

Seven considerations about dingoes as biodiversity engineers: the socioecological niches of dogs in Australia

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Abstract. Australian dingoes have recently been suggested as a tool to aid biodiversity conservation through the reversal or prevention of trophic cascades and mesopredator release. However, at least seven ecological and sociological considerations must be addressed before dog populations are positively managed.

1. Domestication and feralisation of dingoes have resulted in behavioural changes that continue to expose a broad range of native and introduced fauna to predation.
2. Dingoes and other dogs are classic mesopredators, while humans are the apex predator and primary ecosystem engineers in Australia.
3. Anthropogenic landscape changes could prevent modern dingoes from fulfilling their pre-European roles.
4. Dingoes are known to exploit many of the same species they are often presumed to 'protect', predisposing them to present direct risks to many threatened species.
5. The assertion that contemporary dog control facilitates the release of mesopredators disregards the realities of effective dog control, which simultaneously reduces fox and dog abundance and is unlikely to enable increases in fox abundance.
6. The processes affecting threatened fauna are likely a combination of both top-down and bottom-up effects, which will not be solved or reversed by concentrating efforts on managing only predator effects.
7. Most importantly, human social and economic niches are highly variable across the ecosystems where dingoes are present or proposed. Human perceptions will ultimately determine acceptance of positive dingo management.

Outside of an adaptive management framework, positively managing dingoes while ignoring these seven considerations is unlikely to succeed in conserving native faunal biodiversity but is likely to have negative effects on ecological, social and economic values.

Keywords: apex predators, *Canis lupus dingo*, free-ranging dogs, human values, mesopredator release hypothesis, reintroduction, threatened species, trophic cascade

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Introduction

The success of humans is built on the mastery of useful species (livestock, grains) and the downfall or management of competing species, particularly predators and parasites. Humans have historically besieged wild apex predators throughout the world, leading to the endangerment of many wild canid species (Ray *et al.* 2005; Sillero-Zubiri *et al.* 2007). Wild carnivores have been and are still viewed by many as competitors for human resources (e.g. Treves and Karanth 2003; Baker *et al.* 2008) and have been extirpated in many areas of co-occurrence with humans (Williamson 1996; Berger *et al.* 2001; Sillero-Zubiri *et al.* 2007).

This includes ~25% of Australia where dingoes (*Canis lupus dingo*) and other wild dogs have been largely eradicated to accommodate sheep (*Ovis aries*) production (Fleming *et al.* 2001). Conversely, there is a growing literature that proposes that dingoes might be positively managed to provide gains for Australian native biodiversity (Glen and Dickman 2005; Glen *et al.* 2007a). Both retention and encouragement of extant populations and active reintroductions where dingoes are locally extinct are proposed, with the expectation that lower-order prey species will benefit (Johnson *et al.* 2007; Ritchie and Johnson 2009).

The primary mechanism suggested to provide biodiversity benefits is the suppression or reversal of trophic cascades by inhibiting mesopredator release (see ‘mesopredator release hypothesis’ (MRH) below) (Crooks and Soulé 1999) following the maintenance or encouragement of dingo populations. The MRH predicts that when a higher-order predator (such as lions (*Panthera leo*) or grey wolves (*C. l. lupus*)) is removed, lower-order predators – such as leopards (*P. pardus*) and painted dogs (*Lycaon pictus*) or coyotes (*C. latrans*) and red foxes (*Vulpes vulpes*) – will increase in abundance. The consequence of this process is a trophic cascade (Hairston *et al.* 1960), which often results in amplified pressure on smaller prey species. Reversal of trophic cascades may result in fundamental ecosystem changes, even to vegetation. For example, reintroduced wolves reduced elk (*Cervus elaphus*) populations with consequent recovery of aspens (*Populus tremuloides*) (Ripple and Beschta 2007), though these results have been disputed by Kauffman *et al.* (2010). The analogous process suggested for Australian ecosystems is positive management of dingoes, which then suppress foxes and feral cats (*Felis catus*), thereby providing reversal of the trophic cascade and release of prey threatened by fox and cat predation (Dickman *et al.* 2009; Ritchie and Johnson 2009). Such effects are predicted to occur at a continental scale (Letnic *et al.* 2011).

When contemplating reintroductions, the International Union for Conservation of Nature recommends that the probable consequences of any such actions should be evaluated from ecological, economic and social viewpoints (IUCNSSC 1995). Here, we outline some of the assumptions, both explicit and implicit, that affect the current debate. We discuss seven theoretical and pragmatic issues that must be considered before drafting policies about reintroduction (Dickman *et al.* 2009), promotion or expansion of extant dingo populations.

Initially, we consider terminology that affects discussions about positive dingo management. Next we discuss the derivation of dingoes and how this might affect their role in Australian ecosystems. The importance of scale, the direct risks of dingoes, and the likely impacts of anthropogenic changes to Australian ecosystems on the functional role of modern dingoes are also discussed. Before dingoes are positively managed, there are also imperative human dimensions that must be addressed to move the discussion from theorising to practical implementation. Finally, to avoid being branded as naysayers, we offer ideas to assist policy and decision makers in evaluating propositions for positive dingo management.

Some definitions

Word definitions are very important because how we interpret words influences our conceptual understandings. To reduce misinterpretations, we propose the following definitions for terms that we will use throughout.

‘apex predator’: top predator with no predator of their own (Buskirk 1999); ‘apex’ describes trophic position.

‘canid’: any member of the family Canidae.

‘control’: population reduction through poisoning, trapping, shooting and exclusion.

‘dingo’: a type of dog, native to Asia and introduced to Australia by humans. We will use this term when referring specifically to members of the subspecies *C. l. dingo*.

‘feral animal’: wild-living animal, derived by domestication, that has subsequently escaped, reverted more or less to wildness and become naturalised (Butler 2010).

