

FORUM

Dingoes can help conserve wildlife and our methods can tell

Dale G. Nimmo^{1*}, Simon J. Watson², David M. Forsyth³ and Corey J. A. Bradshaw⁴

¹Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Burwood, Vic. 3125, Australia; ²Department of Zoology, La Trobe University, Bundoora, Vic. 3086, Australia; ³Department of Environment and Primary Industries, Arthur Rylah Institute for Environmental Research, 123 Brown Street, Heidelberg, Vic. 3084, Australia; and ⁴The Environment Institute and School of Earth and Environmental Sciences, The University of Adelaide, Adelaide, SA 5005, Australia

Summary

1. Management of apex predators is among the most controversial wildlife management issues globally. In Australia, some ecologists have advocated using the dingo, *Canis dingo*, as a tool for conservation management, due to evidence that they suppress invasive mesopredators.

2. Hayward & Marlow (*Journal of Applied Ecology*, 51, 2014 and 835) questioned the capacity of dingoes to provide benefits to native biodiversity due to their inability to eradicate foxes and cats. They also argued that indices of abundance commonly used in studies of mesopredator release by dingoes (namely, track-based indices) invalidate the conclusions of the studies. Hayward & Marlow caution conservation practitioners against incorporating dingoes into conservation programmes.

3. Counter to their claims, we summarise research showing that the suppression of invasive mesopredators (cf. eradication) can enhance populations of native species and is therefore a meaningful conservation objective. We highlight literature supporting the hypothesis that dingoes suppress mesopredator abundance and activity, which in turn benefits native biodiversity.

4. We show that Hayward & Marlow overlook many studies of carnivores that show track indices capture a large amount of the variation in the density of medium- and large-sized carnivores.

5. *Synthesis and applications.* Practitioners cannot afford to wait to act given the perilous state of Australia's mammal species, and we argue that the evidence is sufficiently strong to justify managing dingoes for biodiversity conservation.

Key-words: abundance indices, apex predator, *Canis dingo*, conservation biology, dingo, mesopredator release, trophic cascades, *Vulpes vulpes*

Introduction

The importance of apex predators for biodiversity conservation has become increasingly apparent over the last few decades (Ritchie & Johnson 2009). Apart from *Homo sapiens*, Australia has only one remaining terrestrial apex predator: the dingo *Canis dingo*. There is mounting evidence that dingoes can have positive effects on small-

and medium-sized native Australian mammals (<5.5 kg) through reducing predation by suppressing mesopredators (red fox *Vulpes vulpes* and feral cat *Felis catus*) (reviewed in Letnic, Ritchie & Dickman 2012). These findings have led ecologists and conservation managers to advocate the cessation of lethal control of dingoes for biodiversity conservation (Ritchie *et al.* 2012; Colman *et al.* 2014). However, dingoes also impart economic and social costs through the predation of domestic livestock (Fleming & Korn 1989), and some researchers have questioned their benefits for biodiversity (Allen *et al.* 2013;

*Correspondence author. E-mail: dale@deakin.edu.au

Hayward & Marlow 2014). Consequently, as for many other apex predators around the world, dingo management in Australia is highly contentious (Letnic, Ritchie & Dickman 2012).

Hayward & Marlow (2014) dismiss the putative benefits of dingoes for native biodiversity, particularly medium- and small-sized mammals, due to their inability to eradicate (as opposed to suppress) invasive mesopredators. They then question the ability of practitioners and researchers to evaluate the benefits of using dingoes, due to limitations with common monitoring methods (namely, track surveys). Here, we respond to both conceptual and methodological issues raised by Hayward & Marlow (2014). Our intention is to provide evidence for an alternative perspective – (i) that suppression of mesopredators is a worthwhile conservation objective, (ii) that dingoes can help achieve this objective and (iii) that track indices can still play an important role in assessing whether this objective is being met.

