Reviving Ecological Functioning Through Dingo Restoration

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Contents

Abstract

Invasive species are regarded as one of the top five leading causes of the global extinction crisis. The majority of threatened species recovery plans therefore call for lethal control of invasive species, particularly predators. Vast resources are expended to combat the threats posed by invasives, and considerable research efforts have been devoted to developing best practice pest control practices; with little success overall. The reason for this may be that although invasive species cause extinctions, they are not the ultimate cause. Instead, the shift to invasive-dominated states is driven by an underlying loss or lack of ecological resilience. One of the leading processes that might result in widespread resilience loss, and release of invasive species, is the control or absence of apex predators.

Across the globe, and in every habitat investigated, apex predators play a keystone role in enhancing ecological resilience to the damaging influence of environmental perturbations. I tested the hypothesis that state shifts to invasive dominance are symptomatic of the disruption of top-down regulation, and that ecological resilience is largely determined by the social stability of apex predators. Australia presents a unique opportunity to examine these ideas because it is here that mammalian invasions and extinctions have been most severe; pest control is intensive and widespread; and only a single large mammalian predator, the dingo (*Canis lupus dingo*), is extant. I studied the interactions between dingoes, invasive mesopredators, herbivores, small mammals and vegetation in a series of sites across the arid zone, representing different levels of predator control (poison-baiting). Four of the sites were monitored over 2-3 years to study the effects of predator control cessation and intensification. This study was therefore conducted on both a spatial and temporal scale, providing not only correlative, but also (quasi) experimental evidence from large-scale predator manipulations.

The results of this study indicate that ecosystem state shifts to invasive-dominated and degraded landscapes are a consequence of predator control. Where threatened species survive, dingoes were consistently found besides them. Where dingo populations were allowed to recover, invasive and opportunistic species declined considerably, and native biodiversity and productivity increased. The ecological benefits of dingoes were more pronounced and consistent when their social stability was considered. The positive influence of dingoes, and the negative effect of predator control, even outweighed the influence of rainfall in the desert. Whether conducted in the name of the pastoral industry or biodiversity conservation, predator control benefitted neither and undermined both. The results of this study suggest that relaxing human intervention, and allowing large predators to re-assume their natural roles, can rapidly restore ecological resilience and reduce the threat of invasive species. I offer an alternative model for ecological restoration, in which the promotion of predators forms the foundation for recovery programs of threatened species.

Declaration

I hereby declare that this submission is my own work. Any contribution made to the research by others, with whom I have worked, is explicitly acknowledged in the thesis. I also declare that the intellectual content of this thesis is the product of my own work, except to the extent that assistance from others in the project's design and conception, fieldwork, analysis and presentation is acknowledged.

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. I give consent to this copy of my thesis when deposited in the University Library, being made available for loan and photocopying, subject to the provisions of the Copyright Act 1968. I acknowledge that copyright of published works contained within this thesis (as listed below) resides with the copyright holders of those works.

All thesis chapters and appendices (excluding the Introduction, Discussion and Conclusion) have been published or accepted for publication, and are presented with minor modifications to allow for a uniform thesis format style.

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Appendix 2: Wallach A.D. and O'Neill A.J. (2009). Artificial water points: hot-spots of extinction or biodiversity? Biological Conservation. 142: 1253-1254.

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Author contribution

This work greatly benefitted from the thoughts, ideas and expertise of several individuals. Adam J. O'Neill (Chapters 2-4 & Appendices 1,2) fully participated in conceiving, designing and carrying out fieldwork, contributed time and equipment, and analyzed results. This study could not have been carried out without him. Brad R. Murray (Chapter 2) supervised the first stage of this study and contributed funding, analysis and editing. John Read (Chapter 3) co-supervised the work in Stuart Creek and Andamooka stations, and assisted with conceiving fieldwork methods, provided funding and contributed analysis and editing. Chris N. Johnson and Euan G. Ritchie (Chapters 3,4) provided statistical and result analysis, contributed funding (CNJ), participated in publication design (Chapter 4) and editing.

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Photography

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CHAPTER 1 - INTRODUCTION

Invasive species: heart of the problem or merely the symptom of a weak heart?

Arian D. Wallach

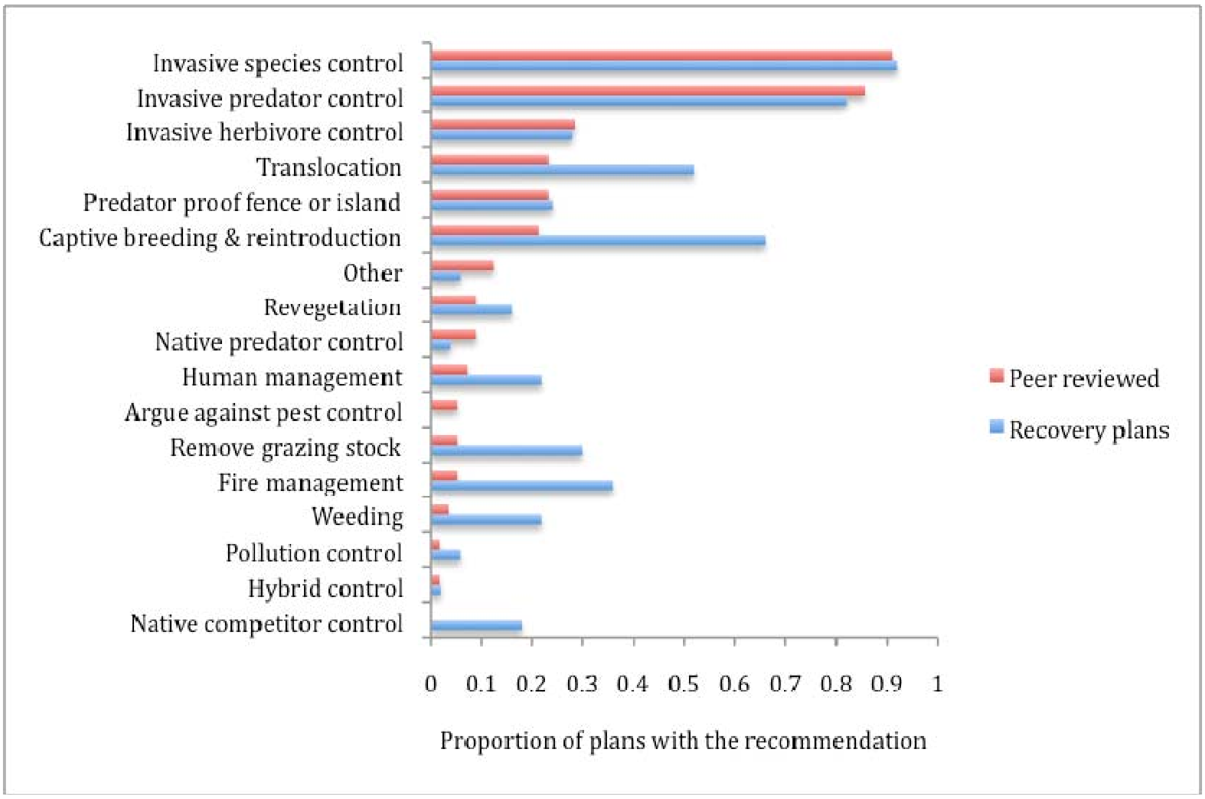
Historical accounts of many ecosystems around the globe describe an abundance and diversity of life, which stands in stark contrast with the impoverished wilderness areas we know today (e.g. Johnson 2006). Observations of several ecosystems subjected to changes (such as climate, nutrient loading, grazing pressure and biotic exploitation) have demonstrated that a loss of resilience is usually the underlying reason why ecosystems shift to degraded states (Scheffer *et al*. 2001). The resilience of an ecosystem is often described as the size of the ‘basin of attraction’ around a state, which determines the maximum amount of perturbation an ecosystem can take before shifting to an alternative state (Holling 1973, Scheffer *et al*. 2001). The few remaining pristine environments display extraordinary resilience in the face of environmental stressors (Sandin *et al*. 2009). Such examples highlight the importance of identifying and strengthening the mechanisms that provide for resilience. Resilience however is invisible and our attention is usually drawn to suppressing perturbations (Scheffer *et al*. 2001).

A convention of intervention

The invasion of exotic species is considered one of the top five global causes of biodiversity loss (Sala *et al*. 2000), due to the mounting evidence that exotic species directly cause extinctions (Vitousek *et al*. 1997, Wilcove *et al*. 1998, Atkinson 2001). Invasive species are drivers not only of individual species decline, but may also induce ecological state shifts to alternative states (Croll *et al*. 2005). Not surprisingly, when ecosystems are invaded by exotic species and native biodiversity declines human intervention in the form of pest control is swiftly applied. Over 90% of recovery plans call for lethal control of invasives, particularly invasive predators (Figure 1). Baxter *et al*. (2008) voiced a common opinion when stating that "*one of the primary goals of conservation biology is… to eradicate or control* [invasive] *predators that threaten native prey populations*". Indeed, no expenses are spared in the war on invasives (Reddiex *et al*. 2006), and if eradication is impossible then indefinite population control is generally considered the next best thing (Baxter *et al*. 2008). The scientific literature has devoted a great deal of attention to the development of best practice pest control, from upper-trigger harvest (Baxter *et al*. 2008) to catching the very first rat ashore (Russel *et al*. 2005).

Australia and New Zealand are in the forefront of invasive species control efforts, largely due to the extensive loss of native species associated with exotic species across these countries (Sinclair *et al*. 1998, Johnson 2006, Salo *et al*. 2007). Poison-baiting with sodium monofluoroacetate (1080) is by far the most popular control method (Reddiex *et al*. 2006). Australia uses approximately 200 kg of 1080 powder (equivalent to over 66 million fox baits) for pest control annually (APVMA 2008). Other methods of pest control include: aerial and ground shooting, trapping, spread of disease agents, fumigation, ripping and blasting of animal warrens, surgical sterilization and immunocontraception (Twigg *et al*. 2000, Nogales *et al*. 2004, Reddiex *et al*. 2006, Strive *et al*. 2007, Bounceback unpublished report). Considering the extent of pest-control-reliant conservation actions (Figure 1), supporting evidence (e.g. reduction in target species, recovery of threatened species) is surprisingly scarce (Reddiex and Forsyth 2006, Warburton and Norton 2009). An extensive review of pest control operations across Australia, for example, revealed that only 0.3% (N = 1,915) has provided reliable information (Reddiex and Forsyth 2006). This is an incredible figure considering the central part that pest control plays in Australian wildlife management. Despite this, the necessity and benefits of pest control remain an axiom, even when evidence suggests otherwise.

Figure 1: Current methods employed to recover threatened (vertebrate) species that are at risk from predation and competition with invasive (vertebrate) species, based on peer-reviewed recommendations and government approved recovery plans. A systematic review (in September 2009) using the search engines *Web of Science*, *Science Direct* and *Google Scholar* (in addition to several government websites for recovery plan searches), and the keywords *recovery plan*, *predator*, *invasive/introduced/exotic* and *threatened*, returned over 2,000 'hits'. I chose the first 56 peer-reviewed recommendations and 50 government-approved recovery-plans focused on native vertebrates threatened by exotic vertebrates. The control of invasive species in general, and predators in particular, is by the far the most popular approach. Captive breeding, reintroductions and translocations are the next most common recovery actions.



Pest control may be worse than pests

Invasive species are as common today as they were a decade ago, threatened species are consistently disappearing from the landscape, and the biotic world is homogenizing

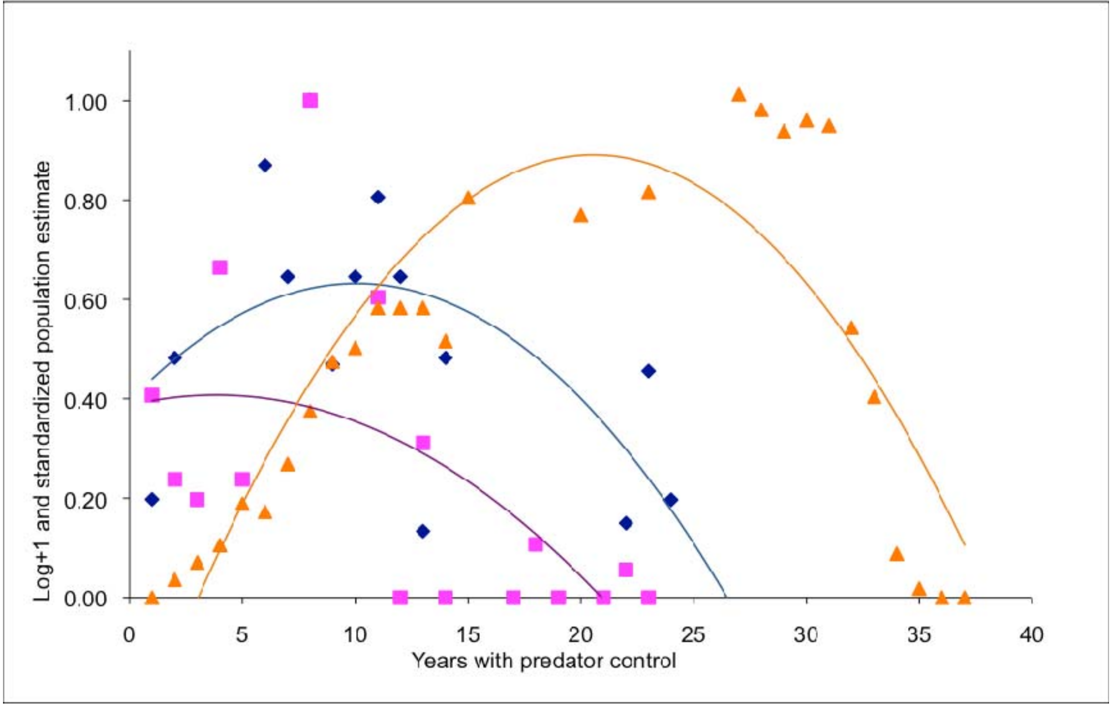
(McKinney and Lockwood 1999). Pest control is not keeping up, and perhaps is not the answer. Successful invasive species cannot be eradicated from mainland environments, rendering control options limited to relatively small areas (Zavaleta *et al*. 2001), and since the target population rapidly breeds back to its original population level (e.g. Rolls 1969, Sharp *et al*. 1999, Thomson *et al*. 2000, Burrows *et al*. 2003), intervention is required indefinitely.