‘free-ranging dog’: any dog (*Canis lupus* ssp.) that lives completely in the wild or metabiologically (where anthropogenic resources provide part or all of their needs commensally). This includes free-living dingoes, ‘wild dogs’, domestic breeds and crosses between them and is shortened henceforth to ‘dog’ when referring to these animals generally.

‘management’: processes and actions that actively or passively reduce (i.e. control), maintain or enhance wildlife populations to achieve a goal (Caughley and Sinclair 1994).

‘mesopredator’ (mostly 2–15 kg mean bodyweight, Buskirk 1999): a middle predator, which may be suppressed by an apex predator and released when the apex predator is removed; ‘meso’ describes trophic position.

‘mesopredator release hypothesis’: (MRH) extension of the trophic cascade hypothesis (see below) where intermediate predators, when unconstrained by higher-order predators, cause prey populations to decline (Crooks and Soulé 1999).

‘positive management’: management actions where wild populations are enhanced or maintained by human intervention, including such actions as reintroductions, cessation of control, or encouragement.

‘reintroduction’: process whereby a species or subspecies (e.g. the dingo) is reintroduced into areas where they are locally extinct (IUCNSSC 1995).

‘trophic cascade’ = green world hypothesis (Hairston *et al.* 1960): Three-level process by which predators (top trophic level) suppress their prey (second trophic level), and thereby release the third trophic level (vegetation or smaller prey), which causes the abundance of the third trophic level to increase. In the simple system described by Hairston *et al.* (1960), predators caused plant biomass to increase by consuming herbivores. Oksanen *et al.* (1981) argued that this system only worked with simple and odd-numbered trophic systems.

1. Derivation of dogs including dingoes

Dogs were probably the first species derived by domestication of wild animals by humans ~15 000 years ago (Scott and Fuller 1974; vonHoldt *et al.* 2010). Domestication may have been through raising of wolf cubs, orphaned or stolen from dens (Scott and Fuller 1974), or by the progressive ‘taming’ of wolves associated with human camps either naturally, as suggested by Coppinger and Coppinger (2001), or through direct selection by culling of any commensal wolves with a tendency for aggression (Trut *et al.* 2009). All dogs were derived by human selection and domestication from grey wolves, and, according to recent DNA evidence (vonHoldt *et al.* 2010), initially from Middle Eastern wolves and from later interbreeding with local wolf populations. Ancient breeds such as the dingo and the New Guinea singing dog (*C. l. hallstromi*), were selected by people living east of the Himalayas (Savolainen *et al.* 2004; Pang *et al.* 2009). Most likely,

selection occurred in southern China less than 16 300 years ago and numerous wolves were involved (Pang *et al.* 2009). Molecular confirmation by Vila *et al.* (2003) and Ciucci *et al.* (2003) of natural hybridisation between wolves and dogs supports the contention of Pang *et al.* (2009) that there were multiple natural crosses, and purposeful out-crossing of dogs with wolves continues today (for example, Ciucci *et al.* 2003; and www.pets4you.com/wolf.html (accessed 24 October 2010)). Descendants of original dingoes are still present in south-east Asia (Corbett 2001).

Domestication leads to genetically based behavioural changes in many canids, including foxes (Lindberg *et al.* 2005; Trut *et al.* 2009), dogs (Trut *et al.* 2009) and wolves (Saetre *et al.* 2004). Although the divergence time between dogs and grey wolves is evolutionarily short, there are large behavioural differences between the species and there are great differences in the behavioural signatures of different breeds of dog (Scott and Fuller 1974). Saetre *et al.* (2004) have identified substantial brain gene expression changes in dogs when contrasted with wolves and coyotes, indicative of strong selection pressure for tame behaviour. The associated changes (e.g. to smaller body and proportional brain size; from obligatory to facultative hypercarnivory; increased number and changed colour morphs, vocalisations and other behaviours, etc.) are likely to have resulted from changes to only a small number of hypothalamic genes with multiple functions (Saetre *et al.* 2004; see also foxes in Lindberg *et al.* 2005). The consequences of genetic changes (through domestication and subsequent feralisation) for the roles of dogs in Australian ecosystems are generalist diets, flexible foraging tactics, and the rapid acceptance of anthropogenic resources and reversion to commensal habits when opportunity arises. In short, dogs benefit from anthropogenic environmental manipulations and water and food subsidies, which likely have major impacts on their abundance and potentially on their ecological functions.

Being selected by humans from wolves, no dog is a native species of anywhere except in the broadest definition of 'native' (see Butler 2010; Corbett 2001). Although considered indigenous wildlife in much current legislation (e.g. *Territory Parks and Wildlife Conservation Act 2005*), it is an Anglocentric artifice to nominate any animal present in Australia before 1788 as indigenous. Dingoes and other free-ranging dogs in Australia are all feral animals by definition, in that they are the wild living descendants of a domesticated animal (Corbett 2001; Price 2002; Butler 2010). In Australia, dogs are introduced animals, with archaeological, morphometric and genetic evidence pointing to likely introduction of the dingo arriving with Asian traders from ~4000 years ago (Corbett 1985; Savolainen *et al.* 2004), a process that might have continued until the 1920s (Corbett 2001). Although dingoes are found in other parts of the world (Corbett 1985, 2001), they are an iconic and charismatic species with significant cultural and intrinsic value to most Australians (Atkinson 2008; Smith and Litchfield 2009; Hytten 2009). The feral domestic dog component of Australian free-ranging dog populations has been contributing to the dog gene pool since early European settlement (Fleming *et al.* 2001). The dogs of south-eastern Australia are mostly dingo-like hybrids (Jones 2009) and the impact of their positive management on biodiversity is largely unknown or assumed to be similar to dingoes (Claridge and Hunt

2008). The key question is not 'are they native' but 'should they be treated as though they are'? The dingo's exotic origin is well established but its ecological roles are not. Dogs were derived by human selection, which means that their functional roles in modern ecosystems may not be readily likened to apex predators elsewhere (including grey wolves), which have not undergone such extensive genetic and phenotypic changes over the past 15 000–16 000 years.

