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Wild dogma: An examination of recent "evidence" for dingo regulation of invasive mesopredator release in Australia

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Abstract There is growing interest in the role that apex predators play in shaping terrestrial ecosystems and maintaining trophic cascades. In line with the mesopredator release hypothesis, Australian dingoes (*Canis lupus dingo* and hybrids) are assumed by many to regulate the abundance of invasive mesopredators, such as red foxes *Vulpes vulpes* and feral cats *Felis catus*, thereby providing indirect benefits to various threatened vertebrates. Several recent papers have claimed to provide evidence for the biodiversity benefits of dingoes in this way. Nevertheless, in this paper we highlight several critical weaknesses in the methodological approaches used in many of these reports, including lack of consideration for seasonal and habitat differences in activity, the complication of simple track-based indices by incorporating difficult-to-meet assumptions, and a reduction in sensitivity for assessing populations by using binary measures rather than potentially continuous measures. Of the 20 studies reviewed, 15 of them (75%) contained serious methodological flaws, which may partly explain the inconclusive nature of the literature investigating interactions between invasive Australian predators. We therefore assert that most of the "growing body of evidence" for mesopredator release is merely an inconclusive growing body of literature only. We encourage those interested in studying the ecological roles of dingoes relative to invasive mesopredators and native prey species to account for the factors we identify, and caution the value of studies that have not done so [*Current Zoology* 57 (5): 568–583, 2011].

Keywords Activity index, Apex predator, *Canis lupus dingo*, Experimental design, Mesopredator release, Sampling

1 Introduction

Invasive terrestrial vertebrates can have dramatic effects on ecosystems. They contribute to species loss through a variety of mechanisms, including predation, competition, habitat destruction, and the introduction of parasites and pathogens (Rolls, 1969; Long, 2003; Salo et al., 2007; Henderson, 2009). When invasive species are predators, they can alter food webs through increased predation on species not adapted to the new predator (Dickman, 1996). When they are prey, they can have similar effects by bolstering the food resources available to predators (Smith and Quin, 1996; Coman, 1999). These outcomes can sometimes be mediated by larger, native predators and man. For example, native apex predators can limit the impact of invasive mesopredators (Crooks and Soulé, 1999; Hayward and Somers, 2009), while humans can regulate the system negatively or positively, through landscape alteration or the promotion of top-order predators (Sergio et al., 2008; Prugh et al., 2009; Roemer et al., 2009).

Interactions between predators can be an important factor in determining the direction of ecological systems (Gese and Knowlton, 2001; Glen and Dickman, 2005). The mesopredator release hypothesis (Crooks and Soulé, 1999) predicts that when a higher order predator is removed, lower order predators increase their abundance, which often results in amplified pressure on smaller prey species. These interactions can cause trophic cascades (Ripple and Beschta, 2004; Ritchie and Johnson, 2009), where the effects of increased mesopredator and herbivore abundance can flow through the food chain ultimately causing undesirable outcomes for faunal and floral biodiversity. Conversely, an increase of apex predators can reduce herbivore and mesopredator abundance and indirectly promote vegetation growth (Ray et al., 2005; Hayward and Somers, 2009).

In Australia, these processes are thought to occur between dingoes, red foxes and feral cats, with effects being felt by several prey species across entire ecosystems (Glen et al., 2007). Dingoes were brought to the island continent by indigenous Australians about 5,000

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years ago (Savolainen et al., 2004) as smaller mesopredators to the then extant 'wolf sized' thylacine *Thylacinus cynocephalus*. Thylacines were quickly replaced by dingoes as top-order predators, becoming extinct on the mainland within a few hundred years, and surviving only on the dingo-free isle of Tasmania until Europeans completed their extinction process over 4,000 years later (Corbett, 2001; Johnson, 2006). With dingoes well established as the top-order predator, foxes and cats were later introduced with the arrival of Europeans, and remain mesopredators throughout their extended range (Johnson, 2006).

The value of better understanding the functional relationships between mammalian predators cannot be understated (Glen and Dickman, 2005). Australia has the worst record for mammalian extinctions in the world, and predation by these three predators are believed to be major factors in the demise of many species (Dickman, 1996; Corbett, 2001; Johnson, 2006). On the other hand, over recent years there has been an increasing amount of literature discussing the potential role of dingoes as an indirect "saviour" (Catling and Burt, 1995b, pg. 542) of biodiversity conservation through their perceived top-down regulation of foxes and cats (e.g. Johnson et al., 2007; Letnic et al., 2009a; Wallach et al., 2009a). Despite reports claiming to provide evidence for the net protection of threatened species in this way, there is still much uncertainty about the ecosystem function of dingoes or the mechanisms for how this protection is thought to occur (Robley et al., 2004; Visser et al., 2009).

In contrast to mesopredator release theory, Hayward et al. (2010) recently reported that foxes and cats were positively associated with dingo presence, suggesting that resource availability was the major factor driving mesopredator populations. Experimental studies in a variety of ecosystems have likewise shown mesopredator populations to fluctuate independently of poison baiting campaigns directed at dingoes (Eldridge et al., 2002; Allen, 2005). For example, Allen (2005) reported that cat populations remained relatively constant throughout periods of above and below-average rainfall in both baited and unbaited treatment areas, concurring with others (such as Hayward et al., 2010) that bottom-up factors were driving cat population dynamics. Moreover, additional studies (e.g. Fenner et al., 2009) have failed to detect the numerical or behavioural responses expected of prey species in response to top-predator control.

In support of dingo regulation of mesopredators, Letnic et al. (2009a) and Wallach et al. (2009a) purported to show that the presence of dingoes indirectly protects dusky hopping-mouse *Notomys fuscus*, yellow-footed rock-wallaby *Petrogale xanthopus xanthopus*, and malleefowl *Leipoa ocellata* populations from predation by foxes and cats. Smith and Quin (1996) used generic distribution maps to compare range distributions of rodent genera with other species and found that threatened rodents were more abundant in areas with high dingo densities. Johnson et al. (2007) likewise analysed distribution maps and suggested that the persecution of dingoes triggered the continental collapse of marsupial populations by foxes and cats. These and many other additional studies (discussed below) attempt to lend support to the notion that Australian dingoes regulate mesopredators and structure entire ecosystems through maintenance of trophic cascades.