Not only is pest control often highly ineffective and costly (Russel *et al*. 2005, Seymour *et al*. 2005, Baxter *et al*. 2008), its application may have adverse, even catastrophic, consequences (Courchamp *et al*. 2003a). The successfully established exotic species integrates into the complex web of ecological interactions (Glen and Dickman, 2005). Eradication or control may therefore cause further ecological damage. For example, fox (*Vulpes vulpes*) control can lead to increased cat densities (*Felis catus*), which may in turn devastate small mammal populations (Risbey *et al*. 2000); eradication of cats can cause increased predation of rats (*Rattus* spp.) on birds (Rayner *et al*. 2007); and rat control can increase seabird predation by house mice (*Mus musculus*) (Wanless *et al*. 2007). The recent successful eradication of cats from Macquarie Island, Australia, resulted in a dramatic increase in rabbits (*Oryctolagus cuniculus*) causing extensive grazing damage, even though the eradication was conducted within an integrated pest management framework (Bergstrom *et al*. 2009).

Several authors have documented cases of endangered species developing ecological dependencies involving exotic species, further complicating management decision making (Van Riel *et al*. 2000, Zavaleta *et al*. 2001, King *et al*. 2006, Rodriguez 2006). Van Riel *et al*. (2000) provided several examples of exotic plants apparently becoming keystone species in island archipelagos, providing habitat for endemic snails and birds after displacing native plants. Myers *et al*. (2000) described a similar case of an endangered rodent in California that depends on exotic annuals for its existence. The exotic saltcedars (*Tamarix* spp.) in western North America are associated with the decline of 41 threatened species. However, the proposal to initiate biological control was initially rejected because an endangered native songbird depends on this plant for nesting (Myers *et al.* 2000, Zavaleta *et al.* 2001). It is unknown, in fact, how long a pest-control-dependant system can function. But what is apparent is that once this course of action is chosen, the need for intensive ecosystem management only increases (Goodrich and Buskirk 1995).

The main evidence supporting predator control for the recovery of native wildlife abundance is cases of subsequent population size increase of native prey (e.g. Kinnear *et al*. 2010, Innes *et al*. 1999, Moorhouse *et al*. 2003, Engeman *et al*. 2005, Donlan *et al*. 2007). But the opposite also occurs. In Australia, for example, several predator control (poison-baiting) treatments have been followed by threatened species declines (e.g. black-flanked rock-wallaby, *Petrogale lateralis*: Read 2003; bilby, *Macrotis lagotis*: O'Neill 2002; rufous hare-wallaby, *Lagorchestes hirsutus*: Lundie-Jenkins *et al*. 1993; bridled nail-tail wallaby, *Onychogalea fraenata*: Fisher *et al*. 2001; and malleefowl, *Leipoa ocellata*: Benshemesh *et al*. unpublished). Particularly interesting are the cases of eventual population collapse following several years, even decades, of population growth (Figure 2). A similar parabolic trend in bay scallops (*Argopecten irradians*) was observed following overharvesting of sharks in the Atlantic Ocean. This ‘quadratic lift symptom’ may serve as a warning sign that the increase in a threatened species does not necessary constitute recovery. In fact, pest-control-induced recovery programs generally do not achieve the goal of establishing self-sustaining populations (Atkinson 2001, Scott *et al*. 2005).

Figure 2: Examples of three threatened species that recovered, but than collapsed, following predator control: woylie *Bettongia penicillata ogilbyi* (Western Shield unpublished report) = yellow (F=48.85, p=0.02); Whitaker's skink *Cyclodina Whitaker* (Hoare *et al.* 2007) = pink (F=4.34, NS); and Kaki *Himantopus novaezelandiae* (Keedwell *et al.* 2002) = blue (F=20.62, p=0.05). Data points were estimated from displayed figures, and analysis used original (untransformed) data.



Invasive species: ultimate or proximate causes of extinction?

Invasive species (particularly predators) are considered to be the ultimate cause of extinction and decline for many threatened species. This ‘ultimate model’ suggests that invasives are destructive because they are a recent addition to a largely naïve ecosystem that has evolved without them (Atkinson 2001, Short *et al.* 2002, Courchamp *et al.* 2003a, Salo *et al.* 2007). Ineffective anti-predator behavior is considered the main reason why native species are sensitive to novel predators (Cox and Lima 2006). This may be true in some cases (Blumstein *et al.* 2002), but not in others (Blumstein *et al.* 2001); and anti-predator behavior can, and does, develop in many species (McLean *et al.* 1995, Griffin and Evans 2003, Berger *et al.* 2007). A particularly interesting case of adaptation to exotic species was the discovery that the introduction and spread of the toxic cane toad (*Bufo marinus*) in Australia has been followed by an adaptive morphological change of toad-vulnerable snakes. The arrival of the toad is exerting selection pressure for increased body size and reduced head size (corresponding with reduced gape size), thereby increasing snake tolerance of cane toad toxin (Phillips and Shine 2004).

Some authors have argued that invasives are not necessarily drivers of extinctions, but instead suggest that changes in environmental conditions (e.g. due to anthropogenic disturbance) may be favoring invasives over natives (Gurevitch and Padilla 2004; Didham *et al*. 2005). This view is certainly supported in instances where native species do not recover despite the removal of exotics (e.g. MacDougall & Turkington 2005; Reld *et al*. 2009). However, this interpretation fails to encompass the numerous cases of native species persisting on exotic-free islands, and increasing following successful control or eradication (Johnson 2006). I propose instead that although invasive species may directly cause extinctions, they are not the ultimate cause. The ‘proximate model’ suggests that the shift to invasive-dominated states is driven by an underlying loss or lack of ecological resilience. One of the leading hypotheses that might illuminate the cause behind resilience loss in many ecosystems is the widespread control and absence of apex predators (Prugh *et al*. 2009).

Top-down regulation of invasive species

Across the globe, and in every habitat investigated, researchers are finding compelling evidence for a keystone role of large predators in enhancing ecological resilience to the damaging influence of ecological stressors (Wilmers and Getz 2005, Wilmers *et al*. 2006, Casini *et al*. 2008, Sandin *et al*. 2008). By suppressing the abundance and changing the behavior patterns of invasive and other opportunistic species, top predators protect animal diversity and vegetation communities. Striking examples include coyotes (*Canis latrans*) suppressing mesopredators such as cats and foxes thereby indirectly protecting birds (Crooks and Soulé 1999); vegetation recovery following the reintroduction of wolves (*C. lupus*) through trophic cascade (McLaren and Peterson 1994, Smith *et al*. 2003, Ripple and Beschta, 2003); kelp forest ecosystem recovery linked with sea otters (Soulé *et al*. 2003); and evidence that coral reef survival is related to the abundance of sharks (Sandin *et al*. 2008). The loss or lack of large predators therefore may be the ultimate cause behind the outbreak of invasive species and their destructive influence.

The spread and increase of exotic species parallels the global population rise of many opportunistic native species (Prugh *et al*. 2009). Indeed, most of the damage caused by exotic species is attributed to a small number of highly opportunistic mesopredators or herbivores such as rats, cats, foxes, goats, rabbits and pigs (Courchamp *et al*. 2003a, Johnson 2006). Salo *et al*. (2007) compared the effect of native against exotic predators on native prey, and concluded that exotic predators are more harmful. However, since these exotic predators are essentially mesopredators, their analysis may not necessarily reflect the destructive influence of invasive predators *per se*, but of mesopredator release (Crooks and Soulé 1999) more generally. Ritchie and Johnson (2009) found that on average an increase in the abundance of an apex predator is likely to have a fourfold negative effect on mesopredator abundance. Once released from the influence of an apex predator native mesopredators, like their feral counterparts, can devastate biodiversity (Ritchie and Johnson 2009). Examples of native mesopredators causing species decline are numerous, such as: raccoons (*Procyon lotor*, Engeman *et al*. 2005), opossums (*Didelphis virginiana*), skunks (*Mephitis mephitis*), foxes (Crooks and Soulé 1999), coyotes (Berger *et al*. 2008) and golden eagles (*Aquila chrysaetos*, Courchamp *et al*. 2003b) in North America; endemic deer mice (*Peromyscus maniculatus elusus*) on Santa Barbara Island (Millus *et al*. 2007); southern black-backed gulls (*Larus dominicanus*) in New Zealand (Keedwell *et al*. 2002); baboons (*Papio anubis*) across sub-

Saharan Africa (Prugh *et al*. 2009); and cownose ray (*Rhinoptera bonasus*) in the Atlantic Ocean (Myers *et al*. 2007).

Putting it to the test

Australia offers a unique opportunity to test whether invasive species are ultimate or proximate causes of biodiversity loss, because here invasive dominance is prevalent, extinction rate is high and attributed to exotic mesopredators, pest control is intensive, and a single top predator, the dingo (*C. l. dingo*), is extant and widely controlled (Johnson 2006). Replacing the thylacine (*Thylacinus cynocephalui*) about 5,000 years ago (Savolainen *et al*. 2004), the dingo is the only large mammalian predator that has survived to this day in mainland Australia (Johnson 2006). Since European occupation dingoes have been controlled over much of the continent (Fleming *et al*. 2001). Historically, dingo control has mainly been driven by the pastoral industry in an effort to reduce livestock losses (Allen and Sparkes 2001). In more recent times, growing concern about the negative impacts of invasive species, particularly mesopredators (foxes and cats), has spurred conservation agencies to take a lead role in predator control (Reddiex *et al.* 2006). The widespread use of 1080 to control of invasive species concurrently affects dingoes that are highly susceptible to this toxin (McIlroy 1986).

Recent studies have provided compelling evidence for a keystone effect of dingoes in the suppression of invasive mesopredators and opportunistic herbivores (native and exotic), and a net benefit to native prey (reviewed in Glen *et al*. 2007). O’Neill (2002) observed that dingoes exert a strong effect on the abundance and behavior of foxes, thereby promoting the survival of threatened species, and suggested that predator control is the main reason behind many recent and historial extinctions. Johnson (2006) reviewed the main drivers of extinction over the past 50,000 years and concluded that the recovery of dingo populations is crucial if we are to save Australia's dwindling biodiversity. Johnson *et al*. (2007) found that across the continent extinction of marsupials occurred mainly where dingoes were scarce, and Johnson and VanDerWal (2009) presented an analysis demonstrating that dingoes limit the upper density of foxes. The Dingo Barrier Fence (DBF), one of the longest man-made construction spanning across 5600 km, was built for the purpose of eradicating dingoes from sheep grazing areas in the southern part of Australia. The higher intensity of dingo control efforts inside the DBF over the past 100 years largely accounts for the different ecological states on either side of the fence, with mesopredators and large herbivores (e.g. kangaroos *Macropus* spp.) common inside the DBF, and small mammals and vegetation more abundant outside the DBF (Letnic *et al*. 2009).

Research typically focuses on top predator abundance as a gauge of top-down regulation intensity. However, abundance alone may not be a fully reliable indicator of top-down effects, particularly when the top predator is social (Haber 1996, Post *et al*. 1999, Gehring *et al*. 2003, Vucetich *et al*. 1997, 2004). Dingoes, like all wolves, form long-term social bonds that may persist for generations if human intervention is minimal (Corbett 1995, Haber 1996, O'Neill 2002). The social (pack) structure influences an array of biological features which are likely to have cascading ecological influences, such as: population size and age composition, group size, survival rates, hunting abilities, prey preferences, territory size and stability, social behavior, genetic identity and diversity (Haber 1996, Knowlton *et al*. 1999, Post *et al*. 1999, O'Neill 2002, Gehring *et al*. 2003, Vucetich *et al*. 1997, 2004, Brainerd *et al*. 2008). Cascading effects of changes in wolf population size on prey dynamics and vegetation growth is well documented (e.g. McLaren and Peterson 1994), but similar processes have also been demonstrated to result from changes in pack structure (Post *et al*. 1999). The maintenance of healthy ecosystem states in Australia may therefore depend not only on dingo abundance, but also on the integrity of their complex social behavior.