2. Dogs are atypical apex predators

In the Americas, Eurasia and Africa, where canids evolved, larger ursids, felids and canids (i.e. typical apex predators) dominate smaller ones in competitive interactions, be they direct or by interference (Crabtree and Sheldon 1999). Apex predators are typically obligate hypercarnivores (i.e. meat constitutes >70% of their diet; Van Valkenburgh 1988), which means they are forced to consume large prey in order to meet their high energy demands (Carbone *et al.* 2007). Hence, lions preferentially select species such as zebra (*Equus burchellii*), buffalo (*Syncerus caffer*), gemsbok (*Oryx gazelle*), and blue wildebeest (*Connochaetus taurinus*) (Lehmann *et al.* 2008; Hayward 2009), while polar bears (*Ursus maritimus*) prefer seals or sea lions (Otariidae) (Derocher *et al.* 2004). Carbone *et al.* (2007) report that as carnivore body size increases some apex predator species are unable to obtain sufficient prey individually, and are instead forced to hunt cooperatively. Wolves are a good example of this. Although individually they are capable of capturing small prey species (Fox 1971), wolves must use cooperative hunting tactics to secure enough prey to meet their individual energy requirements (Carbone *et al.* 2007; Vucetich *et al.* 2011).

In contrast, dogs can be mesopredators at the larger end of the bodyweight range or act as small apex predators. Despite assertions to the contrary (Purcell 2010), dogs are not typical hypercarnivorous apex predators, comparable in function to grey wolves, polar bears, or lions. They are flexible in their hunting and foraging tactics, being hypercarnivorous, mesocarnivorous (meat 50–70% of diet: Van Valkenburgh 1988), hypocarnivorous (meat <30% of diet: Van Valkenburgh 1988) and saprophagous (scavenging on dead material) according to opportunity or need (Fiennes and Fiennes 1968; Thomson 1992b; Manor and Saltz 2004; Purcell 2010). They can hunt individually or in groups of two or more (Thomson 1992b; Corbett 2001; Fleming *et al.* 2001) – behaviours retained from wolves – and their diets are general and opportunistic (Corbett 2001; Fleming *et al.* 2001; Vernes *et al.* 2001; appendix 1 of Mitchell and Banks 2005). Dogs are capable of meeting their individual energy requirements from either small or large prey species (Corbett 2001; Carbone *et al.* 2007). When dingoes were introduced and spread over Australia, these characteristics likely gave them a competitive advantage over larger thylacines (*Thylacinus cynocephalus*) (Wroe *et al.* 2007). Thylacines likely hunted singly and took small prey (1–5 kgs: Wroe *et al.* 2007), which overlaps with the size of prey taken by single dogs (Corbett 2001; Vernes *et al.* 2001; appendix 1 of Mitchell and Banks 2005). Although smaller than thylacines (mean adult weight 24 kg: Wroe *et al.* 2007), dingoes (mean adult bodyweight = 12.4–17.4 kg, but smaller in Asia: Corbett 2001) supplanted them as the largest predator. Where humans were few, dingoes likely ascended to apex predator status as superior

competitors and were beneficiaries of the anthropogenic changes in Australia's ecological history.

Former mesopredators-turned-apex-predators rarely maintain ecological processes similar to historical apex predators because of their 'fundamentally different relationships with people and ecosystems' (Prugh *et al.* 2009, p. 784). Although dogs currently occupy non-human apex predator status in much of Australia, their mesopredator history means that we cannot automatically expect them to focus their direct impacts on large herbivores like typical apex predators. This is supported by our collective knowledge of dog diets (Corbett 2001; Vernes *et al.* 2001; Mitchell and Banks 2005) and social structure (Thomson *et al.* 1992; Corbett 2001). Hence, their potential impacts on small (and often threatened) prey species must be well established before dingoes are managed positively.

To consider any wildlife species as the apex in systems containing humans is exclusivist, which is not problematic except when humans and 'the environment' are considered as separated in such a world view. Anthropocentric standpoints can limit our understanding of systems by excluding humans and thereby imposing restrictions on the conceptual space in which we all think. Before the arrival of humans in Australia, there was a range of marsupial predators including the largest and most likely apex predator, *Thylacaleo carnifex* (110 kg; Johnson 2006). Being omnivorous, humans might have been involved in the extinction of megafauna in the late Pleistocene, possibly through hunting of megaherbivores and competition with megapredators (see arguments in Johnson 2006). Consequently, humans were the apex predator when dingoes arrived and still are the apex predator in many Australian ecosystems, particularly agro-ecosystems where dogs are controlled (control \cong predation: Caughley and Sinclair 1994). The historic and continuing effects of humans on vegetation, water availability, and other landscape features are likely to affect prey assemblages and relative abundances into the future. As demonstrated by our vertebrate pest management failures, humans can be unreliable apex predators, but are nonetheless able to regulate ungulate numbers in agro-ecosystems and facilitate the extinction of competitors, such as the thylacine in Tasmania. Johnson (2006) and others have noted the importance of Australia's first peoples in changing landscapes. Likewise in North America, there is an argument that first peoples were the 'ultimate keystone predator' and ecosystem engineers (Kay 1998). Thus, dingoes as dogs are and always were mesopredators (an appellation that fits well with generally accepted definitions of such: Roemer *et al.* 2009), and we cannot ignore the role of modern humans as the apex predator in many Australian ecosystems. Viewing the functional roles of dogs and humans in this way may influence our expected outcomes of positive dingo management.