Conceptual issues

SUPPRESSING MESOPREDATORS BENEFITS NATIVE BIODIVERSITY

Critical weight-range mammals are those species between 35 g and 5.5 kg that are thought to be most negatively affected by Australia's invasive mesopredators – red foxes and feral cats (Burbidge & McKenzie 1989). Hayward & Marlow (2014) argue that because dingoes cannot *eradicate* foxes and cats, their benefits to critical weight-range mammals are limited. By contrast, there are clear examples where fox suppression (cf. eradication) has led to increases in the abundance, survival and activity of critical weight-range mammals. For example, Dexter & Murray (2009) showed that the total abundance of all mammals, including the critical weight-range southern brown bandicoot *Isodon obesulus* and long-nosed potoroo *Potorous tridactylus*, was higher in areas where foxes had been suppressed (but not eradicated). Likewise, Claridge *et al.* (2010) showed that the activity of southern brown bandicoots increased following suppression of foxes, and Kovacs *et al.* (2012) showed that the survival of the bushrat *Rattus fuscipes* was twice as high when fox activity was low. Robley *et al.* (2014) showed that large-scale and long-term fox suppression increased occupancy rates of common brushtail possums *Trichosurus vulpecula*, long-nosed potoroos and southern brown bandicoots. Hayward & Marlow (2014) themselves acknowledge the positive effects of dingoes on hopping mice *Notomys* spp., a genus that has lost four of its 10 species since European colonization (Van Dyck & Strahan 2008).

These studies indicate that mesopredator suppression can cause substantial, and positive, changes to the abundance of native mammal species. There are additional considerations when using dingoes rather than lethal control (e.g. 1080 poison baiting) to suppress mesopredators:

principally, predation by dingoes of native species (Allen & Fleming 2012). When considering the suppression of mesopredators in the context of ceasing active dingo control (or reintroducing dingoes into their former ranges), the aim should be for a net benefit. The hypothesis to test is that a reduction in mesopredator predation on native mammals (due to suppression of dingo density) is sufficient at least to offset any direct predation by dingoes, resulting in higher abundances of native species in the presence of dingoes. Studies conducted in different regions, using a variety of sampling techniques (i.e. live trapping, spotlighting, in addition to track indices), have repeatedly demonstrated that many native species are more common where dingoes are present or abundant compared to where they are absent or rare (Letnic *et al.* 2009; Wallach *et al.* 2010; Letnic & Dworjanyn 2011; Colman *et al.* 2014).

OVERLOOKED BENEFITS: DINGOES ALSO LIMIT LARGE HERBIVORE ABUNDANCE

Hayward & Marlow (2014) focus solely on the effects of dingoes on mesopredators, overlooking the well-studied effects of dingoes on large, native herbivores (Caughley *et al.* 1980; Pople *et al.* 2000; Choquenot & Forsyth 2013; Letnic & Crowther 2013). Recent theoretical (Choquenot & Forsyth 2013) and empirical (Letnic & Crowther 2013) studies have shown that dingoes place an upper limit on the abundance of kangaroos. Over-abundant herbivore populations have resulted in the decline of many native animal species globally, primarily by reducing vegetation biomass and simplifying the structure of plant communities (Foster, Barton & Lindenmayer 2014).

Methodological issues

TRACK INDICES OF CARNIVORES OFTEN PERFORM WELL

Hayward & Marlow (2014) draw on examples of two rodent species, an insect and one carnivore to support their claim that track indices do not closely reflect true abundances of carnivores. We agree that validating track indices for carnivores is important (as is validating population estimates), and there remains a need for this in the context of mesopredator release due to dingo control. However, in contrast to the examples cited by Hayward & Marlow, there are many validated counter-examples showing that tracks provide a good index of variation in the absolute abundance of carnivores. For example, Funston *et al.* (2010) found that tracks on trails explained 96% of the variance in the true density of large carnivores (lions *Panthera leo*, leopards *Panthera pardus*, cheetahs *Acinonyx jubatus* and spotted hyaenas *Crocuta crocuta*). Stander (1998) found that spoor density was strongly and linearly related to known densities of leopards *P. pardus* ($R^2 = 0.98$), as well as combined densities of lions *P. leo*

and wild dogs *Lycaon pictus* ($R^2 = 0.98$). Similarly, Houser, Somers & Boast (2009) found that spoor density was positively and linearly correlated (97% of variance explained) with known densities of cheetahs *A. jubatus*, and Jhala, Qureshi & Gopal (2011) found that pugmarks (paw prints) explained 84% of the variation in the density of tigers *Panthera tigris*.

Hayward & Marlow (2014) also raise concerns that track indices vary considerably over days or seasons. Many studies of mesopredator release have reduced this variability by using reporting rates (e.g. number of detections/total number of surveys – Letnic *et al.* 2009, 2011; Colman *et al.* 2014) instead of continuous indices that sum incursion events over the sampling period (i.e. counting multiple incursions within a single night).

ESTIMATION OR INDEXATION IS A QUESTION OF CONTEXT AND FEASIBILITY

Hayward & Marlow (2014) advocate other measures of abundance or occurrence when quantifying dingo–mesopredator interactions, such as those derived from distance sampling, mark–recapture and occupancy modelling. We agree that in most cases, population estimates are preferable to indices of abundance. However, the decision to estimate or index true abundance is often driven by feasibility. We question how feasible the methods proposed by Hayward & Marlow (2014) are in the context of studying the trophic role of dingoes.

