the removal of dingoes from the ecosystem generates a release of mesopredators, my predator removal experiment is the first study to rigorously test these claims in closed systems at meaningful scales. The results of my study align with previous experiments conducted by (Allen, Allen, et al. 2013; Allen, Allen, et al. 2014) in open systems, who likewise found that repeated temporary dingo removals did not produce the expected mesopredator release of foxes, cats or goannas either.

Many studies, including Allen, Allen, et al. (2013) demonstrated that mesopredator release did not occur after poison baiting in open systems because dingo populations quickly reinvaded the baited areas, such that dingo populations could not be suppressed low enough or for long enough to potentially allow the trophic cascade to begin. Although extensive research has been carried out on dingo-mesopredator relationships (see Chapter 3 review Table 3.2), my study is the first and only study that has adequately dealt with the issue of post-control migration of dingoes back into the treatment areas. This was made possible due to the construction of predator-proof enclosures inside the DBF since 2015 by graziers responding to growing dingo predation upon their sheep.

Some potential limitations of my study include the following. (1) Passive tracking indices have been criticised because the absence of footprints can mean both species absence and species present but not detected (Hayward & Marlow 2014). The generally low detection rates of carnivores, especially those that habitually avoid detection, can diminish the reliability of abundance indices if the indices are not generated properly (Engeman 2005). But I did collect them properly, and my PTI surveys were performed on a sufficiently comprehensive spatio-temporal scale that was able to reliably monitor both predator and prey species populations whilst accounting for otherwise confounding seasonal and habitat differences (Allen et al. 2011b). (2) The inability to detect a mesopredator release of cats and foxes following the removal of dingoes may have been influenced by factors other than predator removal because the bottom-up effects of rainfall interact concurrently with top-down predation effects (Claridge 2013; Allen et al. 2018). Australia experienced its highest mean annual temperatures on record between 2011–2020 at 0.94 C above average, with 2019 being the hottest and driest year on record at 1.52 C above average (Burea of Meteorology 8 January 2021). A possible factor influencing our results may be the fact that all of our data was collected during a period of high aridity. It is more likely that mesopredator populations, like prey species, are more regulated by food availability than predation (Holt & Polis 1997), given that highly variable spatiotemporal rainfall and primary production reduces the capacity of Australian ecosystems to support consistent top-down predation (Morgan et al. 2017). (3) I acknowledge that even though the baiting program targeted dingoes, it is likely that some foxes consumed 1080 baits as both canids have exhibited a numerical decline after baiting programs (Mitchell & Banks 2005; Fleming et al. 2012). Having said that, foxes are known to engage in bait caching whereby they bury and retrieve 1080 baits after long extended periods during which the water soluble 1080 can decrease in toxicity (Berry et al. 2014), thus making foxes sometimes more difficult to kill during baiting programs (Towerton et al. 2016). Moreover, bait avoidance by foxes is well documented and selection can quickly remove cavalier individuals over successive baiting events which shifts the remaining conspecifics towards more neophobic individuals (Allsop et al. 2017). Furthermore, three properties inside the Tambo cluster did not participate in baiting and these areas may have provided a refuge from baiting to both dingoes and foxes. While some cats do eat baits, the baiting program is less likely to have affected cat numbers because cats tend to specialize on live prey and are more inclined to eat carrion during the drier winter months and thus exhibit lower uptake of larger dingo baits (Burrows et al. 2003).