3. Europeans altered Australian landscapes

We cannot know whether Australian systems were stabilised at a dynamic equilibrium or were still in a state of flux when Europeans arrived. Likewise, we should not expect that all changes to ecosystem dynamics caused by the introduction of the dingo were completed by the time Europeans arrived, as this ignores the long-term stochasticity of Australian climate cycles and the resulting resource pulsing that occurs (e.g. Letnic *et al.*

2005; Letnic and Dickman 2006; Williams *et al.* 2009). Part of the reasoning for considering dingoes as biodiversity conservation tools lies in the expectation that they will fulfil their pre-European ecological roles (whatever they were) and restore ecosystem processes towards a pre-European state (Johnson 2006). However, it is precisely the post-European state that may prevent modern dingoes from fulfilling their pre-European roles. Dingoes might have become a stable part of predator-prey interactions in Australian systems before European arrival, but natural landscapes have changed dramatically since then through a variety of mechanisms (DEWHA 2001; Hamblin 2001). This may influence the current and future ecological roles of dingoes in unexpected ways.

Most of the landscape change stems from the expansion of pastoralism across the continent (Letnic 2000; McKenzie *et al.* 2007; Davies *et al.* 2010). Across much of Australia, destructive overgrazing by sheep occurred for several decades in the 19th and 20th centuries (Barnard 1962; Allen 2011). During the mid to late 20th century, the introduction of bores (Davies *et al.* 2010), tropical grasses (Bortolussi *et al.* 2005b), *Bos indicus* cattle (Bortolussi *et al.* 2005a), and the eradication of contagious bovine pleuropneumonia in 1967 (Newton 1992) changed northern Australian landscapes substantially. Permanent, artificial waters have been established in areas where continuous livestock grazing was previously impossible (Barnard 1962; James *et al.* 1999) and there are now few places in Australia that are further than 10 km from a water point (James *et al.* 1999; Fensham and Fairfax 2008).

The effects of livestock grazing and the creation of artificial water points not only change habitats but can also facilitate predation on threatened species by increasing the population size and ranges of water-limited predators such as dingoes (James *et al.* 1999; Box *et al.* 2008; Davies *et al.* 2010). Although their distribution has changed, dingo numbers in Australia have almost certainly increased since the expansion of pastoralism, permanent water points (Corbett 2001) and outback mining (T. Newsome, G. Ballard, P. Fleming, unpubl. data). Corbett (2001) concludes that following the introduction of rabbits, permanent water and livestock in central Australia, subsequent high dingo densities were ultimately responsible for the demise of nine native mammals following the extended droughts in 1925–30 and 1958–65. Vegetation changes associated with pastoralism (Letnic 2000) cannot be ignored as a factor that will influence the role that dingoes might play after their restoration (Allen 2011). In summary, Australia has shifted from a continent of 'natural' ecosystems (pre-human) through human-influenced ecosystems (by indigenous Australians) to agro-ecosystems since European arrival, with significant consequences for landscape-, wildlife-, and dog-related processes. These new and still-changing Australian landscapes mean that we cannot return to pre-European ecosystem conditions and must expect that positive management of dingoes will have unpredictable and possibly negative impacts on threatened fauna and ecosystems (Coutts-Smith *et al.* 2007; Allen 2011).

4. Spatial scale, predation risk and ecological niches are important

Macdonald (2009) in his seven awkward questions preceding predator reintroductions asks, 'does the generalization adequately

describe the particular?', suggesting that spatial scale must be included in discussions of the mechanisms driving invasive predators and trophic cascades. This is because there is often a discrepancy between large-scale observations and small-scale experimental results (e.g. Altieri *et al.* 2010). Across large spatial scales, patterns of dog distribution have positively correlated with the presence of some small and threatened mammal species and negatively with foxes and cats (e.g. Smith and Quin 1996; Johnson *et al.* 2007; Letnic *et al.* 2009b; but see Allen 2011 for a critique of the methods used in the latter two studies). However, assessments of broad-scale distribution patterns often cannot describe the fine-scale relationships between predator and prey (MacKenzie *et al.* 2006; Allen 2011; McLachlan and Ladle 2011). The mechanisms that drive predation inherently occur at local scales, where predation events occur day by day, one individual at a time. Investigating the risks and impacts of dingoes at finer scales therefore requires a more detailed understanding of their behavioural ecology beyond a broad evaluation of the distribution and abundance of predators (e.g. Johnson *et al.* 2007). For example, Letnic *et al.* (2009a) and Letnic and Dworjanyn (2011) report that the presence of dogs protects dusky hopping-mice (*Notomys fuscus*) from excessive predation by foxes across large scales. However, are there not direct risks of dogs to hopping-mice at the local/fine scale? Where dogs are more abundant than foxes, e.g. at the sites studied by Letnic *et al.* (2009a), could not the risk of dogs be greater than the direct risk of foxes, and their presence ultimately provide no net benefit to populations of hopping-mice? Dogs eat threatened species too (including hopping-mice: Corbett and Newsome 1987; Pavey *et al.* 2008; Allen *et al.* 2011b), yet the direct risks of dog predation to threatened species has not been widely assessed as it has for fox and feral cat predation (e.g. DEWHA 2008a, 2008b; Dickman *et al.* 2009).