Reviews of the available literature discussing the ecological role of dingoes in Australia have been conducted before (e.g. Robley et al., 2004; Glen and Dickman, 2005; Glen et al., 2007; Visser et al., 2009). Each has described a lack of clear and conclusive evidence for the beneficial role of dingoes in suppressing invasive mesopredators for biodiversity benefits. To investigate more fully the potential reasons for this, we explored the structure and design of field studies that investigated the dingo's ability to suppress mesopredators, maintain trophic cascades, or provide net benefits to threatened prey species. Some of the shortcomings found in desktop studies have been addressed elsewhere (Allen, 2011). This required an examination of recent studies that used passive activity indices (i.e. tracking stations) for monitoring populations of invasive predators in Australia. We focus our discussion of the results as they relate to dingo behaviour and ecology, though the methodological limitations we identify equally apply to other species in Australia and around the world.

2 Study Selection

We searched for all recent studies that used track-based activity indices to make inferences about the effects of dingoes on foxes and cats and/or threatened species. Track-based indices have become a standard field technique in Australia for assessing predator populations. Three international databases (Web of Science, Zoological Record, and CSIRO Online) were accessed in February 2010 and searched using the following terms:

For Web of Science and Zoological Record:

• Dingo OR wild dog AND fox
• Dingo OR wild dog AND cat
• Dingo AND mesopredator

For CSIRO Online:

• Dingo (in 'Abstract' only)

After removing duplicates from 505 search results, 28 original studies were further considered. Of these, studies that used 'active' tracking plots (i.e. baiting efficacy studies that used tracking plots with a lure/attractant, such as Eldridge et al., 2000) or simply compared indexing techniques (such as Allen et al., 1996; Mahon et al., 1998; and Edwards et al., 2000) were excluded. This was done to avoid studies that did not focus on dingo-mesopredator or dingo-prey interactions (in the case of bait efficacy studies) and those that were an experimental exercise in method development (in the case of technique comparisons). Studies comparing tracking plot techniques are relevant to this discussion (and are referenced in the text), but outside its scope.

To the remainder we added Fillios et al. (2010), Wallach and O'Neill (2009), and Wallach et al. (2010) which were recent publications not detected in the searches but are directly related to earlier reports (i.e. they're based on the same research projects) specifically identified in our review. Other known studies not detected in our literature search (e.g. Newsome et al., 2001; Purcell, 2009) remained excluded to maintain objectivity in study selection. However, such studies are valuable and are referred to in our discussion where appropriate. Ultimately, 20 dingo-related studies published between 1995 and August 2010 that used passive sand plots were assessed (Table 1). We do not attempt to critically explore each of these, but rather, we discuss key design issues arising from some of the more recent and noteworthy studies.

Table 1 Some recently published dingo studies and their potential methodological weaknesses as related to dingoes

Author	Study topic	Original dataset	General conclusion for dingoes	Potential methodological weaknesses when using tracking plots
Allen, 2000	The effects of 1080 baiting on dingoes and calf predation	A	1080 baiting sometimes reduces dingo activity, but this doesn't always reduce calf predation	Nil
Burrows et al., 2003	The effects of 1080 baiting on dingoes, foxes, & cats	B	Broadscale 1080 baiting was highly effective at controlling dingoes and foxes	Invalid assumptions when calculating the activity of predators Data confounded by seasonal differences in predator activity Invalid comparisons between species
Catling and Burt, 1995a	The effect of habitat on small mammals in eastern Australian forests	C	Abundances of dingoes and small mammals positively correlated with habitat complexity	Data confounded by seasonal differences in predator activity Invalid comparisons between habitats
Catling et al., 1999	The effects of cane toads on native fauna	D	Dingoes were negatively affected by the arrival of cane toads	Used binary counts over potentially continuous measures
Corbett, 1995	Dingo regulation of feral pigs	E	Dingoes do not regulate pig populations	Used binary counts over potentially continuous measures
Edwards et al., 2002a	Habitat selection by dingoes and cats in central Australia	F	Cats preferred woodland habitats and dingoes used both woodland and open habitats equally	Invalid assumptions when calculating the activity of predators Data confounded by seasonal and habitat differences in predator activity
Edwards et al., 2002b	Impact of rabbit warren ripping on wildlife, including dingoes	G	Dingo activity changed with time but an effect of ripping was not detected	Invalid assumptions when calculating the activity of predators Data confounded by seasonal and habitat differences in predator activity Data confounded by 1080 baiting campaigns
Fillios et al., 2010	The effect of dingoes on kangaroos	H	Live kangaroos and kangaroo carcasses were 14-fold and 32-fold more abundant in the absence of dingoes	Data influenced by seasonal and habitat differences in predator activity
Johnson and VanDerWal, 2009	Dingoes ability to limit fox abundance in eastern Australian forests	C	Dingoes set an upper limit on fox abundance	Source data confounded by seasonal and habitat differences in predator activity Source data used binary observations over potentially continuous observations Invalid comparisons between species
Koertner and Watson, 2005	The impact of 1080 baiting for dingoes on quolls	I	Baiting reduced the activity of dingoes and foxes, but not quolls	Used binary observations over potentially continuous observations

(*to be continued on the next page*)

Table 1 (*Continued*)