For example, there is doubt regarding the cost-effectiveness of distance sampling for estimating the density of cryptic and typically low-abundance carnivore populations across large, remote regions. Edwards *et al.* (2000) encountered densities as low as 0.7 cats 100 km⁻¹ using spotlighting transects in Australia's semi-arid rangelands. Distance sampling requires a recommended minimum of 60 observations to estimate a robust detection function (Buckland *et al.* 2001). Thus, to meet this requirement would require >8500 km of transects. By contrast, the minimum number of cats recorded km⁻¹ for track surveys were 5–55 times higher (Edwards *et al.* 2000). Similar results were obtained for dingo monitoring, with the maximum number of dingoes recorded km⁻¹ being 10–125 times greater for track surveys than spotlighting, and spotlight surveys failed to detect animals in areas that were known to be occupied from track surveys (Edwards *et al.* 2000).

Other simple and inexpensive survey methods, such as scat counts, can also outperform more costly measures when surveying carnivores. For example, in the north-eastern USA, scat surveys out-performed camera traps for detecting occupancy by coyotes *Canis latrans*, as camera traps frequently (i.e. in 57% of cases) failed to record coyotes where scat surveys confirmed their presence (Gompper *et al.* 2006; Kays, Gompper & Ray 2008). Gompper *et al.* (2006) found scat counts could be used to census coyote abundance, because the number of scats

was strongly related to the number of individuals at a site ($R^2 = 0.93$). Similarly, Jhala, Qureshi & Gopal (2011) found that a simple model combining tracks and scats of tigers that explained 94% of variance in tiger densities could be built at 7% of the cost of population estimates derived from camera-trap mark–recapture methods. These simple, inexpensive measures will continue to be an integral tool for practitioners monitoring the trophic outcomes of predator-management interventions on tightly constrained budgets.

Hayward & Marlow (2014) also promote occupancy modelling to study mesopredator interactions. However, many studies of dingo–mesopredator interactions show that dingoes and mesopredators often co-occur; it is the upper limit of abundance indices where the effects of dingoes on mesopredators are commonly observed (Johnson & VanDerWal 2009; Letnic *et al.* 2011; Brook, Johnson & Ritchie 2012). Thus, while occupancy modelling can answer some questions about mesopredator release (e.g. changes in site occupancy following predator manipulation), the method would overlook important relationships that require data beyond occupancy. We would be concerned if researchers changed their ecological questions merely to satisfy the requirements of their preferred statistical models (Banks-Leite *et al.* 2014).

WHAT ARE RELATIVE ABUNDANCE INDICES REALLY MEASURING?

One argument against the use of indices is the uncertainty associated with what is really being measured: abundance, activity or some mix of both. In the context of the biodiversity benefits arising from dingoes suppressing mesopredators, this question is not as important as it might first appear. We have provided case studies showing that track indices closely reflect known abundances of medium- and large-sized carnivores. However, it does not matter if dingoes suppress mesopredator abundance or activity; what matters is that a reduction in the signs of mesopredators (e.g. tracks) corresponds with an increase in native prey species' abundance.

There are plausible scenarios of how a reduction in either the abundance or activity of invasive mesopredators could affect native species as both can reduce predation pressure (Ritchie & Johnson 2009). Even the mere presence of apex predators can alter the behaviour of lower-order predators or other prey by creating 'landscapes of fear' (Laundré, Hernández & Altendorf 2001): areas in the landscape that mesopredators avoid in the presence of apex predators (Sergio *et al.* 2007). Such changes in perceived risk can reduce predation pressure on prey species (Ioannou, Payne & Krause 2008). There is strong evidence that dingoes alter the behaviour of both cats (Brook, Johnson & Ritchie 2012; Wang & Fisher 2012) and foxes (Forsyth *et al.* 2014), and in doing so, dingoes can create conditions favourable for native biodiversity without having a direct effect on mesopredator abundance. So long as

the outcome of dingo management is to increase those phenomena that practitioners value (in this case, the abundance of native prey species), then the question of the mechanism (abundance, activity, or both) underlying that response is largely irrelevant. We are reassured by many studies that have confirmed increased trapping success or sightings of native prey species in the presence of dingoes (Letnic *et al.* 2009; Letnic & Koch 2010; Letnic & Dworjanyn 2011; Colman *et al.* 2014).