Where broadly applied predation risk assessments have been conducted, predation risk has been determined by assessing the vulnerability characteristics of the potential prey (Coultts-Smith *et al.* 2007; Dickman *et al.* 2009; Mahon 2009) and most studies do not approach the assessment of risk by exploring the ability of the predator. The latter approach may be more relevant to dingo reintroductions where threatened prey populations may not have been exposed to dingoes for many decades, and not under the altered vegetation, fire and cover conditions of post-pastoralism ecosystems (also see Letnic 2000). This was highlighted by Berger *et al.* (2001) and Gittleman and Gompper (2001), who described the immediate declines of naïve prey species following predator reintroductions. Swift extinctions of susceptible prey were avoided only because adults survived the initial wave of predation, adapting quickly to the new predators and passing this knowledge on to successive generations. However, rapid extinction risk is greatly increased where both adults and juveniles are preyed upon (Berger *et al.* 2001; Gittleman and Gompper 2001), and adults of no native or threatened Australian species are outside the weight range of dog predation (Corbett 2001; Vernes *et al.* 2001; Mitchell and Banks 2005).

Where predation risk has been specifically assessed for individual species, such as northern hairy-nosed wombats (*Lasiorchinus krefftii*) or bridled nail-tail wallabies (*Onychogalea fraenata*), dingo predation has been identified as one of the most likely mechanisms for population extinction, requiring intensive

predator-control activities to protect them (Banks *et al.* 2003; Lundie-Jenkins and Lowry 2005; Augusteyn 2010). Dog predation is recognised as a known or potential threat in 14 national threatened species recovery plans (www.environment.gov.au), and dog predation is a listed Key Threatening Process for threatened species, populations, and communities in New South Wales (Major 2009). Because dogs are well known to prefer small-medium prey species (Corbett 2001), the direct risks of dogs should not be overlooked or assumed to be less than their perceived indirect effects on mesopredators.

But what are the functional ecological roles of dogs? Dogs are a classic, invasive mesopredator species (Williamson 1996; Boitani 2001) and, indeed, were successfully introduced into Australia despite a probable low propagule (Savolainen *et al.* 2004; and see Bomford *et al.* 2009 for characteristics of successful invasives). They are medium-sized, generalist and opportunistic foragers, and are highly adaptable to a wide range of habitats, which undoubtedly contributed to their ubiquitous distribution throughout continental Australia. In addition, dingoes were often commensal with pre-European humans (Smith and Litchfield 2009), and become so again where access to anthropogenic food is actively encouraged (e.g. recent events on Fraser Island: Shorten 2010) or not prevented, for example, at refuse-disposal sites. The possible consequences of this invasive capacity of dogs have not been adequately addressed, and one may ask if the biodiversity conservation outcomes are any greater if a species is extinguished by a dog instead of a fox or feral cat.

Where there are multiple sympatric predators, as there are in many Australian ecosystems, facilitation may occur. Facilitation occurs when the surplus of kills made by the larger predator provides a resource subsidy for subordinates, thereby availing them of energy sources that would otherwise be too large for them to acquire through hunting (e.g. lion kills used by black-backed jackals (*C. mesomelas*): Kruuk 1972), or when other resources (e.g. badger (*Meles meles*) setts, used by red fox and raccoon dog (*Nyctereutes procyonoides*) in Poland: Kowalczyk *et al.* 2008) provided by the larger species benefits the smaller species. Facilitation allows more species or numbers of subordinate predators to co-occur than would have been possible without it. Hence, dingoes could benefit foxes through kleptoparasitism.

Australia has many ecosystems, each with different processes and drivers, so it is reasonable to expect a generalist predator like the dog to have different roles and fill different ecological niches in different places (Visser *et al.* 2009). The roles of introduced predators in different Australian ecosystems are likely to differ according to structural complexity and ecological carrying capacity, and we should not assume that research in xeric environments is applicable in mesic environments. The consequences of positive dog management are likely divergent: beneficial for native fauna in some ecosystems and detrimental in others, and may change in the future.

5. Does dog control release foxes and cats?

The belief that contemporary dog-control programs (e.g. poisoning, trapping, or shooting) will cause mesopredator release (e.g. Wallach *et al.* 2009; Letnic *et al.* 2011) is misguided and contrary to published evidence (see references below). Although Johnson and Van Der Wal (2009), Letnic *et al.* (2011), and others

have reported negative correlations between dog and fox abundances (but see the methodological criticisms by Allen (2011), Allen *et al.* (2011a) and subsequent discussions in Letnic *et al.* (2011) and Allen *et al.* (2011b)), manipulative experiments have failed to find anything but sympatry or parapatry between them. In fact, whenever manipulative experiments *have* been conducted, no evidence for mesopredator release has been demonstrated following contemporary dog-control programs in arid, semiarid, temperate or tropical areas (e.g. Fleming 1996; Eldridge *et al.* 2002; Allen 2005; Claridge *et al.* 2010).

Only manipulative experiments (Platt 1964; Glen *et al.* 2007b) can provide conclusive evidence for the negative impacts of dog control on non-target species. Such experiments have not provided unequivocal evidence of control-induced mesopredator release. For example, in a long-term fox-control experiment in south-east New South Wales, Claridge *et al.* (2010) found no evidence of mesopredator release: fox indices declined at the treatment sites with no change in the nil-treatment indices; cat indices declined independent of treatment; and dog indices increased at one treatment site, exhibited no change at another, and declined at the nil-treatment site. If MRH were evident, cats should have declined where dog abundance went up and cat numbers should have increased where dogs were unchanged but neither occurred. Allen (2005) also found fox and cat populations to fluctuate independently of dog control, as did Eldridge *et al.* (2002). In contrast, Risbey *et al.* (2000) found a 3-fold increase in cat abundance index after fox control in an unreplicated experimental manipulation of mesopredator abundance in Western Australia. Dogs were not present there and cats were shown to reduce prey abundance in the absence of foxes, which supports the concept that MRH operates when there are three levels (i.e. apex predator, mesopredator and prey: Oksanen *et al.* 1981) but adds no information to the debate about dog control releasing fox and cat populations.