The scale and intensity of pest control in Australia (Reddiex *et al*. 2006, Figure 1) reflects a common belief that the Australian ecosystem is incapable of adjusting to the arrival of alien species (*ultimate model*). Here I present an alternative view that the loss of functional top-down regulation across Australia is the ultimate reason behind state shifts to invasive dominated ecological states (*proximate model*). If the ultimate model is correct (Figure 3a), pest control (e.g. 1080 poison) is expected to suppress invasive species (and the top predator alongside) and promote biodiversity. But if the proximate model is correct (Figure 3b), pest control will inadvertently increase invasive species dominance and decrease biodiversity by disrupting top-down regulation. Here 'pest control' refers to generalist methods used to suppress the abundance of exotic species that also affects the apex predator, regardless of the target species.

Three hypotheses were tested in this study: (1) *Species threatened by invasive mammals will only survive in the presence of dingoes*; (2) *Dingo abundance and social stability are not linearly related*; and (3) *the recovery of dingo populations suppresses invasive and opportunistic mesopredators and herbivores, allowing small native mammals and vegetation to recover*. The following chapters (Chapters 2-4), and supporting material (Appendix 1,2) present the main results of a temporal and spatial field study conducted at a series of sites across the South Australian arid zone.

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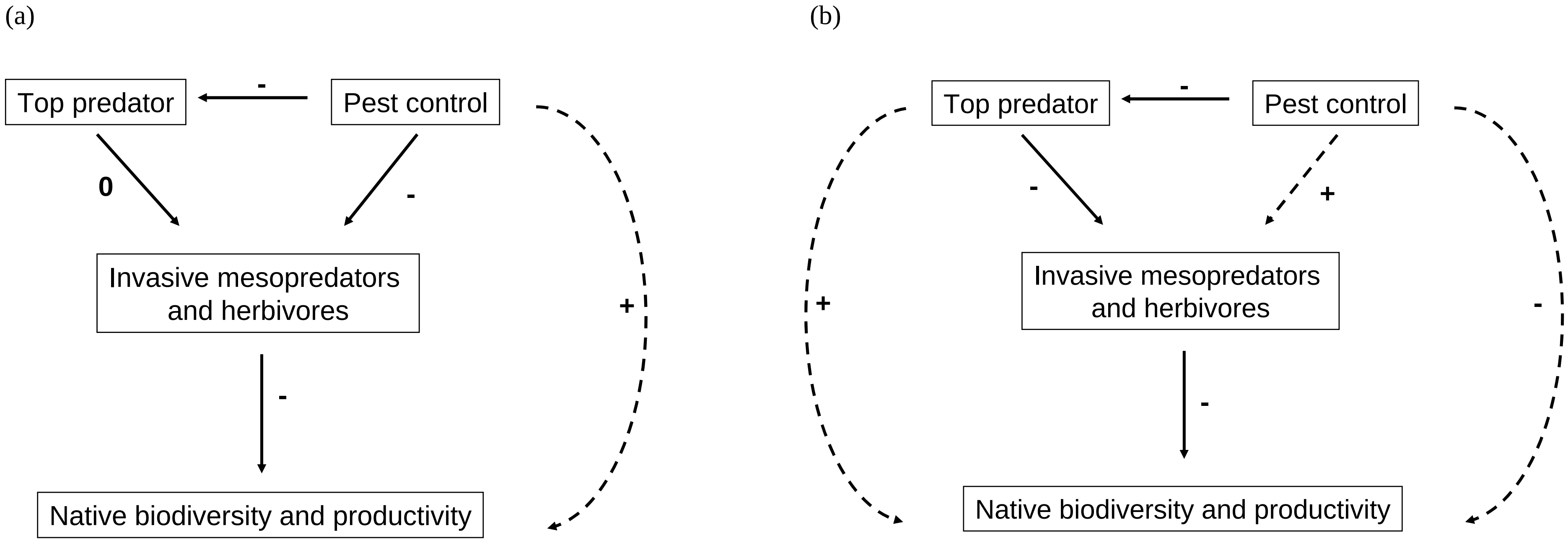
Figure 3: Two theoretical models of the potential influence of pest (predator) control on biodiversity. In *model a* invasive species (e.g. foxes) are assumed to be an ultimate cause of extinction, while top predators (e.g. dingo) are mainly bottom-up driven and their effect relatively negligible. If *model a* is correct, pest control (e.g. 1080 poison-baiting) is expected to suppress invasives and promote biodiversity. Alternatively, *model b* suggests that invasives are merely a proximate cause of biodiversity loss, while top predators are keystone ecosystem regulators. *Model b* would be supported if pest control triggered a release of invasives and a loss of biodiversity, by disrupting top down regulation.



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Chapter 2

Wallach A.D. Murray B.R. and O'Neill A.J. (2009). Can threatened species survive where the top predator is absent? Biological Conservation. 142: 43-52.

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CHAPTER 2

Can threatened species survive where the top predators is absent?

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Chapter 3

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CHAPTER 3

More than mere numbers: the impact of lethal control on the social stability of a top-order predator

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ABSTRACT

Population control of socially complex species may have profound ecological implications that remain largely invisible if only their abundance is considered. Here we discuss the effects of control on a socially complex top-order predator, the dingo (*Canis lupus dingo*). Since European occupation of Australia, dingoes have been controlled over much of the continent. Our aim was to investigate the effects of control on their abundance and social stability. We hypothesized that dingo abundance and social stability are not linearly related, and proposed a theoretical model in which dingo populations may fluctuate between three main states: (A) below carrying capacity and socially fractured, (B) above carrying capacity and socially fractured, or (C) at carrying capacity and socially stable. We predicted that lethal control would drive dingoes into the unstable states A or B, and that relaxation of control would allow recovery towards C. We tested our predictions by surveying relative abundance (track density) and indicators of social stability (scent-marking and howling) at seven sites in the arid zone subject to differing degrees of control. We also monitored changes in dingo abundance and social stability following relaxation and intensification of control. Sites where dingoes had been controlled within the previous two years were characterized by low scent-marking activity, but abundance was similar at sites with and without control. Signs of social stability steadily increased the longer an area was allowed to recover from control, but change in abundance did not follow a consistent path. Comparison of abundance and stability among all sites and years demonstrated that control severely fractures social groups, but that the effect of control on abundance was neither consistent nor predictable. Management decisions involving large social predators must therefore consider social stability to ensure their conservation and ecological functioning.

INTRODUCTION

The long-term survival and ecological functioning of socially complex species such as wolves (*Canis lupus*) may depend on more than merely their numerical status (Haber 1996, Knowlton *et al.* 1999, Post *et al*. 1999, Gehring *et al*. 2003, Vucetich *et al*. 1997, 2004, Brainerd *et al.* 2008, Chapron *et al*. 2008). The stability of their social units (packs) may be as important as their population size, but often only the latter is considered (Haber 1996). Wolves are eusocial (Andersson 1984), with breeding restricted to the dominant pair in the pack (alphas), while the other pack-members assist in rearing the young (Brainerd *et al*.

2008). Young wolves have a long period of parental dependency, which provides the basis for the transfer of complex information between generations (Haber 1996, Macdonald 1983). Under natural conditions wolf-packs may show extraordinary stability. For example, Haber (1996) reported on a wolf-pack that retained a distinct family lineage for over half a century, and a female that maintained alpha status for over 13 years until she died naturally at 18 years old. Few such examples are known however, due to the high level of human intervention in wolf populations. Many profound implications of wolf control remain largely invisible when only numbers are considered.

The control of wolves fractures their social structure, which may lead to changes in age composition, group size, survival rates, hunting abilities, territory size and stability, social behavior, genetic identity and diversity (reviewed in Haber 1996). Controlled populations tend to have a higher proportion of young, breeding pairs and litters, due to the loss of pack structure which regulates breeding (Knowlton *et al.* 1999). Brainerd *et al*. (2008) assessed the impacts of breeder loss on wolf-pack dynamics and found that packs often disperse following the loss of the alpha pair. They also found that pups have a higher chance of survival in persisting larger packs. Following control, territory boundaries dissolve, and dispersing individuals (floaters) immigrate into vacant areas (Thomson 1992c, Sillero-Zubiri and Macdonald 1998, Brainerd *et al*. 2008). Complex behaviors that are learned and developed within stable packs, such as cooperative hunting techniques, may be lost, leading to simplification and aberration of social traditions (Haber 1996).

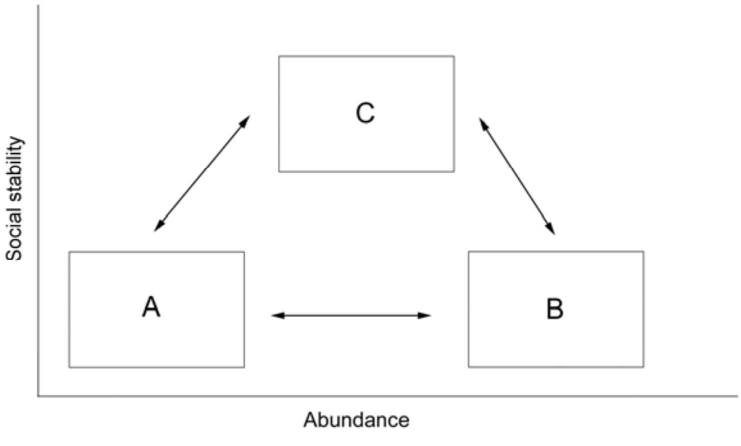
The dingo (*C. l. dingo*) was introduced to Australia about 5,000 years ago possibly by Asian seafarers (Haber 1996) and became established over the whole of the mainland. Replacing the thylacine (*Thylacinus cynocephalus*) and Tasmanian devil (*Sarcophilus* *harrisii*) (Johnson 2006), the dingo is now the largest terrestrial mammalian predator in Australia. Although dingoes differ from wolves in that they underwent a period of semi-domestication prior to their arrival in Australia (Savolainen *et al*. 2004), they are distinct from domestic dogs and display biological, behavioral and ecological traits characteristic of other wolf species (Catling *et al*. 1992, Thomson 1992a,c, Corbett 1995, Glen *et al*. 2007).

Since European occupation, dingoes have been targeted for lethal control over much of the continent, primarily because they prey on livestock (Allen and Sparkes 2001). Poison-baiting with sodium monofluoroacetate (1080) is the most common method of control (Reddiex *et al*. 2006). The Dingo Barrier Fence (DBF), the world’s longest man-made construction, spanning over 5,000 km, was built with the intention of eradicating dingoes from the southern parts of Australia where sheep-farming is common. Along the South Australian section of the DBF a 10-30 km buffer zone is intensively baited on the northern side to reduce the threat of reinvasion. Most pastoral stations north of the DBF also control dingoes because they are considered a threat to cattle (Allen and Sparkes 2001).

Despite their keystone role as top-order predators (Johnson *et al*. 2007), dingoes are also controlled in many conservation-designated areas. They are directly targeted because of a common belief that predator control will assist the recovery of threatened species (Reddiex *et al*. 2006), and to reduce their impact on neighboring pastoral stations. Dingoes are also indirectly affected because 1080 poison-baiting is extensively used to control red foxes (*Vulpes vulpes*), cats (*Felis catus*) and wild dogs (*C. familiaris*) (Reddiex *et al*. 2006). Secondary poisoning may also occur when rabbits and other herbivorous animals are poison-baited (McIlroy and Gifford 1991), which is a common practice in Australia (Reddiex *et al*. 2006).

Nevertheless, dingoes remain abundant and they occur over much of mainland Australia, including areas inside the DBF (Wallach *et al*. 2009). Although they are remarkably resilient in the face of eradication efforts, very little is known about the effects of control on the integrity of their social structure. In this study we investigate the effects of dingo control on their abundance and social stability, and hypothesize that the two variables are not linearly related. We propose a theoretical model in which populations can fluctuate between three main states: (A) below carrying capacity and socially fractured, (B) above carrying capacity and socially fractured, or (C) at carrying capacity and socially stable (Fig. 1). We predict that control fractures pack structure and drives the population into unstable states (A or B) that are more likely to fluctuate with resource availability, and that relaxation of control allows the recovery of social stability and stabilization of population size (C).

Figure 1. Theoretical model of the relationship between dingo abundance and social stability.



METHODS

Study sites

We assessed dingo abundance and territorial behavior at seven sites across the South Australian arid zone representing different management practices. At five sites dingoes have been controlled within two years of our field work, mostly with 1080 poison-baiting: Mungerannie (26^{o}33'S, 139^{o}42'E), Red Lake (southern area of Stuart Creek station; 30^{o}11'S, 136^{o}51'E), Andamooka (30^{o}32'S, 137^{o}05'E), Vulkathunha-Gammon Ranges National Park (GRNP; 30^{o}29'S, 139^{o}14'E) and Nantawarrinna (30^{o}46'S, 139^{o}02'E). There are very few places in the arid zone where permanent water is available and dingoes are not controlled (Wallach and O’Neill 2009), but after extensive surveys we located two sites: Pandie Pandie (26^{o}33'S, 139^{o}42'E) and Curdimurka (northern section of Stuart Creek station; 29^{o}28'S, 137^{o}03'E), where dingo control has been minimal for at least five years. Pandie Pandie, Mungerannie, Curdimurka and Red Lake are outside the DBF, while Andamooka, GRNP and Nantawarrinna are inside the DBF. Study sites were 200-500 km^{2}, and each included at least three permanent water sources.