Author	Study topic	Original dataset	General conclusion for dingoes	Potential methodological weaknesses when using tracking plots
Letnic et al., 2009a	Dingoes' role in protecting dusky hopping-mice from predation by foxes and cats	H	Areas with dingoes provide dusky hopping-mice with refuge from predation by foxes	Insensitive measures of grazing pressure used Data influenced by seasonal and habitat differences in predator activity
Letnic et al., 2009b	Relationships between dingoes & multiple other wildlife species in arid areas	H	Dingoes regulate trophic cascades in arid Australia to the benefit of small mammals	Data influenced by seasonal and habitat differences in predator activity Used binary observations over potentially continuous observations Inadequate measures of grazing pressure used
Moseby et al., 2006	Population dynamics of hopping-mice	J	The presence of dingoes might assist hopping-mice through control of foxes, cats, and rabbits	Used binary observations over potentially continuous measures
Pavey et al., 2008	Population dynamics of rodents and predators	K	Dingo populations increased during a rodent outbreak	Invalid assumptions when calculating the activity of predators Invalid comparisons between species
Southgate et al., 2007a	Bilby distribution and fire	L	Bilby presence associated most strongly with probability of dingo occurrence	Data influenced by seasonal and habitat differences in predator activity Used binary observations over potentially continuous observations Invalid assumptions when calculating the activity of predators
Southgate et al., 2007b	Modelling predator and herbivore distribution	L	Dingo occurrence was positively associated with 'mean annual rainfall' and 'proximity to drainage'	Data influenced by seasonal and habitat differences in predator activity Used binary observations over potentially continuous observations Invalid assumptions when calculating the activity of predators
Wallach and O'Neill, 2009	Dingo suppression of mesopredators	M	Dingo abundance indicates the presence of threatened species	Data influenced by seasonal and habitat differences in predator activity Invalid assumptions when calculating the relative abundance, "Index of abundance", and territorial activity of predators Data influenced by the presence of pet dogs and people Invalid comparisons between species
Wallach et al., 2009a	Dingoes' role in protecting yellow-footed rock wallabies and malleefowl from predation by foxes and cats	M	The presence of dingoes protects yellow-footed rock wallabies and malleefowl from fox and cat predation	Data influenced by seasonal and habitat differences in predator activity Invalid assumptions when calculating the relative abundance, "Index of abundance", and territorial activity of predators
Wallach et al., 2009b	The impact of dingo control on pack structure and social stability	M	Dingo control negatively influences the pack structure and social stability of packs	Data influenced by seasonal and habitat differences in species activity Invalid assumptions when calculating the relative abundance, "Index of abundance", and territorial activity of predators Data influenced by the presence of pet dogs and people Used binary observations over potentially continuous observations
Wallach et al., 2010	The effect of dingo control on invasive species	M	Dingo removal promotes invasive-driven ecological states	Data influenced by seasonal and habitat differences in species activity Invalid assumptions when calculating the relative abundance, "Index of abundance", and territorial activity of predators Data influenced by the presence of pet dogs and people

3 Summary of Review Findings

Of the 20 studies reviewed, 14 studies (70%) were potentially confounded by seasonal factors, 13 studies (65%) were potentially confounded by habitat factors, 10 studies (50%) violated or made invalid assumptions, 9 studies (45%) used binary counts over continuous measures, and 9 studies (45%) were potentially con-

founded by additional factors (Table 1), indicating that multiple studies contained multiple methodological weaknesses. In total, 15 of the 20 studies (75%) contained serious methodological weaknesses, with only one study avoiding each of these issues. As an aside, two other studies outside the scope of the review (i.e. Newsome et al., 2001; and Purcell, 2009) also avoided these issues.

4 Assessing Dingo Activity or Relative Abundance

Using dingo activity as a measure of relative abundance is a standard and useful tool for dingo research. It is most often determined by recording the number of tracks, intrusions, or foot prints on tracking plots placed along roads (e.g. Allen and Engeman, 1995; Allen et al., 1996; Mahon et al., 1998; Edwards et al., 2002a). This technique (and variations of it) has also been used successfully around the world to monitor a wide range of other carnivore and herbivore species of all sizes (with examples in Eldridge et al., 2002; Engeman et al., 2002; Allen, 2005; Engeman and Evangelista, 2006; Blaum et al., 2008; Evangelista et al., 2009; Purcell, 2009). Wilson and Delahay (2001) and Engeman (2005) outline a widely applicable framework for indexing and sampling animal populations using tracking plots (and other means) and describe the principles governing their proper use for making reliable inferences about species abundance. However, many dingo-related studies have not applied these principles. The principles described in these reports are simple reflections of elementary statistical sampling and design. Hence, studies not accountting for them may offer unreliable evidence due to biased data or confounded inferences.

Several important factors can be easily overlooked when using indices to assess the activity or relative abundance of dingoes, including seasonal variability of activity and the potential for activity to be influenced by habitat. Other methodological weaknesses can limit the ability of studies to accurately portray reality, such as insufficient sampling effort, and, to a lesser extent, reducing sensitivity to population change by using binary data (e.g. presence/absence, or the proportion of sand plots with or without animal tracks) rather than potentially continuous measures. Fundamentally, indices are only useful when they are correlative of density (Caughley, 1977), and in most circumstances, the relationship between indices and population density is impossible or impractical to determine. Other factors can arise when simple indices are unnecessarily complicated to include additional assumptions that are extremely difficult, if not impossible to validate. These general considerations are also important when indexing species other than dingoes.

4.1 The influence of season and habitat

The effect of season on species activity is most obvious for reptiles that reduce their activity (or even hibernate) during cooler months (see Allen, 2005; or Purcell, 2009, for sand plot examples). This behaviour reflects activity changes, not abundance changes, because reptiles do not die off each winter, they just become less active. Dingoes do not hibernate like reptiles, but seasonal activity changes do occur. For this reason, observations made at different times of the year cannot be accurately compared or pooled for analysis (Fleming et al., 1996; Engeman, 2005). This is because comparison of indices obtained from different times/seasons would confound relative abundance differences with behavioural differences, whereas pooling across seasons would mask differences that could be more appropriately identified within a season.

Habitat or land use may also influence species activity (Wilson and Delahay, 2001; Engeman, 2005). For instance, ‘open’ habitats (such as sandy deserts or grasslands) may afford a more even distribution of activity across the landscape because there are no physical barriers to movement patterns, whereas ‘closed’ habitats (such as rocky ranges, or dense forest) may direct movements on to the road (i.e. where sampling occurs). Alternatively, the availability and proximity of predation refuges may influence the activity of smaller prey species. Other, more subtle differences may occur between land uses within a similar overall habitat, such as the size of the seed bank available to granivorous species. Such subtle differences may be undetectable when sampling parameters such as recent rainfall, vegetation diversity and richness, or contemporary grazing pressure from herbivores.