ARE TRAIL-BASED SURVEYS PREDICTABLY BIASED?

Hayward & Marlow (2014) contend that it is ‘almost ubiquitous’ that when apex and mesopredators co-occur, trails are used primarily by apex predators, whereas sympatric mesopredators largely avoid them. In the absence of apex predators, they argue, mesopredators will make greater use of trails. If this were true, then changes in mesopredator track densities on trails in dingo-free areas could simply reflect their greater use of trails and would therefore be an artefact of sampling rather than a meaningful change in the abundance or activity of mesopredators. While we ultimately agree that sampling on and off trails is preferable to avoid sampling bias, the type of bias outlined by Hayward & Marlow (2014) is far from ubiquitous. Brook (2013) found no evidence of an interaction between road use and effective dingo control on cats throughout northern Australia. Read & Eldridge (2010) found that foxes tended to follow roads for longer distances in the presence of dingoes, speculating that foxes might follow dingoes along roads to reduce the likelihood of ambush or to locate carrion left behind by them. Similarly, Mahon, Bates & Dickman (1998) found that both dingoes and foxes selected roads for travel in sympatry. It is therefore inaccurate to claim that mesopredators ubiquitously use trails more in the absence of apex predators, and, therefore, it is incorrect to claim that the conclusions of mesopredator-release studies are an artefact of their sampling methods.

Finally, it is wrong to imply that all studies of mesopredator release from dingoes rely solely on trail surveys. Such studies have employed other measures – including on- and off-trail camera traps, driven spotlight transects, on- and off-trail track surveys, and off-trail transects – and have arrived at similar conclusions to those studies that use trail-based track surveys: that is, that dingoes alter the activity or abundance of mesopredators (Wallach *et al.* 2010; Brawata & Neeman 2011; Letnic *et al.* 2011; Brook, Johnson & Ritchie 2012; Wang & Fisher 2012; Forsyth *et al.* 2014).

PRACTITIONERS MUST ACT (AND MONITOR)

Practitioners seldom act with perfect knowledge of the community or ecosystem they are managing (Kinnear, Summer & Onus 2002). Unfortunately, the time and

resources required to plan and implement randomized and replicated management-scale experiments together with the most cutting-edge approaches for estimating populations are rarely available in these situations (Parkes *et al.* 2006). While such types of studies should remain the ultimate goal of researchers and practitioners, in the absence of these studies, practitioners must act based on available information to prevent further decline of Australia’s biodiversity. In our evidence-based opinion – supported by research done using different experimental designs, sampling protocols, and analytical techniques, and across different ecosystems – there is strong support for the use of dingoes as a management tool to enhance the conservation of native animals.

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Data accessibility

This Forum article does not contain data.

References

- Allen, B.L. & Fleming, P.J.S. (2012) Reintroducing the dingo: the risk of dingo predation to threatened vertebrates of western New South Wales. *Wildlife Research*, **39**, 35–50.
- Allen, B., Fleming, P., Allen, L., Engeman, R., Ballard, G. & Leung, L.K.-P. (2013) As clear as mud: a critical review of evidence for the ecological roles of Australian dingoes. *Biological Conservation*, **159**, 158–174.
- Banks-Leite, C., Pardini, R., Boscolo, D., Cassano, C.R., Püttker, T., Barros, C.S. & Barlow, J. (2014) Assessing the utility of statistical adjustments for imperfect detection in tropical conservation science. *Journal of Applied Ecology*, **51**, 849–859.
- Brawata, R.L. & Neeman, T. (2011) Is water the key? Dingo management, intraguild interactions and predator distribution around water points in arid Australia. *Wildlife Research*, **38**, 426–436.
- Brook, L.A. (2013) *Predator guild interactions in northern Australia: behaviour and ecology of an apex predator, the dingo Canis lupus dingo, and an introduced mesopredator, the feral cat Felis catus*. PhD thesis, James Cook University, Australia.
- Brook, L.A., Johnson, C.N. & Ritchie, E.G. (2012) Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. *Journal of Applied Ecology*, **49**, 1278–1286.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (2001) *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, New York, NY.
- Burbidge, A.A. & McKenzie, N.L. (1989) Patterns in the modern decline of western Australia’s vertebrate fauna: causes and conservation implications. *Biological Conservation*, **50**, 143–198.
- Caughley, G., Grigg, G.C., Caughley, J. & Hill, G.J.E. (1980) Does dingo predation control the densities of kangaroos and emus? *Wildlife Research*, **7**, 1–12.
- Choquenot, D. & Forsyth, D.M. (2013) Exploitation ecosystems and trophic cascades in non-equilibrium systems: pasture – red kangaroo – dingo interactions in arid Australia. *Oikos*, **122**, 1292–1306.
- Claridge, A.W., Cunningham, R.B., Catling, P.C. & Reid, A.M. (2010) Trends in the activity levels of forest-dwelling vertebrate fauna against a background of intensive baiting for foxes. *Forest Ecology and Management*, **260**, 822–832.