Red Lake, Andamooka, Nantawarrinna and Curdimurka were surveyed more than once to study the effects of management changes on dingo abundance and social stability. At Red Lake dingo control was relaxed, in Andamooka and Nantawarrinna dingo control intensified, and at Curdimurka there were no management changes and dingoes were generally not disturbed. Red Lake is inside the buffer zone and was baited annually until 2006. We surveyed this site in 2006 and for two years (2007, 2008) following relaxation of control. Rainfall was below average during the study period (www.bom.gov.au). Red Lake borders Andamooka station and the two sites are separated by the DBF. At Andamooka dingoes have been controlled with shooting and sporadic low-intensity baiting between 2001 and 2007. In May 2008 Andamooka was subjected to an intensive poison-baiting treatment and we monitored this site several months before (October 2007) and after (October 2008) this event. Conditions were favorable in both years following an above-average rainfall event in early 2007 (www.bom.gov.au), which increased prey availability (Wallach unpublished data). Nantawarrinna has a long history of dingo eradication efforts, but since the station was de-stocked in the 1990's, dingo control has been conducted irregularly. In mid 2008, Nantawarrinna was subjected to an intensive poison-baiting treatment and we monitored this site several months before (December 2007) and after (November 2008) this event. Rainfall was below average during the study period (www.bom.gov.au). Curdimurka was surveyed in November 2007 and September 2008, and rainfall was below average (www.bom.gov.au).

Relative abundance

Relative abundance of dingoes was assessed by the passive track survey method described previously in Wallach *et al.* (2009). In short, relative density (R_{de}) was determined by dusting randomly located 500-m transects (at least 1 and 2 km apart for off and on road transects, respectively) and counting the number of dingo crossings over three days, giving an average value of tracks/500m/day (9 - 25 transects/site). Transects were located both on unformed dirt roads and off roads, where possible. We also estimated the relative distribution (R_{di}) of dingoes (proportion of the study site occupied) by recording the presence or absence of fresh dingo tracks in random 2-ha plots scanned for 30 min (21 - 39 plots/site). An Index of Abundance (IA) was calculated as follows:

$$IA = R_{de} \times R_{di}$$

Social stability

Intensive persecution has taught many dingoes to avoid human contact (Wallach *et al*. 2009) hence opportunities for direct observations of wild dingoes are limited. Furthermore, any attempt to capture animals for radio collaring may bias the sample toward naïve floaters. Our first aim therefore was to develop an indirect method of assessing social stability. We surveyed the frequency of social stability indicators, scent-marking and howling, under differing degrees of control.

Scent-marking with scats, urine and ground-rakings are well known forms of social communication in canids (e.g. dingo: Thomson 1992a, Corbett 1995; other wolves: Sillero-Zubiri and Macdonald 1998, Zub *et al*. 2003). Scent-marking communicates pack size and composition, individual social and breeding status, and is used to advertise ownership and territory boundaries (Sillero-Zubiri and Macdonald 1998). A reduction in scent-marking following the breakdown of a wolf pack (due to control or disease) may be followed by a rapid shift in territory boundaries and infiltration of floaters (Sillero-Zubiri and Macdonald 1998). Like scent-marking, howling communicates a diversity of messages such as identity, location, age, size, aggressiveness, social and breeding status, and pack size and composition (dingo: Thomson 1992a, Corbett 1995; other wolves: Harrington 1986, 1987, Sillero-Zubiri and Macdonald 1998). Howling and scent-marking are both more common among pack members than among floaters (dingo: Corbett 1995; other wolves: Rothman and Mech 1979, Nowak *et al.* 2007; coyote *C. latrans*: Gese and Ruff 1998).

We surveyed dingo scat abundance and location to assess scent-marking intensity, because annual variation in deposition rates is small (Corbett 1995, Sillero-Zubiri and Macdonald 1998, Zub *et al.* 2003), detectability is high, and in our study sites scats normally endure for roughly 3-6 months, although some persist much longer (Wallach unpublished data). Scats are long-term visual cues, especially in low rainfall regions, and are placed to maximize their visual effect (Barja 2009). They are often found concentrated at distinct focal points such as road junctions, elevated objects and carcasses (Corbett 1995, Sillero-Zubiri and Macdonald 1998, Barja *et al.* 2004). The positioning of scats on conspicuous objects can assist in the identification of canid territorial marking (Barja *et al.* 2005). Hence we consider the strategic deposition of dingo scats in prominent locations, relative to randomly located scats, to be an indicator of territoriality and pack stability.

The locations of 890 dingo scats (122±48 scats/site), mostly from outside the DBF, were recorded while surveying the 2-ha plots (described above), to determine the degree to which scats were placed randomly or at focal points. Focal points that could potentially provide a resource are referred to as resource points. A scat was considered to be a scent-mark if it was deposited on a distinct focal point, was part of a latrine, or if it was found on a conspicuous object. We then conducted a scat survey of the most prominent focal points at each site (average of 80 focal points/site) to determine the level of scent-marking activity. We recorded all dingo howling events at the study sites that we camped in for a minimum of two weeks (all sites apart from the GRNP). We also estimated the age of dingoes (whether young: <1 year, or mature: >1 year) based on their size and appearance, during occasional clear, direct observations.

Statistical analyses

We compared scent-marking at different resource points with a Kruskal-Wallis test, and we tested the relationship between scent-marking and howling activity with a Spearman's rank correlation test. A site was considered 'controlled' if baiting or shooting had been conducted within the past 2 years. We compared abundance and scent-marking between sites with (N = 5) and without (N = 2) control using a Mann-Whitney U-test, and we used the average of multiple years for sites that were surveyed more than once. A Chi-square test was used to compare the number of young and mature dingoes in controlled and non-controlled sites. A best-fit regression analysis was employed to assess the relationship between scent-marking, howling and abundance with the time elapsed since control, between scent-marking and abundance, and between howling and abundance. We also compared dingo control intensity, scent-marking, howling and abundance with both average annual rainfall and recent rainfall (accumulation of one year prior to the study). Control intensity was quantified as the maximum time any of our study site was not controlled (standardized at 6 years), minus the time elapsed since control was applied at each site. When comparing the change in abundance and scent-marking following management changes we used a Mann-Whitney U test because some of the samples (e.g. resource points and transect location) were not tied even though the sites were.

We constructed and compared generalized linear models (using a Poisson distribution and log link function) of dingo scent-marking and howling with the Akaike's Information Criterion (AIC). We used an information-theoretic approach (ITA) and constructed all possible configurations (best subsets) of independent variables that may predict each response variable. We compared the support for models according to differences in their AIC scores (Burnham and Anderson 2002), as well as calculating Akaike model weights (*wi*) (Link and Barker 2006). We retained all models that were within a 95% confidence set (Burnham and Anderson 2002). The relative importance of predictor variables was calculated by summing w_i across all models in which the variables occurred. The candidate models included: (i) time elapsed since control, (ii) poison-baiting frequency (baiting/year), (iii) distance from human activity centers (e.g. towns, camping grounds), (iv) dingo abundance, and for howling only:

(v) breeding season (between April-August, following Thomson (1992a). Howling frequency was arcsine-transformed prior to analyses in accordance with recommendations in Quinn and Keough (2002).

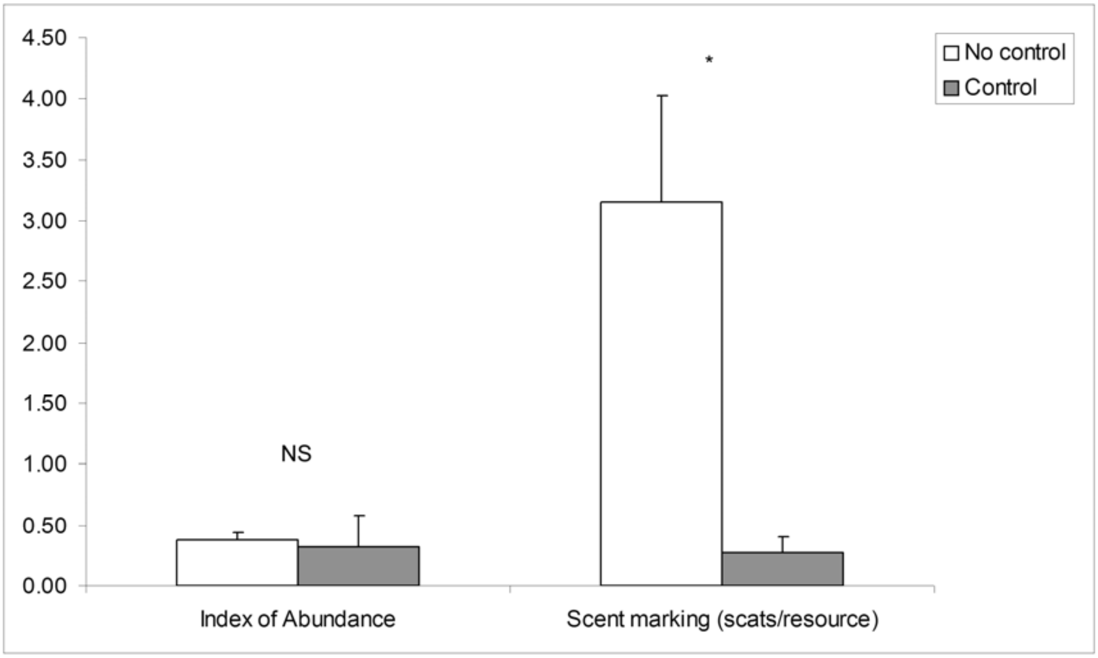
RESULTS

The location of dingo scats found on the 2-ha plots was not random, and 97% (N = 890) were found on clearly defined focal points; including water points, rabbit warrens, carcasses, trees where eagles nested and fed, roads, gates and isolated trees. Scats were often deposited on conspicuous objects and were part of latrines. Water points, rabbit warrens, carcasses and eagle nests were the most common and intensively scent-marked resource points, and up to 80% were scent-marked in a given area. Dingoes scent-marked water points (12.84 ± 3.22 scats/water point; N = 69) more intensively than rabbit warrens (1.32 ± 0.23 scats/warren; N = 555), carcasses (0.89 ± 0.27 scats/carcass; N = 204) or eagle nests (3.64 ± 1.25 scats/nest; N = 32) (Kruskal-Wallis: H = 39.76, d.f. = 3, p<0.001).

Scent-marking and howling frequency were not significantly correlated (Spearman (r_s) $_{0.05\ (2),\ 10}$ = 0.23, p = 0.52), and were predicted by a different set of variables (Table 1). Scent-marking activity was explained by four models that included four variables. Time since control was by far the most important and positive predictor of scent-marking. Relatively weaker predictors were dingo abundance, poison-baiting frequency and distance from human activity (Table 1). Conversely, howling frequency was explained by seven models that included four variables. Distance to human activity was the strongest predictor of howling (howling frequency increased as distance from human centers increased); followed by time since control, poison-baiting frequency and timing of the breeding season. Dingo abundance did not feature in any of the top-models predicting howling (Table 1).

Sites where dingoes had been controlled within the previous 2 years were characterized by low scent-marking activity (Mann-Whitney Z = 1.97, $p < 0.05$; Fig. 2), but abundance was similar between sites with and without control (Mann-Whitney Z = 1.16, p = 0.25; Fig. 2). Dingo abundance was however reduced at sites that had been poison-baited within the past 3 months (Mann-Whitney Z = 2.32, $p < 0.05$). Of 15 dingoes observed in the controlled sites, 93% were young (N = 15), while 75% of dingoes observed in the non-controlled sites (N = 20) were mature ($\chi^2 = 16.13$, d.f. = 1, $p < 0.0001$). Scent-marking and howling increased linearly the longer an area was allowed to recover from control (scent-marking: $R^2 = 0.94$, d.f. = 10, $p < 0.001$, howling: $R^2 = 0.46$, d.f. = 9, $p < 0.05$), but we found no significant relationship with dingo abundance ($p > 0.05$). Dingo control intensified and scent-marking decreased as average annual rainfall increased (control intensity: $R^2 = 0.38$, d.f. = 9, $p < 0.05$, scent-marking: $R^2 = 0.39$, d.f. = 9, $p < 0.05$), while no significant effect was found for howling, abundance or recent rainfall.

Figure 2. Comparison of abundance and scent-marking between sites with and without dingo control (average + se).