Confounding seasonal or habitat factors with population assessments may mean that even if two populations are the same size in reality, their activity index values may well be different, or, even if the values are the same, the true population sizes may still be different. To illustrate this, consider the likely result of comparing a reptile population sampled at one site in summer to a population of reptiles sampled at another site in winter. The indices are likely to suggest a smaller population at the second site simply because of the season the site was sampled. Furthermore, if the first site was in a sandy

desert and the second was nestled amongst some rocky ranges, the resulting indices may also reflect habitat characteristics and not true abundance. This was well-demonstrated by Evangelista et al. (2009) when track plots on roads were ineffective at intercepting the daily movements of Ethiopian wolves *Canis simensis* because adjacent vegetation was only a few centimetres high and consequently did not impede travel by wolves. These issues should guide the way researchers sample populations and analyse data obtained using methods potentially influenced by activity.

Dingo activity naturally fluctuates throughout the year in response to seasonal breeding patterns (Corbett, 2001; Fleming et al., 2001). Independent of dingo abundance, dingoes' use of roads (and therefore off roads) fluctuates likewise (Fig. 1). Significant, yet normal changes often occur in just a few weeks, with the most marked decreases occurring between April (mid fall) and August (late winter), or between the mating and whelping seasons (for examples, see Thomson, 1992a; Eldridge et al., 2002; Allen, 2005; Allen, 2006; Allen and Miller, 2009; or Purcell, 2009). Some studies have inadvertently ignored this behavioural change by comparing a sample/s obtained from a given site and season to a sample/s obtained from a quite different site and season, rendering comparisons indecipherable.

For example, to make inferences about the protective influence of dingoes on dusky hopping-mice populations and other species, Letnic et al. (2009a) used tracking plots at three sites along the New South Wales section of the predator-proof Wild Dog Barrier Fence (referred to hereafter as the 'dog fence', Yelland, 2001). Each of the three sites had 'paired' sub-sites located on either side of the dog fence, where the relative abundance of several species, including dingoes, foxes, and cats were assessed.

Unfortunately, paired sub-sites were located on properties with differing historical and contemporary land uses either side of the dog fence (e.g. properties grazing sheep only, cattle *Bos taurus*/*B. indicus* only, or sheep and cattle), prohibiting reliable comparisons between them (Allen, 2011). In an earlier study on dingoes and kangaroos (Newsome et al., 2001, pg. 71), the same areas on either side of the dog fence surveyed later by Letnic and colleagues were described as two entirely different "ecological universes", with marked differences in landform, habitat, water run-off, artificial water point densities, faunal assemblages and resulting ecological processes. It may also be argued that the other sites sampled (the information presented in Letnic et al., 2009a; Letnic et al., 2009b; Fillios et al., 2010; and Letnic and Koch, 2010, are each based on a single field study) also compared two different ecological universes, where the sub-sites on one side of the dog fence

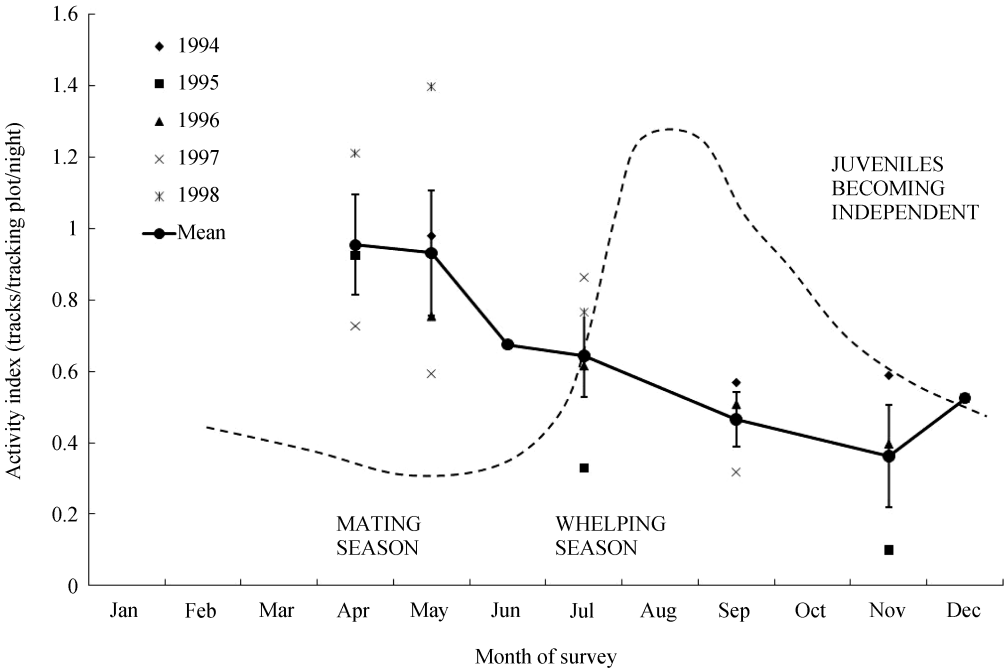

Fig. 1 Mean activity index for dingoes at a central Queensland site across drought (1994–1996) and flush (1996–1998) years showing normal seasonal changes in activity (solid line) independent of their theoretical abundance (dashed line), from Allen (2005)

adjoined either rugged ranges (those surveyed by Wallach et al., 2009a) or near-permanent river systems, while sub-sites on the other side of the fence did not.

The purpose of sampling matched pairs is to control all factors except for the effect of interest. However, having sub-sites of different historical and contemporary land uses essentially means that sub-sites assessed in this way are not properly paired. Such different land use and habitat contexts usually confound comparisons across the dog fence or diminish the prospect of accurately determining a cross-fence effect when pooling activity indices between sub-sites (Fleming et al., 1996; Wilson and Delahay, 2001; Engeman, 2005). Moreover, individual sites (each with paired sub-sites) were sampled in different seasons (Letnic et al., 2009a). Inferences from pooling them together for analysis achieve utility when assuming the effect of season is constant, which is known to not be true for many species, including dingoes.

Furthermore, the results of Letnic et al. (2009a) were then contrasted with the relative abundance of irruptive hopping-mice, whose fine-scale abundance and distribution are known to fluctuate significantly in response to localised rainfall events independent of alternative factors (Moseby et al., 2006; Van Dyck and Strahan, 2008; Waudby and How, 2008). By sampling sites in different seasons (surveys were conducted in March/April, September and November of 2007), explanations for the hopping-mice results become extremely difficult to interpret. This is because their abundance at the various sites may simply have reflected the spatio-temporal variation in a dynamic population and/or the size and quality of the seed bank available to them.