The implicit assumptions in the suggestion that dog control facilitates the release of foxes and cats is that dog control either selectively removes dogs while leaving foxes and cats, or that foxes and cats will recover more quickly than dogs after control (Allen, *in press*). Although control of cat populations is problematic and variably efficacious (e.g. Short *et al.* 1997; Wickstrom *et al.* 1999), dogs and foxes are approximately equally controlled by effective dog-control programs and, moreover, dog control usually affects fox populations first (Fleming 1996; Fleming *et al.* 1996; Burrows *et al.* 2003). This is because the most effective control programs for dogs use extensive (e.g. Fleming *et al.* 1996; Thomson 1984) or repeated baiting (e.g. Fleming 1997) with meat baits containing more than 4 mg of compound 1080 (Fleming *et al.* 2006; Glen *et al.* 2007b) or, in some states, strychnine (Allen and Fleming 2004). As 3 mg is the nominal dose most commonly used for fox control (Saunders *et al.* 1995) and both species will readily eat meat baits (Allen *et al.* 1989; Glen *et al.* 2007b), all foxes that consume baits placed for dogs will likely die (McIlroy 1981; McIlroy and King 1990). Indeed, where they are sympatric, fox population indices may be reduced more than dog indices in canid-control programs (e.g. Fleming 1996). Foxes and cats are also common non-target species captured during dog-trapping programs in eastern Australia (G. Ballard and B. Allen, unpubl. data).

For foxes to be released by dog control through more rapid recovery, their rate of increase must exceed that of dogs. Both dingoes and foxes are monoestrous (fox: Lloyd and Englund 1973; dog: Jones and Stevens 1988; Corbett 2001) and whelp a similar number of young in late winter or spring (dog mean litter size 4.0–5.5; Jones and Stevens 1988; Thomson 1992a; Thomson *et al.* 1992; Corbett 2001; range 1–10 pups per litter: Corbett 2001; fox mean Australian litter size 3.04–5.4; McIlroy *et al.* 2001; Saunders *et al.* 2002; range 1–11 cubs per litter: Saunders *et al.* 2002). Although domestic dogs of similar size to dingoes can cycle twice during the breeding season, there is no evidence that wild dogs can raise two litters to independence in a year (Jones and Stevens 1988; Daniels and Corbett 2003). The calculated finite rates of increase for foxes range from 0.95 to 1.07 (McLeod and Saunders 2001) and mortality rates of female foxes are high in their first year ($q_x = 0.7$: Saunders *et al.* 2002). Dogs likely have a relatively high finite rate of increase ($\lambda = 0.99$ –1.3, estimated from Fleming *et al.* 1996) and, as adults, have no predators other than humans. Therefore, with similar potential rates of increase to dogs, and similar seasonality in breeding, fox populations are unlikely to rebound more quickly than dog populations following dog control and Fleming *et al.* (1996) found no evidence of disproportionate population recovery of the species between annual control programs.

Furthermore, there is an implicit assumption that dog-control programs are always effective at eliminating dogs, or at least have broad-scale and long-term negative impacts on dog populations. Although Fleming *et al.* (1996) and Thomson (1986) found substantial reductions in dog indices, Eldridge *et al.* (2000), Twigg *et al.* (2000), Allen (2005), Allen (*in press*) and others have reported variable effectiveness of baiting programs for dogs, where some control programs fail to reduce dog activity indices and some actually increase indices (Allen 2006b). Thomson (1986), Fleming *et al.* (1996), and Allen (2006b) each reported that aerial baiting programs for dogs provide only a temporary sink, which is refilled by dogs (and foxes) during the following year or two. Where dog populations are unresponsive to control there is no opportunity for mesopredator release to occur through immigration (Allen *in press*).

Although dogs are known to kill foxes (e.g. Fleming 1996), regulation of subordinate predators by dogs has not been demonstrated in Australia (Glen *et al.* 2007a; Allen *et al.* 2011a). Most importantly, concerns over the potential cascading effects of dog control are founded in the expectation that dog control somehow produces negative consequences for threatened species. Given that ‘no studies published to date have found significant reductions in populations of non-target animals following 1080 baiting’ (Glen *et al.* 2007b, p. 195), calls to suspend dog control on biodiversity conservation grounds clearly remain unjustified. Dog control may still be useful in mitigating livestock losses or protecting threatened species without fear of releasing foxes or cats.

6. Focussing on predators as system drivers is simplistic

The mechanism required to generate faunal biodiversity benefits from positive dingo management, as argued by Letnic *et al.* (2009a, 2009b, 2011) and Johnson *et al.* (2007), is essentially a top-down process. For mesopredator release to occur, the higher-

order predator must be limiting the abundance of the lower-order predator(s), which in turn is limiting prey and so on. However, carnivory and social predominance among predators do not necessarily imply limitation or regulation (Caughley *et al.* 1980; Sinclair and Pech 1996), and trophic interaction intensity varies with complexity (Atwood *et al.* 2009). Moreover, 'populations are not affected by weather or predation or food or disease, but by an interaction of all those factors. We should not delude ourselves into looking for *the* mechanism 'regulating' mammalian populations; instead, we should strive to understand how various mechanisms interact to affect those populations, and under what circumstances specific mechanisms will be particularly important' (Holmes 1995, p. 11).

Analysing data collected over 90 years, Elmhagen and Rushton (2007) showed that, even though both top-down and bottom-up factors influenced mesopredator population growth, the bottom-up effect of landscape productivity was 9.7 times greater than the top-down removal of apex predators. Sergio *et al.* (2008) likewise reported that apex predators can be associated with high biodiversity in a bottom-up manner, greatly cautioning the use of top predators as biodiversity conservation tools. Where prey populations are obviously limited by bottom-up factors (such as refuge dependence, e.g. Tuft *et al.* (2011), and forage availability fluctuations, e.g. Letnic and Dickman (2006)), attempting to unravel top-down processes without accounting for bottom-up factors is counterproductive, particularly in multipredator/multiprey systems (Gese and Knowlton 2001).