The relationship between dingo abundance and scent-marking followed a bell-shaped curve (quadratic best fit: $R^2 = 0.84$, d.f. = 9, $p < 0.001$; Fig. 3). Scent-marking activity was reduced at low densities and began to increase exponentially at IA = 0.2. One site (Andamooka in 2008) had a particularly high dingo abundance index but scent-marking was low, corresponding with the prediction of a state B scenario illustrated in Fig. 1. Although our data is mostly restricted to the left side of the curve (Fig. 3), we found that the quadratic best-fit line was also supported over a linear line after removing Andamooka 2008. Using AIC, we found that a model with the variable 'abundance' (linear) + 'abundance squared' (quadratic) was substantially better supported (>1000 times) than a model with just 'abundance' (linear). Adding this quadratic variable did not change the relative importance of abundance on the scent-marking model in Table 1. Howling frequency followed a similar pattern but was considerably more variable ($p > 0.05$; data not shown).

Figure 3. Relation between dingo abundance and scent-marking activity. Black triangles: Red Lake (2006, 2007, 2008), grey triangles: Andamooka (2007, 2008), grey circles: Nantawarrinna (2007, 2008), grey squares: Curdimurka (2007, 2008), and black diamonds represent Pandie Pandie, Mungerannie and the GRNP.

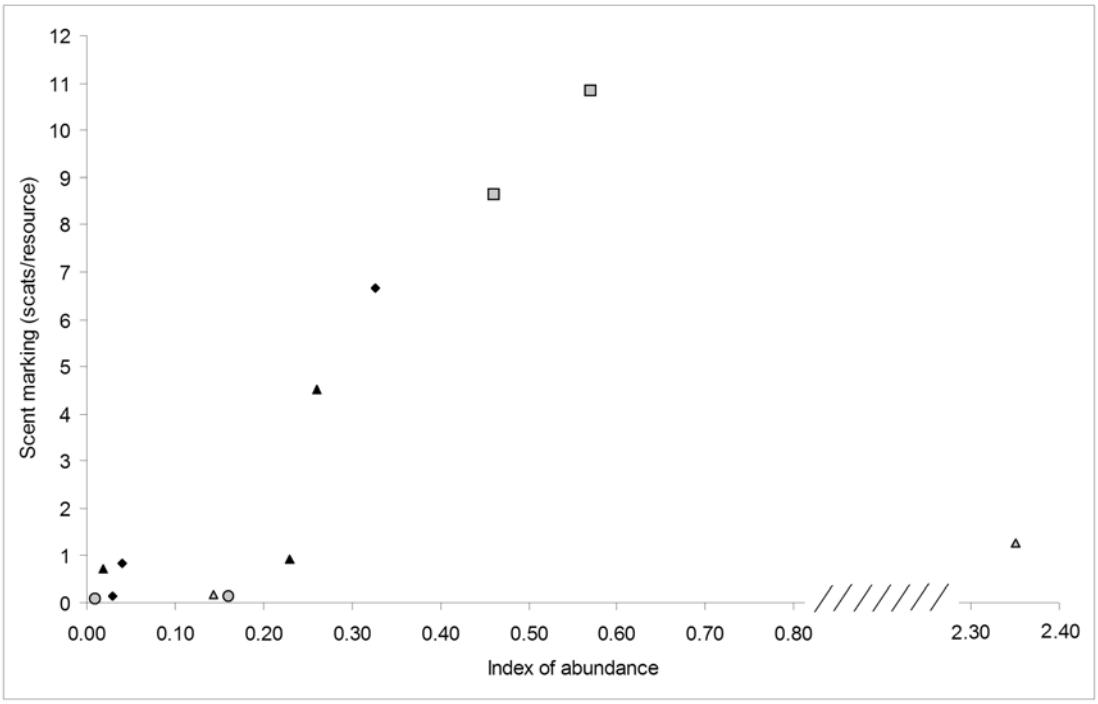


Table 1. Generalized linear models of dingo scent-marking and howling, using best subsets (AIC).

Model			AIC	Δ_i	w_i	Variables	Importance w_i (direction of effect)
Scent-marking	Time since control		22.18	0.00	0.44	**Time since control**	**1.00 (+)**
	Time since control	Dingo Abundance	23.80	1.62	0.20	Dingo Abundance	0.20 (+)
	Time since control	PBF	23.83	1.64	0.19	PBF	0.19 (-)
	Time since control	Human distance	24.07	1.89	0.17	Human distance	0.17 (-)
Howling	Human distance		11.02	0.00	0.21	**Human distance**	**0.51 (+)**
	Time since control		11.22	0.20	0.19	Time since control	0.30 (+)
	PBF		11.56	0.54	0.16	PBF	0.27 (-)
	Breeding season		11.92	0.90	0.14	Breeding season	0.22 (+)
	Time since control	Human distance	12.37	1.36	0.11		
	PBF	Human distance	12.46	1.44	0.10		
	Human distance	Breeding season	12.98	1.97	0.08		

Only models which are within the 95% confidence set for each model set are shown.

Δ_i = model score differences, w_i = Akaike model weights. Variables with importance (w_i) greater than 0.5 are shown in bold, and the direction of effect are indicated in brackets. PBF = Poison-baiting frequency, Human distance = distance from centers of human activity.

One year after the cessation of poison-baiting in Red Lake, dingoes increased in abundance (Mann-Whitney Z = 2.37, $p < 0.05$) but scent-marking remained low (Mann-Whitney Z = 0.49, p = 0.62; Fig. 4a). After two years abundance stabilized (Mann-Whitney Z = 0.38, p = 0.71) and scent-marking increased significantly (Mann-Whitney Z = 6.35, $p < 0.001$; Fig. 4a). Also after two years the first howl was heard (N=14).

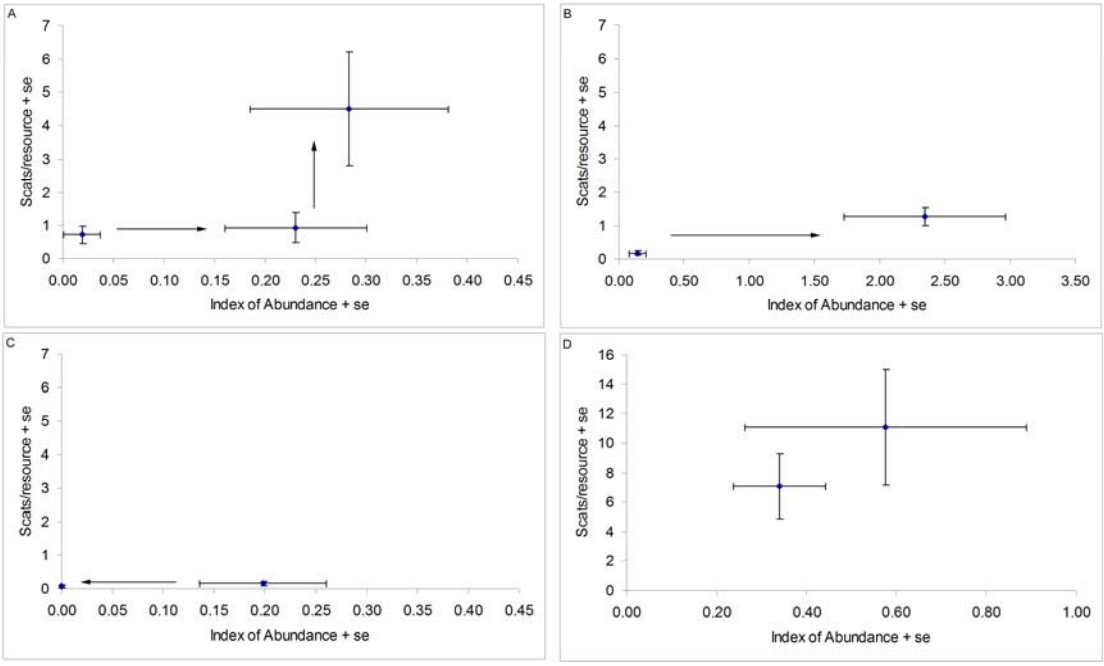
Poison-baiting at Andamooka, coupled with high resource availability, resulted in a 16-fold increase in abundance (Mann-Whitney IA: Z = 2.8, $p < 0.01$; Fig. 4b), bringing the index of abundance to the highest level detected in this study (see also Fig. 3). The size of the tracks and the location of an active den indicated that many of these dingoes were young. This change in abundance was also followed by an increase in scent-marking (Mann-Whitney: Z = 5.22, $p < 0.001$; Fig. 4b), but after correcting for relative abundance, scent-marking was found to have decreased (Mann-Whitney scent-marking/IA: Z = 4.33, $p < 0.001$). No howling events were recorded in either year.

In 2007 dingoes were relatively abundant at Nantawarrinna but incidence of scent-marking was low (N = 18). After Nantawarrinna was poison-baited, dingo abundance dropped to almost zero (Mann-Whitney IA: Z = 2.86, $p < 0.01$; Fig. 4c) and scent-marking remained low (N = 4). Howling was relatively common at Nantawarrinna in 2007 (18% of nights (N=28), with up to four dingoes howling together). A single dingo howled in 2008 (N=14).

Curdimurka was not subjected to dingo control, and abundance and scent-marking activity remained high and relatively stable, although there was a trend of increase for scent-marking (Mann-Whitney IA: Z = 0.41, p = 0.68, scent-marking: Z = 1.72, p = 0.09; Fig. 4d).

Howling frequency was also similar between years (14.29% (N = 14) and 21.43% (N = 14) of nights in 2007 and 2008, respectively).

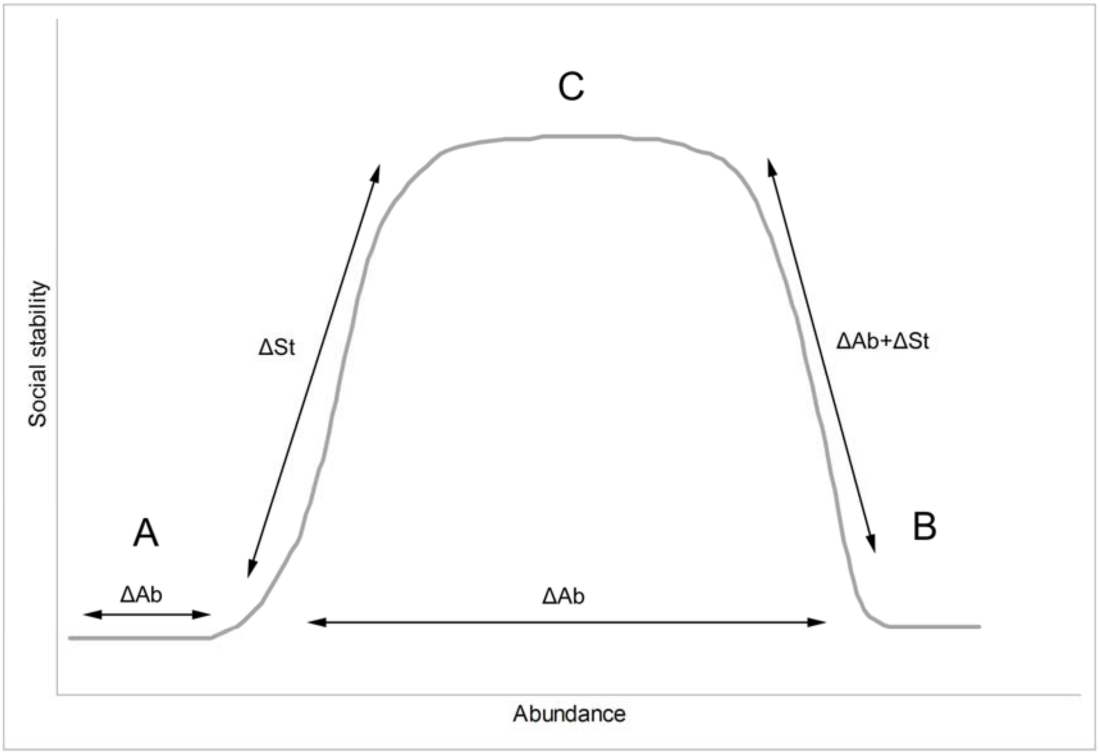
Figure 4. Effect of relaxation or intensification of control on dingo abundance and scent-marking behavior. (a) Relaxation of control (Red Lake 2006-2008); (b) intensification of control during a productive period (Andamooka 2007-2008); (c) intensification of control during a dry period (Nantawarrinna 2007-2008); and (d) no control in both years (Curdimurka 2007-2008). Arrows denote the direction of meaningful significant changes between the years.



DISCUSSION

Our study provides evidence that the relationship between dingo abundance and social stability is not linear, but may rather follow a bell-shaped curve. Lethal control systematically fractures social units and releases population abundance to bottom-up processes, which drives population size in either direction. Fig. 5 illustrates the effect of management on the dynamic relation between dingo abundance and social stability as indicated in this study. Under the influence of control, dingo populations may be driven towards the unstable states of A or B. The changes following relaxation of control indicate that recovery may follow two main phases. Populations recovering from state A will first increase in abundance, potentially driving the population into state B. The next phase is an increase in stability followed by a reduction in population growth rate (A to C) or size (B to C).

Figure 5. Influence of management on the abundance (Ab) and social stability (St) of dingoes.