It would be a natural tendency to consider pooling data across seasons (but not land use practices) for hopping-mice given information indicating they do not appear to be seasonally affected, but it may not have been widely understood that dingo activity indices would be highly affected by season. These issues indicate that once-off, snapshot surveys conducted at different times and in different treatments have a greatly reduced ability for inferring causal processes, as a large number of alternative hypotheses could explain the observations (MacKenzie et al., 2006). Such inferential design issues for activity indices are also found in reports by Wallach et al., 2009a; Wallach and O'Neill, 2009; Wallach et al., 2009b; and Wallach et al., 2010, which also had comparisons invalidated by misapplication of activity indices (Allen, 2010).

For example, Wallach et al. (2009a) surveyed several sites both inside and outside the South Australian section of the dog fence (Fig. 2) to make inferences about the protective influence of dingoes on yellow-footed rock wallabies and malleefowl. Comparisons were made between, and pooled across widely separated "inside" sites and "outside" sites. Not made explicit is that these sites are vastly different in topography, mean annual rainfall, livestock grazing history, contemporary land use, and fauna assemblage. The three inside sites, two of which are in the very rugged northern Flinders/Gammon Ranges (i.e. rock-wallaby habitat), were compared to the three outside sites comprised of comparably flat and stony gibber plains up to 400km away (see Wallach et al., 2009a for details) where rock-wallabies have never been recorded. Mean annual rainfall is approximately two-three times higher in the Flinders/Gammon Ranges than at the other sites (see www.bom.gov.au, noting site differences in local rain events during the course of their study), and the difference in historical and contemporary livestock grazing practices either side of the dog fence cannot be understated (Newsome et al., 2001; Allen, 2011). These confounding effects of season and habitat restrict the ability to make valid inferences from contrasting observations, with data on dingo behaviour and ecology at the outside sites having limited application for assessing the ecological significance of dingoes in rock-wallaby habitat at the inside sites.

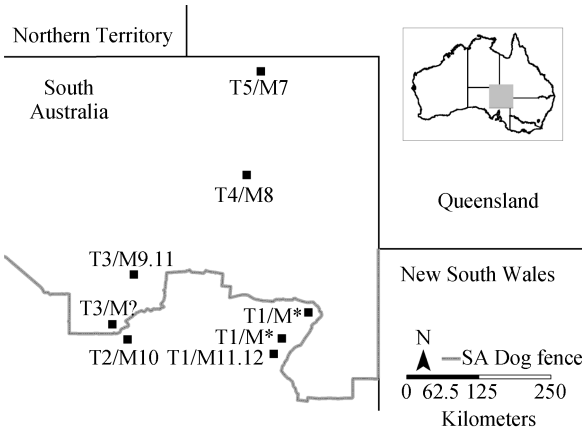

Fig. 2 Location of study sites used in Wallach and O'Neill (2009), Wallach et al. (2009a,b), and Wallach et al. (2010) showing the treatment (T) and month (M) in which sampling was conducted (? = dates not reported; * = sometime between July and February)

In another, more subtle example, Johnson and VanDerWal (2009) re-analysed data from two earlier studies (Catling and Burt, 1995b; Newsome, 2001) to make

inferences about the ability of dingoes to set an upper limit on fox abundance in eastern Australian forests. While the 2009 desktop study was well conducted, the field methods used to obtain the relative abundance values of dingoes and foxes in the original studies were corrupted with seasonal and habitat factors. Catling and Burt (1995b, pg. 538) used tracking plots to record tracks in "late summer or autumn and again in late winter or spring." The exact survey dates were unpublished, but according to the authors, the surveys were conducted across all four seasons. The results were pooled for analysis (before later re-analysis), potentially masking the reported relative abundance differences with seasonal behavioural differences.

Additionally, the Catling and Burt (1995b) data were collected from hundreds of different sites of varying habitat complexity (compare Catling and Burt, 1995a; with Catling and Burt, 1995b). The relative abundance data from the other original study (reported first in Newsome et al., 1983; then Newsome et al., 1997; and finally in Newsome, 2001) were also collected over several years, seasons, and habitats before pooling for analysis and later transcription and re-analysis by Johnson and VanDerWal (2009). Pooling across several years and seasons may be an attempt to reduce the effects of seasonal variability in the analysis, but doing so is questionable for data from multiple sites with significant habitat differences (Engeman, 2005).

Being elementary experimental design concepts, we have tried to emphasise that activity indices obtained from different seasons or habitat types cannot be reliably compared because of the potential disparity between factors affecting the activity of species between seasons or habitats. Sometimes analytical procedures, such as generalized linear modelling, have been applied in attempts to sort out various influences. However, the premise of confounding is that the researcher cannot be sure what effect is actually being evaluated. Regardless, model output is directly related to the quality of data used for model input, and when confounded, analytical results may simply be artefacts of the sampling design. Hence, our criticisms are not with statistical procedures but of the sampling and design issues used to collect the raw data before analytical procedures are even attempted. Once collected, it is difficult to argue that confounded data can then be 'un-confounded' to produce a reliable result.

Habitat usage and seasonal changes in activity by dingoes have three important implications for researchers and managers. First, researchers wanting to monitor a population over multiple years must ensure that observations are made at the same time of year. Alternatively, if comparisons between Population A and Population B are desired, care should be taken to ensure that both populations occupy similar habitats and are observed at the same time. Second, when using tracking plots to measure interventions (such as the effectiveness of control programs), the time difference between pre- and post-control assessments should be as small as possible to avoid confounding the effects of the control program with normal seasonal activity changes. The same concept applies when comparing index values at paired sites, with the data needing to be collected nearly simultaneously for each member of a pair. Third, predator control programs initiated in response to a given activity index value should take into account the season, and its influence on activity, abundance and impacts of dingoes.

The examples discussed above are not the only studies that have suffered from the confounding effects of season and/or habitat, and many others could be equally used as examples (see Table 1). Any wildlife studies that rely on methods influenced by activity patterns (e.g. tracking plot indices, direct counts, camera trapping, aerial surveys, vocalisations, dung/scat counts, pitfall trapping, chew cards etc) should be careful to sample populations in the same habitat and at the same time to avoid data-confounding that could lead to unsubstantiated conclusions.