The stochastic nature of most Australian ecosystems would suggest to us that bottom-up factors play the most important role in ecosystem dynamics – much more than predator effects in any combination. This is most clearly evident in drier regions, where reproduction in a high proportion of faunal species is triggered by rainfall and subsequent vegetation growth (Cogger 2000; Van Dyck and Strahan 2008; Robin *et al.* 2009). Given the irruptive nature of many threatened and non-threatened species, it is difficult to comprehend how dog predation provides a catalyst for significant faunal reproduction events. In contrast, dog predation is more likely to inhibit population growth rates by limiting the abundance of prey faunas already reduced by a lack of resources (Corbett and Newsome 1987; Letnic and Dickman 2006; Pavey *et al.* 2008). This situation is made worse by alternative food sources capable of sustaining predators through difficult times (Sinclair *et al.* 1998; Courchamp *et al.* 2000).

Because the processes that govern community dynamics in Australian ecosystems are likely a combination of bottom-up and top-down factors, ignoring either component will prevent proper determination of threatening processes. This is the case even in the well studied but relatively simple boreal systems in Canada (Krebs *et al.* 2001), where top-down effects as modelled were strong but short-term, while bottom-up effects were lesser but more persistent (Krebs *et al.* 2001). This conclusion is intuitive, in that long-term persistence of species is likely driven by resource availability but population size may be modulated by predation rates. Viewing the top-down role of dogs against known bottom-up processes may highlight alternative management actions that could achieve greater returns for biodiversity conservation. Alternatively, promoting a generalist mesopredator, such as the dog, without removing other known causes of fauna decline is

unlikely to result in threatened species recovery. It may even make it worse (Allen 2011).

7. Dogs and socioecological niches

Dogs, like all wildlife, exist within human socioecological niches that may not be amenable to positive dingo management. Accounting for human dimensions is fundamental when managing conflicts with wildlife (Treves and Karanth 2003; White and Ward 2010) and large predators in particular (Bath 1988; Majic and Bath 2010). In moving from theoretical ecology to real-world management (i.e. from proposing positive management of dingoes to actually achieving it), the biggest stumbling blocks are people and their associated sociopolitical views.

A cognitive hierarchy of human values, beliefs, attitudes, behavioural intentions and enacted behaviours (Fulton *et al.* 1996) impact upon wildlife, both directly and indirectly. The viewpoints of stakeholders are a function of their values, attitudes, experiences and 'knowledge' (Decker and Bath 2010). Importantly, all knowledge is not the same and scientists hold a more restricted definition of what constitutes knowledge than other people (Brunner *et al.* 2005; Parker 2006). Influential community members may distrust 'science' and 'government' (e.g. Shorten 2010), causing an imbalance of power between laypeople, scientists, and land or wildlife managers (Decker and Bath 2010). All knowledge must be included in discussions to enable parity among stakeholders (Decker and Bath 2010).

Essentially, Australians hold diverse value orientations towards dogs, often expressed as various and sometimes conflicting attitudes and behaviours (Coman and Jones 2007). Although several authors have noted that dingoes hold particular status with humans (e.g. Parker 2006; Hytten 2009; Smith and Litchfield 2009), this status is not uniform, let alone uniformly positive. For example, Johnston and Marks (1997) found that 79% of Victorians surveyed regarded wild dogs as pest animals, with 63% preferring eradication as a management option. Although mostly negative, respondents' opinions were not homogeneous and the responses might well have been different if the questions were asked about 'dingoes' rather than 'wild dogs'.

Moreover, arguments surrounding what constitutes a 'dingo' are largely subjective, and the Australian people have not decided what it is they want to positively manage (Coman and Jones 2007). Is it their ecological role, their colour, or something else? A particular morphologically or genetically determined suite of genotypic and phenotypic characteristics may satisfy some scientists, wildlife managers or tourist operators, while other people frequently identify free-ranging 'yellow' dogs as dingoes (e.g. Shorten 2010). This assumed public preference has real-world negative consequences for atypical dingoes, particularly those with non-yellow pelage living in high-visitation conservation areas (Corbett 2001; Fleming *et al.* 2001; Purcell 2010). Although Purcell (2010) argues that all wild-living dogs, regardless of pelt colour or genetic status, should be labelled dingoes and their functional role should be preserved, reserve managers are often under pressure to remove visually atypical dogs, separate from any genetic or functional basis. Reciprocally, yellow-coated hybrids may benefit when dog controllers, after

capturing them, opt to release (rather than euthanase) them simply because they conform to public perceptions (G. Ballard and P. Fleming, unpubl. data).

Dogs in Australia undoubtedly hold a very complex status (Hyttén 2009; Smith and Litchfield 2009), contributing to 'wildly fluctuating contemporary versions of the dingo' (Parker 2006), and making socially acceptable management particularly challenging. Native species are often considered 'good' whilst invasive species are 'bad' (Brown and Sax 2004). Although feral by definition (see above), dingoes are considered to be both native and/or apex predators by some, and are therefore 'good'. The corollary of this is that dingoes, being good, are wanted, and their reintroductions needed to achieve biodiversity conservation. Domestic dogs are typically 'good', yet once they become free-ranging, stray, or wild these same dogs are readily perceived as 'bad' (Trigger *et al.* 2008).

Adding significantly to this confusing social appreciation of dogs is their place in legislation, regulations, and policy, and these vary between States and Territories and are subject to periodic change (Fleming *et al.* 2001). In New South Wales, for example, dogs are the only eutherian carnivore explicitly banned from wildlife refuges and other conservation areas (*NSW National Parks and Wildlife Act 1974*, Clause 70, Section 2c), implicitly acknowledging likely negative impacts of dogs on native fauna. Contrary to this, dingoes have legislated protection in many national parks and reserves (Davis and Leys 2001). Any plan to reintroduce or conserve dingoes will require appropriate legislation and regulation changes in most States and Territories, and a suite of actions and technologies that enable it.