Researchers usually focus solely on abundance, probably because assessing social stability may not always be feasible, due to constraints on research time and resources. This study used a rapid and non-invasive method of assessing social stability that requires efforts similar to those used in estimating abundance. Sites where dingoes have been undisturbed for several years are characterized by consistent scent-marking of available resource points. In the arid zone, water points, carcasses, active warrens or dens, nests and roads are the most common focal points of scent-marking activity. Our stable study sites had an average of 6-10 scats per resource point (Fig. 3), but some scent-posts had over 100 scats. Where dingoes are stable and fear of humans is minimal, howling is heard on most nights and most frequently during the breeding season (Thomson 1992a). Sites that are subjected to dingo control are easily recognized by the paucity of scent-marking, whether population abundance is low or high. Scent-marking appears to be the most consistent indicator of social stability because it can be reliably predicted by the occurrence of control. While control also predicts howling frequency, proximity to centres of human activity is the strongest predictor (Table 1). These differences explain why howling and scent-marking are not always correlated. The importance of scats in canid scent-marking, and their utility as indicators of stability, is probably more applicable in low rainfall regions where scats can endure as visual cues for extended periods of time.

Another observable symptom of pack disintegration appears to be an increase in attack rates on livestock. Allen and Gonzalez (1998) provided experimental evidence suggesting that calf losses are higher where dingoes are baited than where they are left undisturbed. They found, as we did, that baiting does not always reduce dingo numbers. A similar pattern was found at Pandie Pandie (no control) and Mungerannie (annual poison-baiting). We found no signs of dingo predation on cattle at Pandie Pandie (N = 56), while at Mungerannie 14% (N = 44) of carcasses were calves, and all appeared to have been killed by dingoes (Wallach & O'Neill unpublished). Similarly, several weeks after Nantawarrinna was poison-baited in 2008, a neighbouring property lost 24 of 30 sheep to dingoes in one day. The sheep were killed but not eaten (T. Coulthard, personal communication). Long-term data on coyote control also indicate that control does not significantly reduce livestock predation (Conner *et al.* 1998) nor does it improve production (Berger 2006).

In the course of this study, we did not find a single place where dingoes had clearly reached state C. Even at Pandie Pandie and Curdimurka, dingoes have occasionally been shot or poisoned. Although abundance, scent-marking and howling did not change significantly in Curdimurka, there was a trend of increase (Fig. 4d), indicating that dingoes may still be recovering from past control. Similarly, the regression analysis for scent-marking and howling as functions of time since control were linear and did not plateau, although this may be a result of the small sample size. The lack of social cohesiveness in dingo populations appears to characterize the vast majority of Australia. In the arid zone there is a trend of dingo control intensification, and social destabilization, as average annual rainfall increases. Thus, the more potentially productive areas are the most highly controlled against dingoes. The implications of such widespread control are largely unknown, but probably result in reduced fitness and impaired ecological functioning at a continental scale.

Eusocial systems have developed to increase fitness for pairs that are part of multi-generational groups comprised mainly of non-breeding helpers (Andersson 1984, Macdonald 1983). Following control, the remaining individuals may be subjected to reduced survival rates by creating populations with many lone breeding pairs (Brainerd *et al*. 2008). Dingoes, like other wolves, are cooperative hunters, and their hunting abilities are directly related to pack size, age and experience (Thomson 1992b, Allen *et al.* 2000, Sand *et al.* 2006). Control-related fitness costs may also be indirect. For example, reduced group size may increase the loss of kills to scavengers (Vucetich *et al.* 2004), and social fracturing may induce chronic stress levels in a population (Van Meter *et al.* 2008).

The long dependency period of many young social carnivores (e.g. wolves) attests to the vital role of learning within these species (Haber 1996). At Curdimurka we observed a dingo pup (approximately 4 weeks old) actively searching out rabbit warrens and buck heaps and dingo scent-posts for scent-marking. At Pandie Pandie a two-month-old dingo was heard howling daily with the same adult, presumably its mother, and often in chorus with three additional adults that howled regularly together. At Curdimurka we observed a dingo that washed his food. Two pieces of kangaroo meat (from an ant-covered carcass) were washed in a spring approximately 30 m from the carcass. Food-washing is often cited as an example of culture in primates (Sapolsky 2006). Although we do not know how this behaviour developed, it is interesting to note that it occurred in one of the stable sites.

The role of learning is particularly evident in the case of dingoes surviving in the face of eradication efforts. For instance, inside the DBF in South Australia some national parks poison-bait fortnightly (S. Gillam unpublished data), with poison-baits often distributed by aircraft, achieving extensive coverage of large areas that are otherwise inaccessible (Bounceback unpublished report). Despite this, Wallach *et al*. (2009) located dingoes surviving in areas deep inside the DBF, near towns and sheep farms, that have avoided detection for several decades, and found that scent-marking rates were relatively high. Although pack stability is usually disrupted under control, dingoes surviving under conditions of intensive persecution must have retained stability, because survival depends on specialized skills (avoiding contact with humans, livestock predation, and baits) that must be passed on to their offspring.

Hybridization with dogs is considered one of the main threats to dingo survival in Australia, spurring the Victorian State Government to shift the dingo from the vermin list to the endangered species list in 2008. We believe that the rate of hybridization is a direct consequence of dingo control. Like all wolf species, dingoes are highly territorial and aggressive, and it is with great difficulty that outsiders join stable packs (dingoes: Corbett 1995; other wolves: Sillero-Zubiri and Macdonald 1998, Stahler *et al*. 2002). Under natural conditions genetic lines are protected through kin selection, and genetic variation within packs may be small due to inbreeding and aggressive behavior towards outsiders (Haber 1996, Lehman *et al*. 1992). This can give rise to the development of genetic traits unique to each pack, such as coat color (dingo: Thomson 1992c; wolf: Haber 1996). Dingo control may increase the number of floaters that are more likely to breed with dogs (O'Neill 2002). Similarly, hybridization between wolves and dogs has been reported from Latvia where wolf-hunting was common (Andersone *et al*. 2002). We propose that the most efficient way to conserve the genetic identity of dingoes and other wolves is to cease control.

The dingo is the only large terrestrial mammalian predator in Australia, the next largest being the invasive red fox. Australia is now home to a diversity of large prey species, mostly invasive, that have successfully eluded eradication efforts. These include goats (*Capra hircus* 15-80kg), feral pigs (*Sus scrofa* 25-175 kg), six species of deer (*Dama dama, Cervus* spp., and *Axis* spp. up to 300 kg), feral donkeys (*Equus asinus* 300-350 kg), feral horses (*E. caballus* ca. 500 kg), feral cattle (*Bos taurus* 500-900 kg) and camels (*Camelus dromedaries* 600-1000 kg) (Van Dyck and Strahan 2008). Dingoes may have the potential to regulate even the largest of prey (but see Sinclair *et al*. 2003), most likely mainly through risk effects (Creel and Christianson 2008, Ritchie and Johnson 2009), but only under conditions of long-term pack stability can this be reliably tested.

As long as only numbers are considered, the full ecological benefits of dingoes will remain unknown. It is the *pack* that is the top predator, not the individual dingo. Without the pack, a dingo is functionally equivalent to a large fox. Australia has suffered the worst rate of mammalian extinctions worldwide (Johnson 2006) and this crisis is directly linked with dingo control (Johnson *et al*. 2007). The ecological role of the dingo as Australia's top predator has recently moved into the spotlight of research attention (Glen *et al*. 2007). It is vitally important that future research considers the role of social stability, to ensure the conservation and ecological functioning of socially complex top-order predators.

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Chapter 4

Wallach A.D., Johnson C.N., Ritchie E.G. and O'Neill A.J. (2010). Predator control promotes invasive dominated ecological states. Ecology Letters. *In Press.*

Author Contribution

Conceived and designed the experiments: ADW, AJO.
Performed the experiments: ADW, AJO.
Analyzed the data: ADW, JCN, EGR.
Contributed funding/equipment/analysis tools: AJO, ADW, JCN.
Wrote the paper: ADW.

Co-author declaration

I approve the above *author contribution* statement and give permission for the paper/s coauthored by me to be included in the thesis by Arian Wallach.

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Date: 16/11/09

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Date: 16/11/09

CHAPTER 4

Predator control promotes invasive dominated ecological states

Wallach, A.D., Johnson, C.N., Ritchie, E.G. & O'Neill, A.J. (2010). Predator control promotes invasive dominated ecological states.
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CHAPTER 5 - DISCUSSION

Dingo control is the ultimate cause behind biodiversity loss in Australia – a thesis overview

Arian D. Wallach

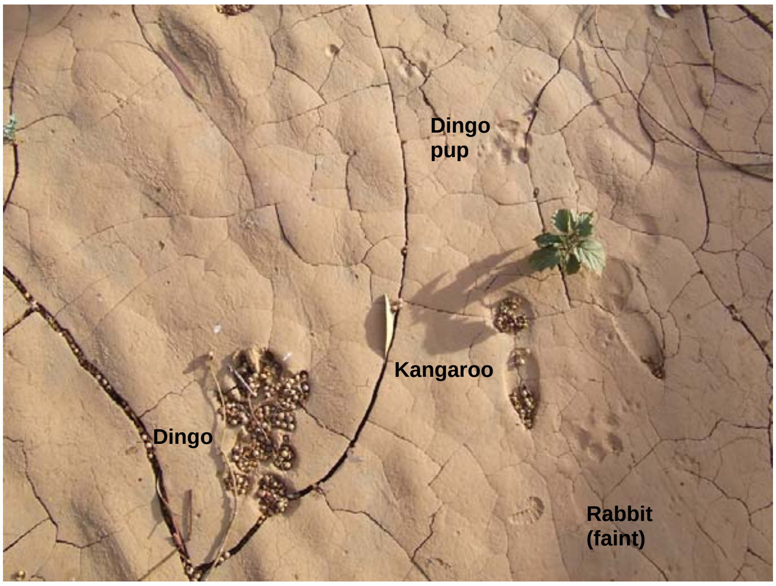
"We regard trophic cascades as a universal property of ecosystem functioning, a law of nature as essential and fundamental to ecology as natural selection is to evolution" Terborgh and Estes (2010)

This study suggests that the disruption of functional top-down regulation across Australia is an ultimate cause behind state shifts to invasive dominated and degraded ecological states. Rather than controlling invasives, predator control promotes bottom-up driven states resulting in the proliferation of opportunistic mesopredators and herbivores, which rapidly deplete their resource base (*proximate model*, Introduction). The three hypotheses tested in this study supported this view: (1) all threatened species surveyed were found to be surviving in the presence of dingoes; (2) social stability, rather than abundance, was a consistent predictor of top-down regulation; and (3) the restoration of dingo populations promoted the recovery of biodiversity and productivity, while predator control was affiliated with invasive and opportunistic species. The aim of this chapter is to discuss the thesis as a whole. I do not offer a comprehensive literature review, as this has been thoroughly presented in the chapters. Instead, I aim to clarify how the various chapters and appendices form a coherent picture.

Threatened species survive only in the presence of dingoes

The survival of several threatened species in areas where dingoes were considered rare or absent posed a major challenge to the general applicability of the top-down regulation hypothesis. However, following our prediction, dingoes were found to be surviving at all sites with threatened species that were surveyed, including areas that were most unlikely to harbor dingoes (Chapter 2). Dingoes were located inside the dingo barrier fence (DBF), where yellow-footed rock-wallabies (*Petrogale xanthopus xanthopus*) survive (Flinders Ranges, Plate 1); and dingoes were also located deep inside the DBF where malleefowl (*Leipoa ocellata*) occur (Adelaide Hills and Yorke Peninsula).

Plate 1: Adult and pup dingo tracks, together with rabbit and kangaroo tracks, near a wallaby colony in the Northern Flinders Ranges.



Dingoes were the most common predator in the two wallaby sites surveyed and were a major controlling influence on competing opportunistic herbivores (Chapter 2,4). The ecological significance of dingoes in the Northern Flinders Ranges became particularly apparent after they were lost to a 1080-baiting treatment in Nantwarrinna. Following predator control, generalist herbivores notably increased in abundance (Chapter 4), vegetation cover was lost from several water points, and wallaby signs disappeared from one location (unpublished data). The Northern Flinders Ranges provides a stark demonstration of an ecosystem that has shifted to an alternative state (Plate 2; and see also Figure 2).

Plate 2: A dead mulga forest in the Northern Flinders Ranges presents a grim view of an ecosystem that has shifted to a degraded state following a century of predator control. Although extensive sections of the Northern Flinders Ranges were declared a National Park or an Indigenous Protected Area and destocked several decades ago; grazing pressure has not eased. Despite the extreme state of degradation, this area supported the highest abundance of herbivores detected in this study. These herbivores were mainly species that can travel large distances (kangaroos and goats) and utilize emerging patches of vegetation.

The discovery of secretive dingoes surviving in association with malleefowl in close proximity to human settlements and sheep farms, provided yet another striking example of the link between dingoes and threatened species survival (Chapter 2). In this region dingoes were presumed eradicated several decades ago, yet they have persisted and their ecological significance is indicated by the high rate of scent-marking activity at active nests (Chapter 2), and the negative correlation between poison-baiting and malleefowl nesting success (Benshemesh *et al.* unpublished). What these results imply is that many, and perhaps all, species threatened by invasives are under the protective influence of dingoes, even in cases where the dingo is presumed absent.