4.2 Assumptions

Activity/population indices do not directly measure absolute density. Nevertheless, some studies have complicated otherwise simple, robust indices in attempts to identify exactly how many individuals are responsible for the tracks observed. This introduces several important assumptions that are almost certain to be violated.

The prospect of individual identification is seductive, and has been accepted because predators are known to casually meander on and off the road as they wander along it (Mahon et al., 1998). For example, Burrows et al. (2003) reported the results of several 1080 baiting exercises using tracking plot methods where it was assumed that identical tracks <2km apart and heading in the same direction were from the same individual. Pavey et al. (2008) likewise assessed the population dynamics of predator species assuming that dingo and fox tracks separated by a minimum distance of 1km and 0.5km respectively were from different individuals. Many other studies have made similar assumptions (e.g. Mahon et al., 1998; Edwards et al., 2000; Edwards et al.,

2002a; Eldridge et al., 2002). If unfounded, these assumptions would lead to erroneous estimates of activity, particularly if the species' use of roads varies throughout the year, as we have discussed for dingoes.

In a different example, Wallach et al. (2009a) attempted to distinguish between individuals based on the size and shape of the footprint. However, the shape of the print can be influenced by the tracking substrate, and front and rear feet of dingoes (and many other species) are of different sizes (Triggs, 2004). Dingoes are also annual breeders (Corbett, 2001), and mean footprint size therefore changes throughout the year according to the proportion of juveniles becoming active in the population (Allen and Gonzalez, 1998; Allen, 2005). This fact is particularly important to the study of Wallach et al. (2009a) because sites were surveyed between July and February (exact dates were not reported), which correspond to the months when juveniles (as distinguished by foot size) are absent, and then present and independent in the population (see Corbett, 2001, and discussion above). Moreover, a multiplicative combination of their 'relative abundance' and 'relative distribution' indices (i.e. a continuous and a binary method) could be argued as providing a potential synergy of assumption violations, leaving little prospect for a valid variance estimate, and unnecessary if the track sampling was representative of animal usage in the area of interest (Allen, 2010).

It may be stating the obvious, but studies that violate the underlying assumptions necessary for valid application of the methodology risk making unsupported inferences (Caughley, 1977; Elphick, 2008), especially when those assumptions reflect real behavioural and ecological issues. If researchers and land managers need sound ecological knowledge to formulate appropriate management strategies, then many recent studies violating these assumptions may not provide such information.

4.3 Sampling design, intensity, and inferences

Dingo activity is not uniformly distributed across the landscape, but is usually influenced by resources (Corbett, 2001; Fleming et al., 2001), thereby contributing to plot-to-plot variability in tracking plot activity indices (Engeman et al., 1998; Engeman and Allen, 2000; Engeman, 2005). Thus, it is also important to consider the overall number and spatial distribution of tracking plots in reference to the area for which inferences are being made. Note also that the objective of such sampling is not measuring the habitat, but rather the population using the habitat – and populations are rarely distributed uniformly within a habitat (Engeman, 2005).

Some studies justify small sample sizes, or the sampling of small areas by referring to the number of home ranges the sampling area is likely to cover (e.g. Mahon et al., 1998; Edwards et al., 2000). However, dingo home range size is influenced by habitat, season, and resource availability (Thomson, 1992b; Corbett, 2001; Fleming et al., 2001; Purcell, 2009), which in turn, influences the number and type (i.e. age or gender) of dingoes (and possibly other animals) using roads (and off roads) and the distance they travel on them (discussed above). Studies using tracking plots over restricted areas risk having large differences in daily activity means, and having the results unduly influenced by dispersal activity, extraterritorial movements, and other such factors. If the area is too small, studies may potentially be sampling only a few individuals, which may not be representative of the population of interest.

Dingo-related studies have expectedly used a variety of sampling intensities. Newsome et al. (1983) placed 45 tracking plots along a 18km transect at one site, 65 along 26km at another, and 105 plots along a 84km transect at another site. Wallach et al. (2009a) used between 9 and 25 randomly placed tracking plots (each referred to as 'transects') per study site, while Southgate et al. (2007b) used 227 random plots. Letnic et al. (2009a) used 25–30 tracking plots spaced 1km apart at each sub-site while Corbett (1995) used 55 plots interspersed throughout one site. Allen (2000, 2005) used 50 plots spaced 1km apart per treatment area and 100 plots similarly spaced in another large scale study (Allen, 2006).

Studies designed primarily to survey other species – assessing invasive predators only incidentally – have expectedly used sampling regimes not ideally suited to dingoes. For example, Catling and Burt (1995a) were interested in small, forest animals with discrete dispersions (as well as dingoes and foxes), and they therefore used a spacing of one tracking plot every 200m on multiple transects ranging from 4km to 7km in length. Catling et al. (1999) used similar methods when surveying for cane toads *Bufo marinus* in the Northern Territory, where 25 plots spaced 200m apart were established along a 5km transect in each site. In a study designed to survey desert rodents, Moseby et al. (2006) recorded dingo, fox, and cat tracks in the 20m spaces between 200 rodent traps placed in 10 lines of 20 traps. In doing so, approximately four kilometres were surveyed inside an 8ha trapping grid (Moseby et al., 2006), potentially

sampling a very limited number of individual predators in a very limited area of predator activity or home range at extensive rangeland sites. Studies based on small sample sizes, or conducted across small areas, should be careful not to extrapolate inferences beyond the range of the data, or the area surveyed.

Based on studies from eastern New South Wales, it has been recommended that at least 25 tracking plots spaced 1km apart should be monitored over three nights to sample dingo populations (Mitchell and Balogh, 2007). Using a smaller number of plots is legitimate (although often imprecise), providing the area surveyed (or number of plots used) is representative of the area for which inferences are being made, otherwise, severe bias can be introduced into the results. In a typical rangeland setting where sheep or cattle are extensively grazed or in large wilderness reserves, studies with a paucity of tracking plots may have limited ability to provide reliable inferences about the dingo population in the area.

The examples discussed suggest that some of the study designs used in various approaches, whether it be the size of the area sampled or the overall number and configuration of tracking plots, may be a cause for the reduced ability of many reports to deliver dependable information. Intuitively, the greater the sampling effort the more sensitive the study will be at detecting presence and trends (Allen et al., 1996; Wilson and Delahay, 2001). Given the logistical constraints to conducting large-scale research projects, variance component analyses across a variety of studies have typically shown that if a labour-saving choice must be made, it is better to sample more plots over less days than vice versa (Engeman, 2005).