It has been suggested that changes in the landscape of fear can potentially alter predator-prey relationships and produce a cascading effect on multiple ecological levels (Gallagher et al. 2017). Fear has the ability to change the way an animal uses the landscape as it attempts to reduce its vulnerability to predation (Laundré et al. 2001). The fundamental tenet of the landscape of fear hypothesis is that species quickly learn to differentiate safe versus dangerous habitat (Laundré et al. 2010). We observed smaller foxes and cats freely moving through the cluster fences during our spotlight surveys. It is therefore conceivable that changes to predator lethality and thus predation risk, occurring inside the clusters in response to the eradication of dingoes, could elicit a migratory response within sympatric predators living outside the fences into the perceived refuge within the fenced areas. This ability to learn could potentially drive a migration of sympatric mesopredators to the inside of the clusters and so cluster fencing may reshape our perspectives and thinking relating to the spatial ecology of animals across heterogeneous landscapes. Laundre et al. (2010) suggest the use of giving up densities, frequency of trapping and levels of vigilance as three viable methods to monitor the landscape of fear. Even though my study did not measure these potential fear effects, I suggest potential landscape of fear effects within cluster-fenced areas should be monitored in future studies. Whatever the fear effects were, if any, they failed to manifest themselves in our study as increased mesopredator migration into areas where dingoes had been removed.

Future studies should continue these predator removal experiments into periods of higher productivity in order to disentangle the effects of climate on predators and, more importantly perhaps, to measure the responses of native species following the removal of dingoes. It is crucial that these studies ensure a demonstrable reduction in dingoes inside the enclosure. Experiments such as this should also be undertaken in different bioregions in order to build upon the evidence presented in our study and gain a broader understanding of the ecological role of dingoes in Australian ecosystems.

The science surrounding the ecological role of the dingo in Australian ecosystems remains polarized due to an emotive view of the species fueled by unsupported beliefs about dingoes arising from the continued use of poorly designed correlative experiments with weak inferential power, as identified in our review (see Table 3.2). Furthermore, many of the authors of these correlative studies failed to acknowledge the weaknesses and limitations in their studies, instead glossing over them and emphasizing their preferred narrative. Many researchers proclaim the dingo as an ecological savior while others caution that such an adaptable 'formerly-mesopredator-but-now-apex predator' may do more harm than good in a system where it has no evolutionary history. Either way, robust discussions on the role of the dingo continue among various stakeholders including scientists, conservation managers and livestock producers (Hayward & Marlow 2014). My results may have important implications for future conservation management decisions given that some conservation decisions have been predicated solely on the findings of unreliable correlative studies, see (Table 3.2). Consequently, decisions based on poor science could lead to further declines or potential extinctions of native species. For example, Letnic et al. (2011) advocate the restoration of dingoes as part of conservation programs due to their perceived ability to reduce the activity of red foxes. Wildlife managers at Taunton National Park made a similar decision to cease dingo baiting based on the "growing body of evidence" that dingoes supress foxes. But after baiting ceased, the critically endangered and last wild population of bridled nailtail wallabies *(Onychogalea fraenata)* precipitously declined until baiting was again resumed, resulting in a rapid increase in the wallaby population (Allen et al. 2011b). I therefore encourage future studies to engage in predator manipulation experiments of higher inferential strength prior to relying on unreliable studies, in order to progress the scientific knowledge of dingo-mesopredator relationships and conserve threatened species more effectively.

My results add to the global understanding of mesopredator release when applied to invasive predators and the benefits that may ensue following their removal from inside fenced areas and the broader landscape. They also add to the growing body of literature that mesopredator release or suppression processes are not ubiquitous. I support the view that large-scale manipulative experiments, conducted over sufficient timescales are the best way of elucidating the ecological roles top predators.

Cluster fenced areas are being erected rapidly in Queensland and other states, and several invasive species currently threatening native wildlife have either been almost eradicated or substantially reduced inside these areas. The decline in pest species currently yielding economic and environmental benefits to livestock growers may potentially and concurrently provide benefits for some of Australia’s threatened species. My research highlights the need for ongoing monitoring of native prey and invasive predator populations inside more cluster-fenced areas in order to determine if these areas may be suitable for re-establishing populations of threatened species. Cluster-fenced areas undergoing sustained predator removal should be considered as a potential resource for trialling the translocation of key locally extinct species into fenced areas. The potential to achieve biodiversity conservation on agricultural land may become a key approach to slow Australia’s extinction crisis and I hope my research contributes to this objective.

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