As reflected in historical legislation changes, a community or society may shift in attitudes towards predators over time. Many wolf reintroductions have been technically successful, but have caused social conflict among people who have to live and work with them (Buller 2008; Chadwick 2010). Similarly, the reintroduction of snow leopard (*Uncia uncia*) into Himalayan National Parks has led to declines in tahr (*Hemitragus jemlahicus*) populations and subsequent perceptions of increased predation of livestock and retaliatory killing of leopards by herders (Lovari *et al.* 2009). Those who accept the notion of positive dingo management today might not in the future, as has been shown by the changes in attitudes of Australians towards dingoes over the past 200 years or so (Breckwoldt 1988; Parker 2006). Although anecdotal evidence and popular media suggest that the average Australian is relatively positive towards dingoes, this could shift as people interact more closely with the animals, and negative experiences associated with dogs (e.g. predation of pets or livestock, predation of local wildlife, threat of dog-borne disease, and direct threats to human safety) literally come closer to home (Allen 2006a).

With so much subjectivity and social heterogeneity inherent in dingo management, how can managers make appropriate decisions about dog management? The deeper drivers of human behaviour (i.e. values) are hard to change, but attitudes, norms, behavioural intentions and behaviours are more malleable. Vitaly, stakeholders must be given the opportunity to develop management-related opinions in an informed and balanced environment that is open to diverse perspectives. All too frequently, contemporary dog-management debates do not fit this model, with some stakeholder groups deriding other groups

that do not share their views. Such behaviour is not conducive to progress.

A framework for positive management

We suggest that proponents of positive dingo management follow the principles already used to achieve negative wild dog management (Fleming *et al.* 2006). These principles encompass an inclusive, community comanagement approach (*sensu* Decker and Purdy 1988), whereby managers engage with the diverse range of stakeholders to create an environment where all involved parties consider both scientific and other evidence, and the sociopolitical issues, before determining and implementing appropriate action. These principles can be applied through an adaptive management framework (Holling 1978). Such adaptive management, with involvement and equity among stakeholders (Chase *et al.* 2000), is required for managing dogs at local and regional scales. This framework allows greater ownership by stakeholders, reduces disenfranchisement of key people affected by the management, and allows stakeholders to adapt procedures as knowledge improves and situations change.

An adaptive approach broadly involves: defining the issue, developing a plan of action with achievable and measurable goals, implementing the plan, monitoring progress, evaluation of the plan, and making adjustments and improvements before reimplementation (Fleming *et al.* 2006). Defining the issue is the most difficult, time-consuming and critical for success. It must take into account all the socioecological components and current knowledge before further planning or implementation can proceed successfully. This is particularly so for the proposed positive management of dogs which, at present, has only just begun the issue-definition phase and is currently lacking experimental support (Glen *et al.* 2007a). This adaptive approach should encourage the involvement of all major stakeholders, and Varley and Boyce (2006) recommend this approach for all reintroductions of predators.

Conclusions

Before positive management of dogs is universally adopted as a 'good thing' for Australian biodiversity, there are seven prior considerations we think are essential. There are others of importance, including those raised by Macdonald (2009, in fig. 19.1), such as the expense of reintroductions, habitat suitability, genetic diversity in the founder stock and the removal of other agents of decline. The differences between Macdonald's (2009) list of concerns and ours arise because most predators nominated for reintroductions elsewhere are close to extinction in the wild, whereas dogs are abundant in many Australian ecosystems. Endangered predators often suffer from decreasing genetic diversity and corresponding loss of fitness, whereas the genetic diversity of free-ranging dogs in Australia is increasing through ingression of domestic genes (Purcell 2010), which might facilitate evolutionary diversification (see Grant *et al.* 2005). We and Macdonald (2009) commonly identify community and political support, adequate monitoring, appropriate scale, prior field experimentation and appropriate reasons for reintroduction as essential precursors to positive management. Critically, it must be demonstrated that Australian ecosystems require the positive management of dogs: 'is reintroduction the right answer'

(Macdonald 2009)? The distribution of dogs throughout Australia may have changed but they are likely in greater abundance now, negating the need for positive management.

Experiments are required to determine the strength of top-down and bottom-up components of community dynamics before deciding on threatening processes and investing in management actions that may have limited bearing on biodiversity conservation or recovery. The key scientific questions to answer are: 'are the indirect effects of dogs on mesopredators greater than their direct effects on prey' and 'do dogs provide a net benefit'? If so, 'is this always the case, will it always be the case, and can these effects be harnessed to restore biodiversity'? Alternatively, 'what can we do to enhance the population viability of threatened species during times of decline without adding another predator'?

Most importantly, the human dimensions of dog management must be acknowledged and accounted for before moving the positive management of dingoes from theory to application. We can answer the scientific questions with experiments but, in essence, the debate about managing dingoes devolves to the management of conflicting human values. Each individual human has values and attitudes that affect their worldview and what they consider is right for 'the environment'. The primacy of native animals over invasive animals is a human construct (Macdonald *et al.* 2007; Schlaepfer *et al.* 2011), as is the primacy of human food production over biodiversity conservation or *vice versa*; an ecosystem does not know or care about its constituent species. These views need not be mutually exclusive and the solutions to this debate are not purely scientific ones. A consultative, adaptive management framework can be employed to decide what management actions, if any, are implemented, and where and when they are enacted. Addressing these seven considerations will be important steps for managers to take before considering dingoes as a suitable biodiversity conservation tool.

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