4.4 Continuous versus binary data

Using binary measures is legitimate (Caughley, 1977), although the reduction of potentially continuous data to binary observations is very easily demonstrated to have less descriptive ability, less sensitivity for detecting change, and result in a greater opportunity for erroneous inferences (Engeman, 2005). This has been well demonstrated for dingoes and many other carnivore species around the world (Allen et al., 1996; Engeman et al., 2000; Engeman et al., 2002), with the prospect for erroneous conclusions increasing with population density (Blaum et al., 2008).

For example, in two separate studies on coyotes and other coexisting species (Engeman et al., 2000; Engeman et al., 2002), the authors demonstrated a loss of sensitivity for detecting changes or differences among track plot indices when data were treated as binary observations, rather than a continuous measure, such as the number of intrusions. Similarly, while using quite different observational methods on rodents, the reduction of continuous measurements to binary counts again resulted in a loss of sensitivity for monitoring populations (Whisson et al., 2005). Recording continuous data from tracking plots takes little additional time, but unfortunately, this has been neglected in many recent dingo-mesopredator studies.

For example, Johnson and VanDerWal (2009) re-analysed data that was originally obtained by recording the number of tracking plots with and without tracks (see Newsome et al., 1983; and Catling and Burt, 1995b for details). Mahon et al. (1998) and Wallach et al. (2009b) also used binary measures to assess the activity of dingoes, foxes, and cats. In another example, Letnic et al. (2009a) collected and used continuous measures, but later reduced the same data to binary counts for further analysis (Letnic et al., 2009b). The density of dingoes at the outside sub-sites sampled was very high, while their paired inside sub-sites had very low densities. This means, according to Blaum et al. (2008), there is a greater likelihood for the outside and inside sub-sites assessed by Letnic et al. (2009a, b) to be indistinguishable even though a substantial difference might exist.

In evaluating the use of binary counts in recent dingo studies, the logical question to ask would be whether the conclusions would be different if continuous data was used. In some cases the answer may be ‘no’, but in other cases the answer may well be ‘yes’. The reason for this is most clearly elucidated by Corbett (1995, pg. 69), who observed that the difference in actual numbers of water buffalo *Bubalus bubalis* between pre- and post-control surveys (described as ‘Phase A’ and ‘Phase B’ respectively) were “probably much greater than that indicated by the index values. This is because sign was deposited by many buffalo along most transects in Phase A but usually only by a solitary buffalo in Phase B and the [binary] index method did not account for such differences”. Hypothetically, there may have been 10 buffalo tracks/transect pre-control and 1 buffalo track/transect post-control, indicative of a large reduction in buffalo activity if continuous measures had been used; but because binary measures were used, the technique did not distinguish between 10 tracks or 1 track, and the methods were insensitive to population change.

In summary, studies using tracking plot activity indices should record and analyse the potentially continuous

number of individual track intrusions on a plot rather than the binary presence or absence of tracks in order to provide a more sensitive picture of population trends and reduce the prospect for erroneous inferences. Using binary data alone does not invalidate the conclusions presented and studies are not confounded because of them, but if binary counts were preferentially analyzed, it would be useful to first collect and then show that reduction of continuous data did not result in a loss of sensitivity. Perhaps the ecological role of dingoes relative to other invasive mesopredators may be better illuminated if more sensitive techniques were used more often.

5 An Appropriate Experimental Design

Having reviewed some of the limitations from some study designs found in the recent dingo-related literature, it is important to understand how an appropriate experiment might be conducted. We advocate the experimental design presented in Glen et al. (2007), and encourage those interested in undertaking field studies of dingoes to follow their recommendations.

In short, they suggested that predator removal or reintroduction experiments be conducted with a BACI (before-after, control-impact) design, with replicated treatments and controls, at scales large enough to permit the occurrence and detection of animal population growth. Study duration should also be sufficient to differentiate between treatment effects and the expected stochastic variations typical of Australian landscapes, such as rainfall and associated primary productivity (Glen et al., 2007). We would recommend that dingo removal experiments are conducted in favour of dingo reintroduction experiments, because it is easier to protect threatened species from generalist predators by preventing their arrival than it is to rescue them once a predator is established. Dingo removal experiments may also elucidate the trophic effects of dingo *control*, which may be a concept more readily applicable to land managers.

With a multi-site and multi-year experiment, appropriate techniques for population monitoring of dingoes, foxes, cats and potential prey species are required in order to obtain adequate data on the various species of interest. As discussed above, we encourage the use of the activity index described by Allen and Engeman (1995) for this purpose for seven reasons (with additional details in Allen et al., 1996; Engeman et al., 1998; Engeman and Allen, 1999; Engeman and Allen, 2000; and Engeman, 2005):

1) It has been shown to be particularly sensitive to changes in dingo populations.

2) It is relatively quick and inexpensive to undertake.

3) It allows the simultaneous monitoring of multiple species.

4) It is not as labour-intensive as density-estimation procedures which are often impractical and invalid to apply.

5) It contains few inherent assumptions.

6) It is capable of detecting the presence of species in low densities.

7) It is objective, repeatable, and able to be subsequently used in common analytical procedures.

For completeness, tracking plot indices should be supplemented with other techniques, such as bird counts or scat collection, to provide additional information on ecological processes at the study site. If the experiment is conducted in areas where livestock are grazed and a measure of grazing pressure is desired, consideration should be given to obtaining information on stock numbers from the landholders as a more reliable measure than scat indices/dung counts (Allen, 2011). Historical and contemporary land use should also be considered when assigning treatments.