A comparison of two sites within the historical range of a threatened species, the kowari (*Dasyuroides byrnei*), lends further support to the notion that dingoes play a vital role in the survival of threatened species (Appendix 1). The kowari has persisted in Pandie Pandie (Plate 3), but is apparently absent from Mungerannie, even though both stations are similarly utilized for cattle grazing, and no known barrier is halting reinvasion. The main difference in management between these two stations was predator control: Mungerranie was baited, while Pandie Pandie generally was not. The consequences of this difference reflected the top-down regulation model, and suggest that the cessation of control in Mungerannie may enable rapid kowari recolonization (Appendix 1).

Plate 3: A dingo in the grass in Pandie Pandie. After five years of reduced predator control, Pandie Pandie was top-down regulated and supported the highest abundance and diversity of small mammals and plants detected in this study (Chapter 4, Appendix 1).

These results support the continent wide trend of higher survival rates of marsupials where dingoes are common (Johnson *et al.* 2007), and suggest that the current war on exotic species, particularly predators (Introduction), is counterproductive. The survival of threatened species in pastoral zones may depend on replacing predator control practices with ‘predator friendly’ methods of production (e.g. guardian animals, van Bommel 2010); and their survival in conservation-designated areas may very well depend on assuming a more relaxed and holistic attitude towards invasive species. A recovery of dingo populations, as an alternative to predator control practices, is expected to benefit both conservation objectives and pastoral production (Chapter 4). This transition however depends upon an understanding of dingo behavior and the key role their sociality plays in their ecological functioning.

Dingo abundance and social stability are not linearly related

The relationship between dingo abundance and social stability is quadratic rather than linear (Chapter 3). Populations may fluctuate between three main States[1]: (A) below carrying capacity and socially fractured, (B) above carrying capacity and socially fractured, or (C) at carrying capacity and socially stable. Lethal control systematically fractures social units and releases population abundance to bottom-up processes, which drives populations towards State A or B. Populations recovering from State A will first increase in abundance, potentially driving the population into State B. The next phase is an increase in stability followed by a reduction in population growth-rate (A ➔ C) or size (B ➔ C) (Figure 1).

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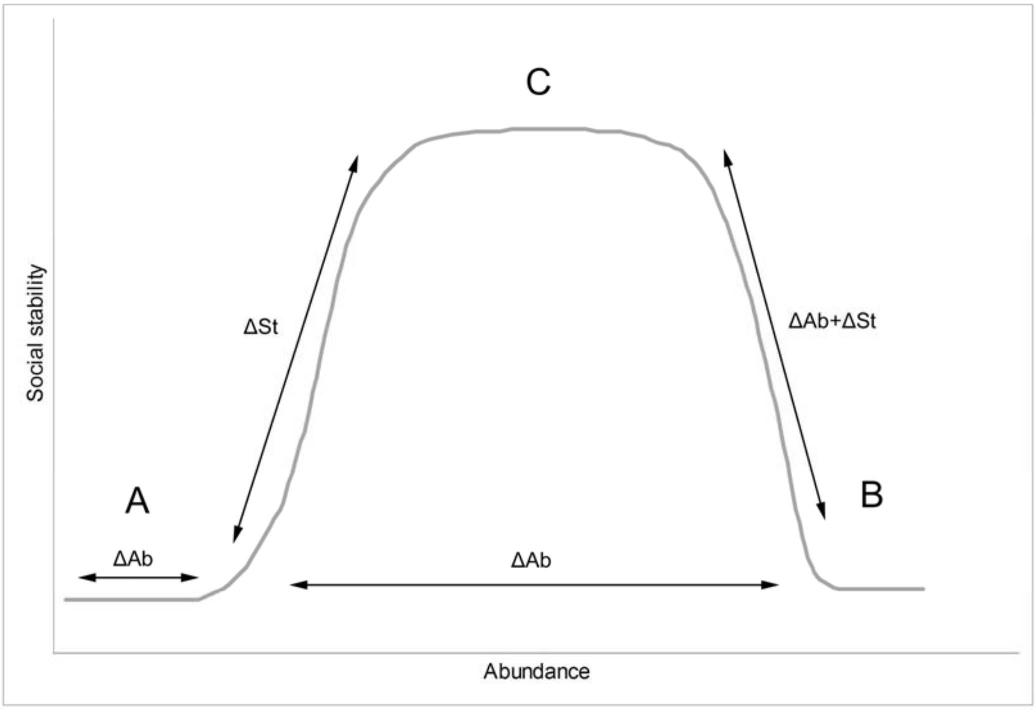
[1] Chapter 2 and Chapter 3 both make use of the term ‘State’ frequently, yet in different contexts. Chapter 2 refers to the three dingo *population States*, while Chapter 3 discusses *ecological states*. To reduce confusion, the word is capitalized when describing dingo populations, while lower case is used when referring to ecological conditions.

Figure 1. Influence of management on the abundance (Ab) and social stability (St) of dingoes (reproduced from Chapter 3).



Following the cessation of control, dingo populations in Red Lake followed an A ➔ C pathway, yet it will take several years for this population to reach State C. Dingoes in Nantawarrinna were showing signs of recovery from State A in 2007, but the poison-baiting campaign in 2008 reversed this process. Following control intensification in Andamooka, dingoes swung from State A to B. Cessation of control at this stage is expected to result in a population size decrease following the B ➔ C pathway. Pandie Pandie and Curdimurka were relatively free from predator control for approximately five years, providing the best representations we found in South Australia of State C populations. A survey of Curdimurka in its sixth year, and the linear relationship between social stability and time since control across sites, indicates that a decade may be required before social stability fully recovers from control. By contrast, population size can easily bounce back within one year if conditions are favorable (Chapter 3). Factoring social stability into the top-down regulation model may therefore provide a more reliable indicator as to when a large predator is merely common, and when it is functioning as an apex predator.

The strength, and in some cases even the direction of effect, of dingo abundance and social stability differ. A generalized linear model (GLM) revealed that dingo social stability (scent-marking rates) was overall the more powerful predictor of top-down regulation effects, while dingo abundance was prone to be bottom-up influenced. Thus herbivore abundance is negatively related to dingo scent-marking, but is positively related to dingo abundance (a weaker variable; Chapter 4). This may explain why several studies have found inconsistent correlations between dingoes and mesopredators and herbivores. For example, Letnic *et al.* (2009) found a negative relation between dingo and fox abundance, but not cats; and a consistent controlling effect of dingoes on kangaroos, but not on rabbits. I suggest that this pattern is attributed to the different behavioral interactions and life history traits of each species. Different intraguild interactions may explain the stronger negative relationship between dingo and fox numbers compared to dingo-cat associations. Dingoes may ‘seek out’ foxes first (see Andamooka, Chapter 4), because they are potentially a more significant competitor than cats, who are also potential prey. The consistent negative relationship between dingo and kangaroo numbers (see Nantawarrinna, Chapter 4) may reflect the high mobility of kangaroos, which enables them to avoid areas of high dingo activity. Rabbits on the other hand are sedentary and unless dingoes are socially stable, dingo-rabbit abundance may be positively correlated due to the shift to bottom-up driven states (GLM, Chapter 4). These differences in inter and intra-guild interactions, under different dingo population States and ecological conditions, deserve further research.

Studies that focus solely on comparing systems under high and low abundances may often be comparing two types of bottom-up driven systems (State A verses B, or low verses high variations of State A). This is most likely to be a widespread situation in regions, such as Australia, where predator control is prolific and State C is rare (Chapter 3). State B is probably a common, but under-appreciated, condition of high top predator numbers but low social stability. This condition is likely to occur where a large resource base can support high predator densities, and the lack of social structure allows for increased reproductive rates and a lack of territorial behavior. Because behavior is often overlooked in ecological studies, State B may mistakenly be assumed to represent a top-down regulated state. In the current study Andamooka was the only site that was productive and unstable enough to sustain a State B scenario, and dingo abundance was the highest detected (even though this site is inside the DBF). Although the increase in dingo abundance was followed by an almost precise one-to-one decrease in foxes, Andamooka could not be described as a top-down regulated site (Chapter 4). Where social stability is considered within an ecological context, the keystone role of large predators as the source of ecological health and resilience becomes consistently apparent.

Dingoes recover wilderness

The principle components analysis presented in Chapter 4 clearly indentified two main ecosystem states and the cause of shifts between them. Predator control (poison-baiting) is the factor that reduces resilience, driving ecosystems from top-down regulated states (PC1) to bottom-up driven states (PC2). Figure 2 provides a schematic illustration of shifts between PC1 and PC2 states in this study. At the top end of the PC1 branch, dingo populations are in State C, small and CWR mammals and vegetation are abundant and invasive species are scarce. The loss of resilience caused by predator control drives sites along the PC1 branch towards, and eventually past, the F_1 bifurcation point and into the basin of attraction of the PC2 branch. Sites that have shifted to the PC2 branch are bottom-up driven, dominated by invasive and opportunistic species, and may have low (State A) or high (State B) dingo numbers. A recovery of sites back onto the PC1 branch will require that conditions be reversed far enough to reach the F_2 bifurcation point. Thus, for example, although scent-marking rates in Red Lake had already surpassed Mungerannie by 2007 (Chapter 3), its PC1 value was still lower in 2008 (Chapter 4).

Figure 2: Illustration of shift between top-down regulated (+PC1) to bottom-up driven (-PC1) ecological states. Sites with positive PC1 values are positioned on the upper branch, while sites with negative PC1 values are positioned on the lower branch. Placement along each branch follows PC1 and PC2 values (Chapter 4). Red arrows indicate the basin of attraction, black arrows denote the direction sites were moving in, and F_1 and F_2 denote the bifurcation points. Sites are: Pandie Pandie (PP), Curdimurka (CU), Mungerannie (MU), Red Lake (RL), Andamooka (AN), Gammon Ranges National Park (GR) and Nantwarrina (NA). Modified from Scheffer *et al.* (2001).

NOTE:
This figure is included on page 125 of the print copy of the thesis held in the University of Adelaide Library.

Causality was supported by comparing community composition before and after intensification and relaxation of predator control (Chapter 4). The increase and initial stabilization of dingo populations in Red Lake following predator control was accompanied by a decrease in mesopredators and herbivores and an increase in small native mammals. In Andamooka, the increase in dingoes was followed by a decrease in foxes; while the decrease of dingoes in Nantawarrinna was followed by an increase in herbivores. Curdimurka served as a non-baited control site and following our prediction, dingoes and small mammals (including CWR mammals) were relatively common, while mesopredators and generalist herbivores remained scarce. Ironically, foxes benefitted from poison-baiting campaigns, due to the loss of top-down control by dingoes (GLM, Chapter 4). Thus, the principle method applied across the country to control foxes, promotes foxes instead.

The negative effect of poison-baiting in our arid study sites even outweighed the positive influence of rain (Chapter 4). The GLM revealed a negative relationship between small mammals and recent rainfall (three years accumulated), and average rainfall was negatively associated with PC1, PC2 and vegetation cover. Curdimurka, on the shore of Southern Lake Eyre supported on average 2.5 times more vegetation cover (at grazing level), and 200 times more small mammals, compared to the Northern Flinders Ranges that receives nearly twice as much rain. The increase in predator control efforts with average rainfall in the arid zone (Chapter 3) has created an unexpected reverse pattern where the more potentially productive zones are the most degraded. Although rainfall does initially increase productivity (Letnic *et al.* 2009), the build up of herbivores and mesopredators that occurs where the top-predator is controlled, eventually overwhelms any newly available resource. This result challenges the popular view that the degraded state of the Australian arid zone is due to the drought.

Shifting to top-down regulation

Extinctions in Australia have been most severe in the arid zone, even though human population density is at its lowest, wilderness areas are vast and connected, and although alien species were introduced in mesic areas (McKenzie *et al.* 2007). This pattern reflects the fact that it is precisely in the arid zone where dingo-control is most effective (Appendix 2). Since Europeans advanced into the Australian deserts, pastoralism became the main land use. Predator control was immediately instigated especially at water points, which became the "life blood" of arid pastoralism. Because dingoes need to drink, they are vulnerable where water availability is restricted, and are effectively controlled by laying poison baits around water points. The establishment of National Parks in the arid zone certainly did not improve these conditions, as predator control is a primary conservation strategy. The consequences of these actions are apparent today in the barren pastoral stations, and impoverished National Parks, where the folly of predator control is most apparent (Plate 2). Yet it is extraordinary how rapidly ecosystems can recover when predator control is relaxed (Plate 3, Chapter 4).

Much publicity has been given to the threat of invasive species, while largely condoning the extensive loss of top-down regulation that has paved the way for this condition. The scale and intensity of pest control in Australia reflects a common belief that the Australian ecosystem is incapable of adjusting to the arrival of alien species, and that human intervention can come to the rescue. Neither of these notions is supported by this study. We cannot assume the ecological roles of wolves, sharks and lions, even though we are certainly capable of determining their fate.