Further to Glen et al. (2007), a conceptual diagram of a study site in such an experiment is shown in Fig. 3. Here, dingoes are subjected to poison baiting in one treatment but not the other (an experimental control). Tracking plots are spaced 1km apart along a transect 50km long in each treatment and are monitored at regular intervals each year, repeating the surveys at the same time each subsequent year. Tracking plot transects are separated by a 50km buffer to avoid populations in the experimental control (unbaited) area being influenced

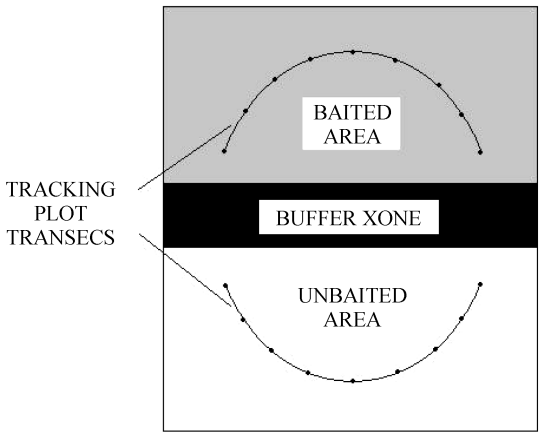

Fig. 3 A diagrammatical representation of a study site used in an appropriately designed dingo removal experiment

by potential changes in the treated (baited) area. Our recommendation to use 50 tracking plots per treatment area attempts to maximise sampling while considering logistical constraints, where (in our experience) only ~100 tracking plots arranged as described can be serviced by one researcher each day.

Because of the subtle habitat differences that can occur in landscapes that appear similar, a trade-off is likely to exist between treatment independence and treatment similarity when deciding on an appropriate buffer. For instance, independence may increase and habitat similarity decrease the further apart two treatments are, and vice versa. It is important not to compare 'apples with oranges', and in this case, we should seek to compare a poisoned 'apple' with an un-poisoned one. Foundational data should be collected to verify this, such as rainfall, vegetation types, and other such information. This can then be used to identify population responses to variables besides predator control. Replication of paired treated and untreated sites helps resolve these issues, especially in the face of background variability.

The types of experiments described have been conducted before in arid, forested, and monsoonal areas (e.g. Eldridge et al., 2002; Allen, 2005; Allen, 2006). Because the role of dingoes in Australian landscapes is potentially so important for threatened species recovery and viable livestock production (Fleming et al., 2001; Glen et al., 2007), these experiments should be repeated in additional systems around Australia in the future to build up a clearer picture of causal processes (Visser et al., 2009).

6 Conclusions

This review of recent dingo-mesopredator or dingo-prey studies indicated that the applied methodologies of 15 out of 20, or 75% of reports contain serious design and/or methodological flaws. Of the five remaining studies, four of them used insensitive measures, suggesting that further detail may be hidden within the data. Reading beyond the results and conclusions of all the studies examined, it is clear that some excellent data is available that might provide more defensible insights into the ecological role of dingoes relative to mesopredators and prey species if they were reanalysed in light of the issues we highlight. Hence, there is currently inconclusive evidence from these studies for invasive mesopredator release in Australia.

Our concern is that the intuitive appeal of the recent "evidence" for the usefulness of dingoes as biodiversity conservation tools will prematurely lead conservationists and land managers to positively manage dingoes despite the clear absence of supporting data. The precautionary approach would be to maintain the current situation until more robust information is available (Cooney, 2004). Moreover, before national or state-based policy changes towards the positive management of dingoes in pastoral areas are proposed on biodiversity conservation grounds, any negative effects of dingo *control* on threatened species – either direct or indirect – need to be better demonstrated. This might be achieved by following the recommended experimental designs described here and in Glen et al. (2007), being careful to not waste time on "'low-information' observations *or* experiments" that do not exclude or even discuss alternative hypotheses (Platt, 1964, pg. 349, emphasis added).

It must also be kept in mind that dingoes are highly capable of predation on the same species that are assumed to derive a benefit from their promotion. Hence, the relative strength of the dingo-mesopredator and dingo-prey interactions will ultimately determine the outcome of positive dingo management. Dingoes are also economically significant predators of livestock (e.g. Hewitt, 2009), and their positive management must not be considered with a narrow focus on only biodiversity issues, which could potentially result in devastating impacts to rural communities and hence the capacity to manage dingoes and biodiversity in rural areas.

Most of the studies we assessed did not contain reliable evidence for the biodiversity benefits of dingoes, which may be why there is still such uncertainty about their role in Australian ecosystems. Moreover, the dynamics of threatened fauna is influenced by more than just predator-prey relationships (Holmes, 1995; Gese and Knowlton, 2001), and predation may be a secondary issue to many others (Mahon, 2009; Visser et al., 2009; Allen, 2011). We therefore assert that much of the "growing body of evidence" so often referred to by an increasing number of authors is merely a growing body of literature only, and is often based on inadequate science.

Observational and purely correlative studies, typified by many of the recent reports (Glen et al., 2007), have the weakest ability to make inferences about causal processes (Gehrt and Clark, 2003; MacKenzie et al., 2006). Whereas, the few experimental studies (e.g. Eldridge et al., 2002; Allen, 2005; and Allen, 2006), which have the strongest inferential ability, have not been emphasized in the literature reviewing or supporting a hypothesis of dingo regulation of mesopredators

or their net protection of threatened species. Part of the reason for this lies with those authors not making the results more widely available outside of 'the grey literature'. Incidentally, our review suggests that good-quality research can be found within such literature. Moreover, it also suggests that peer-reviewed studies published by reputable outlets should not necessarily be blindly accepted as good-quality information just because they are 'peer-reviewed studies published by reputable outlets'.

To conclude, it would be regrettable if this study were viewed as an 'anti-dingo' or 'anti-mesopredator release' paper – it is not. Rather, our intention is that it be viewed as a 'pro-science' paper, because our results indicate that the quality of the science underpinning current knowledge of the ecological role of dingoes is deficient. Moreover, the positive management of top-order predators does not always yield the biodiversity benefits often anticipated (Sergio et al., 2008; Hayward and Somers, 2009), and premature positive management of a generalist predator as capable as dingoes could further threaten many species, populations, or ecological communities (Major, 2009; Allen, 2011). If researchers are to unravel the complexities of the dingo's ecological roles in a dynamic environment, then the quality of research needs improvement. Otherwise, decision-makers and land managers will continue struggling to make sense of the available literature. We encourage the continued interest in dingo trophic regulation research, and hope that this review results in a more balanced and justifiable discussion. Future reports making conclusions from observations without addressing the design and sampling issues discussed here should be interpreted with caution and valued accordingly.

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