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CHAPTER 6 - CONCLUSION

Collaborating with predators

Arian D. Wallach

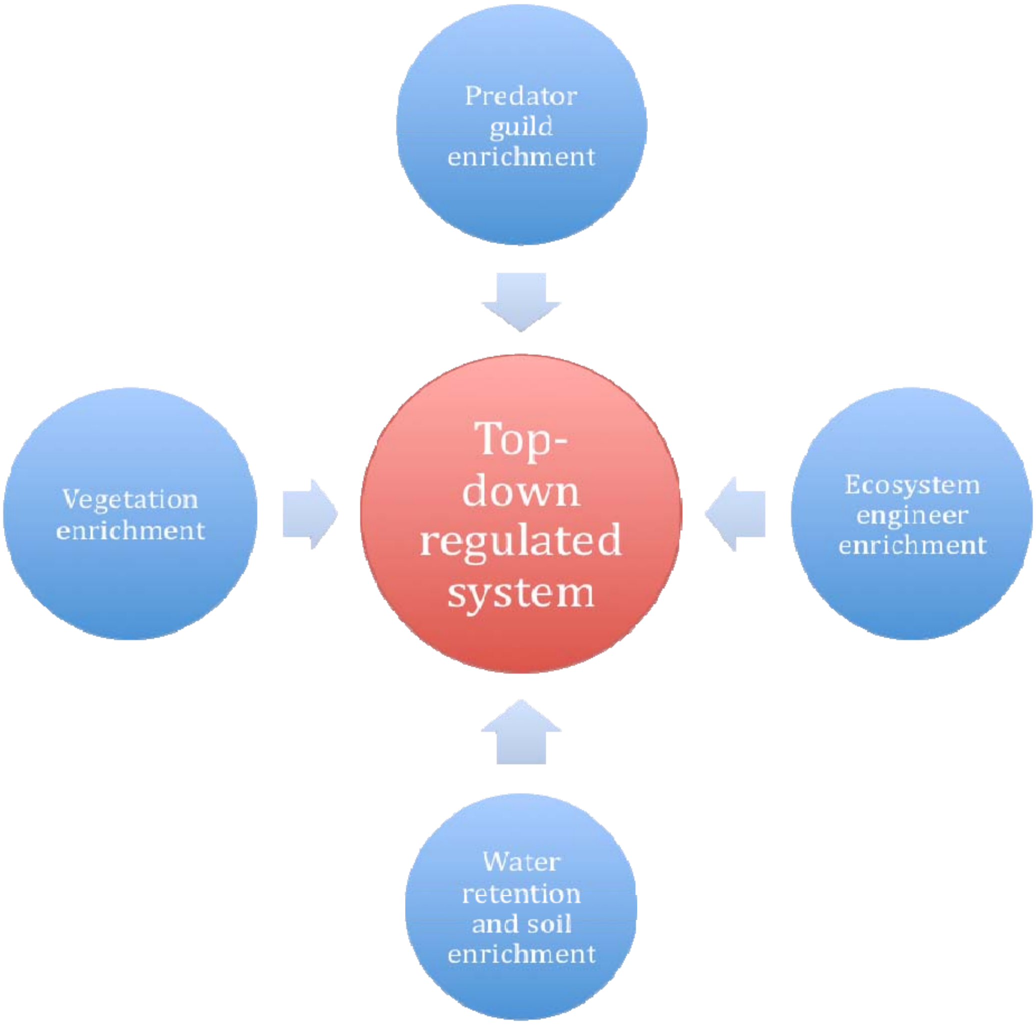
Apex predators are clearly far more successful ecosystem regulators than humans are. But that does not imply that we are without a role to play. Rather than controlling predators, we could instead initiate a ‘collaboration’. The role of the apex predators within this collaboration is to exert top-down control on opportunistic species. Our role is to enrich the degraded ecosystem once top-down regulation is achieved.

The alternative model for ecological restoration we propose here is based upon three principles:

1. The fundamental component of ecological restoration is the apex predator.
2. No distinction is made between native and exotic species.
3. Species interactions that cause biodiversity loss are symptoms of ecological fragility.

Following these principles, restoration is conducted in two main stages: (1) Restoration of top-down regulation, and (2) Ecological enrichment. Human input into these stages is solely additive (e.g. reintroduction) rather than subtractive (e.g. population control). This concept it illustrated in Figure 1.

Figure 1: Top-down ecosystem restoration. Rather than controlling predators to promote prey, apex predator recovery is the foundation of restoring ecological functioning. Two main recovery stages are illustrated: restoration of top-down regulation (red circle) and ecosystem enrichment (blue circles).



Stage one: restoring top-down regulation of ecosystems

The foundation of our proposed restoration begins at the top, with apex predator recovery. The first stage of restoration is therefore to reinstate functional top-down regulation (Figure 1, inner circle). The system can be described as functional when: (1) apex predators are in State C (Chapter 3); (2) mesopredators and generalist herbivores are top-down regulated; and (3) extant native fauna and flora abundance and diversity is increasing. This study indicates that in the Australian arid zone a period of five years of recovery from predator control is often sufficient to restore ecosystems to a top-down regulated state (Chapter 4). In other regions however, predator recovery may take longer and require human assistance.

Apex predators are the foundation of ecological resilience (Terborgh *et al.* 2001, Wilmers and Getz 2005, Johnson 2006, Sandin *et al.* 2008, this study). Therefore, reintroduction is required where they are locally extinct (Hayward and Somers 2009). But what of the regions of the world from which apex predators have been lost entirely, or are naturally absent? For these cases we suggest the introduction of a surrogate or exotic apex predator. This would naturally require a change in attitude towards biotic invasions. As was discussed previously (Introduction, Discussion), the rise and detrimental impact of feral predators parallels the general effect of mesopredator release. We suggest that unlike the devastating effects of introducing mesopredators into apex-predator-free environments (a form of mesopredator release), the introduction of an exotic apex predator will increase ecological resilience, health and vigor. The main difference between apex predators and mesopredators is that apex predators exert top-down regulation upon themselves, while mesopredators do not (Chapter 3, 4). The introduction of the dingo to mainland Australia and an off shore island (Fraser Island) are classic examples of the benefits of exotic apex predators (Letnic *et al.* 2009). Islands are the main environments that are naturally devoid of large predators, and indeed it is on islands that the impacts of invasive species have been most notably detrimental (Courchamp *et al.* 2003). We suggest that invasive dominated islands that do not have an apex predator (e.g. New Zealand) could benefit from the introduction of an exotic apex predator. This approach falls in line with the proposal to *Rewild* North America with African and Asian megafauna (Donlan et al. 2005, 2006).

Stage two: ecological enrichment

Following the reinstatement of an apex-predator-dominated environment, significant recovery of the extant members of the ecological community will most likely occur naturally and rapidly. The restoration of functional top-down regulation will now provide a firm foundation for active restoration of the depleted aspects of the ecosystem (Figure 1, outer circles). The second stage of recovery focuses on reinstating keystone species and processes via enrichment of the predator guild, ecosystem engineers, vegetation and soil.

Predator guild enrichment

Reintroduction of missing predator species is vital to the restoration of depleted ecosystems because predator richness and biodiversity are closely linked (Finke and Denno 2005). For instance, although dingoes control cats (Chapter 4), they cannot exert much influence in the arboreal plane. Cats successfully hunt and reproduce on trees, and it is here that they might continually suppress the recovery of arboreal species such as quolls, possums and birds (Dickman 1996). The reintroduction of pythons, a potentially important predator of cats (Fearn *et al.* 2001, personal observation), could allow quolls and cats to coexist (Plate 1). Dingoes are necessary for python recovery because pythons are potentially susceptible to fox predation (Michael and Lindenmayer 2008). Cats in turn, may also be important for python survival, because cats are successful predators of many venomous snakes (Dickman 1996, Paltridge *et al*. 1997) some of which feed on young pythons (e.g. mulga snakes *Pseudechis australis*, http://www.abc.net.au/news/stories/2008/01/23/2144507.htm).

Plate 1: Enrichment of the predator guild may provide a more complex mosaic of habitats and niches. When the predator guild is poor cats can be damaging in areas where dingoes cannot reach. Reintroducing pythons may help further regulate cats and benefit quolls, possums and birds. Pythons actively seek and kill cats in a similar way that dingoes hunt out foxes (personal observation).

Enrichment with ecosystem engineers

Ecosystem engineers are organisms that create significant physical changes in their environment, modulate resource availability to other species, and thereby create new habitats (Jones *et al.* 1994). Beavers (*Castor candensis*) are perhaps the best-known ecosystem engineers because they create wetlands by cutting trees and building dams. These activities strongly influence tree populations, hydrology, and nutrient cycles on a scale of decades and even centuries (Naiman *et al.* 1994). Ecosystems that have lost their engineers will eventually also loose those engineered habitats and the species that depend upon them. Reintroducing ecosystem engineers is therefore another priority in degraded environments. In Australia, for example, the loss of the greater bilby (*Macrotis lagotis*) and burrowing bettong (*Bettongia lesueur*) from most of their historic range has resulted in habitat simplification and degradation. Both are ecosystem engineers whose extensive digging and burrowing activities create fertile patches that benefit plants and other animals (James and Eldridge 2007, Read *et al*. 2008). Both were driven close to extinction by foxes and cats and their survival is therefore dependent upon dingoes (Chapter 2, Southgate *et al*. 2007).

Vegetation enrichment

Top-down regulation enhances productivity by regulating the abundance and behavior of herbivores. Thus recovery of extant vegetation should occur naturally and rapidly in many places, particularly where ecosystem engineers are present. However, in some cases once an ecosystem has state shifted to a degraded state, the damage can be irreversible without active restoration efforts. Erosion and the lack of vegetation cover can induce a positive feedback that creates a hostile environment for germination. The lack of vegetation can encourage desertification in the same way that vegetation generally encourages more vegetation (Schlesinger *et al.* 1990, Scheffer *et al*. 2001). To reverse this process, revegetation activities may be highly beneficial when coupled with restoration actions to enhance water retention and soil quality.

Water retention and soil enrichment

In arid regions high grazing pressure and low water retention is often a more significant limiting factor to productivity than rainfall. Apex predators modify grazing intensities, but soil compaction, lack of vegetation cover and the loss of engineered water catchments may drastically reduce water retention and soil quality (Handa and Jefferies 2000, Drewry 2006).

High densities of domestic animals may compact the soil to the extent that water cannot easily penetrate the surface, thereby creating a hostile environment for vegetation regeneration. Burrowing animals are probably the best remedy for this condition, although some forms of active restoration could be considered (Van Den Berg and Kellner 2005). The lack of vegetation can reduce water retention due to the lack of shade, root pathways and debris accumulation in creeks. Revegetation in natural or man-made water collecting basins (shallow dams) may create productive pockets from which regeneration can spread (Rosenstock *et al.* 1999). The construction of small dams in creeks to mimic those that would be created by plant debris will create new wetlands that attract birdlife that are essential for seed dispersal and germination (Rosenstock *et al.* 1999). The construction of water catchments in arid environments may serve to overturn the process of desertification that is occurring in many regions of the world.

Man-made deserts

The life threatening desertification process is most commonly related to climate change (Scheffer *et al.* 2001). But the inextricable link between apex predators and productivity may suggest another cause. Humans have successfully annihilated large predators from most of their range. The main driver of these efforts is most often pastoral development. There appears to be a recurring pattern of events throughout the world, and human history, in which pastoral intensification promotes large predator annihilation which in turn shifts ecosystems to bottom-up driven states that eventually collapse (Terborgh *et al.* 2001, Johnson 2006, Sandin *et al.* 2008, this study). In arid and semi-arid regions, this deterioration can rapidly denude entire regions of life supporting systems. We believe that the Gobi Desert, the Sahara Desert and the Australian deserts are all examples of this theme. The mass slaughter of wolves from the Mongolian grasslands in the 1960's (Reading *et al.* 1998) may be the primary cause behind the desertification of this region in recent decades. The rapid transformation of the Sahara from a productive savannah to a wasteland occurred at a period of pastoral intensification (Kuper and Kröpelin 2006). Did humans wipe out large predators from the Sahara to protect their livestock during this period, and was overgrazing rather than climate the mechanism of change? If so, will continued persecution of predators similarly transform the Australian desert into an ocean of sand?

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APPENDICES

Appendix 1

Wallach A.D. and O'Neill A.J. (2009). Threatened species indicate hotspots of top-down regulation. Animal Biodiversity and Conservation. 32.2: 127–133.

Author Contribution

Conceived and designed research methods: ADW, AJO.
Performed the fieldwork: ADW, AJO.
Analyzed the data: ADW.
Contributed funding/equipment: ADW, AJO.
Wrote the paper: ADW.

Co-author declaration

I approve the above *author contribution* statement and give permission for the paper coauthored by me to be included in the thesis by Arian Wallach.

Name: Adam O'Neill

Signature: ____________

Date: 16/11/09

APPENDIX 1

Threatened species indicate hot-spots of top-down regulation.

Wallach, A.D. & O'Neill, A.J. (2009). Threatened species indicate hotspots of top-down regulation.
Animal Biodiversity and Conservation, v. 32(2), pp. 127 -133

Appendix 2

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Author Contribution

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I approve the above *author contribution* statement and give permission for the paper coauthored by me to be included in the thesis by Arian Wallach.

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APPENDIX 2

Artificial water points: hotspots of extinction or biodiversity?

Letter to the Editor

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