- Colman, N.J., Gordon, C.E., Crowther, M.S. & Letnic, M. (2014) Lethal control of an apex predator has unintended cascading effects on forest mammal assemblages. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20133094.
- Dexter, N. & Murray, A. (2009) The impact of fox control on the relative abundance of forest mammals in East Gippsland, Victoria. *Wildlife Research*, **36**, 252–261.
- Edwards, G.P., de Preu, N.D., Shakeshaft, B.J. & Crealy, I.V. (2000) An evaluation of two methods of assessing feral cat and dingo abundance in central Australia. *Wildlife Research*, **27**, 143–149.
- Fleming, P. & Korn, T. (1989) Predation of livestock by wild dogs in eastern New South Wales. *The Rangeland Journal*, **11**, 61–66.
- Forsyth, D.M., Woodford, L., Moloney, P.D., Hampton, J.O., Woolnough, A.P. & Tucker, M. (2014) How does a carnivore guild utilise a substantial but unpredictable anthropogenic food source? Scavenging on hunter-shot ungulate carcasses by wild dogs/dingoes, red foxes and feral cats in south-eastern Australia revealed by camera traps. *PLoS One*, **9**, e97937.
- Foster, C.N., Barton, P.S. & Lindenmayer, D.B. (2014) Effects of large native herbivores on other animals. *Journal of Applied Ecology*, **51**, 929–938.
- Funston, P.J., Frank, L., Stephens, T., Davidson, Z., Loveridge, A., Macdonald, D.M. *et al.* (2010) Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. *Journal of Zoology*, **281**, 56–65.
- Gompper, M.E., Kays, R.W., Ray, J.C., Lapoint, S.D., Bogan, D.A. & Cryan, J.R. (2006) A comparison of noninvasive techniques to survey carnivore communities in Northeastern North America. *Wildlife Society Bulletin*, **34**, 1142–1151.
- Hayward, M.W. & Marlow, N. (2014) Will dingoes really conserve wildlife and can our methods tell? *Journal of Applied Ecology*, **51**, 835–838.
- Houser, A.M., Somers, M.J. & Boast, L.K. (2009) Spoor density as a measure of true density of a known population of free-ranging wild cheetah in Botswana. *Journal of Zoology*, **278**, 108–115.
- Ioannou, C.C., Payne, M. & Krause, J. (2008) Ecological consequences of the bold–shy continuum: the effect of predator boldness on prey risk. *Oecologia*, **157**, 177–182.
- Jhala, Y., Qureshi, Q. & Gopal, R. (2011) Can the abundance of tigers be assessed from their signs? *Journal of Applied Ecology*, **48**, 14–24.
- Johnson, C. & VanDerWal, J. (2009) Evidence that dingoes limit the abundance of a mesopredator in eastern Australian forests. *Journal of Applied Ecology*, **46**, 641–646.
- Kays, R.W., Gompper, M.E. & Ray, J.C. (2008) Landscape ecology of eastern coyotes based on large-scale estimates of abundance. *Ecological Applications*, **18**, 1014–1027.
- Kinney, J., Summer, N.R. & Onus, M.L. (2002) The red fox in Australia – an exotic predator turned biocontrol agent. *Biological Conservation*, **108**, 335–359.
- Kovacs, E.K., Crowther, M.S., Webb, J.K. & Dickman, C.R. (2012) Population and behavioural responses of native prey to alien predation. *Oecologia*, **168**, 947–957.
- Laundré, J.W., Hernández, L. & Altendorf, K.B. (2001) Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, **79**, 1401–1409.
- Letnic, M. & Crowther, M.S. (2013) Patterns in the abundance of kangaroo populations in arid Australia are consistent with the exploitation ecosystems hypothesis. *Oikos*, **122**, 761–769.
- Letnic, M. & Dworjanyan, S.A. (2011) Does a top predator reduce the predatory impact of an invasive mesopredator on an endangered rodent? *Ecography*, **34**, 827–835.
- Letnic, M. & Koch, F. (2010) Are dingoes a trophic regulator in arid Australia? A comparison of mammal communities on either side of the dingo fence. *Austral Ecology*, **35**, 167–175.
- Letnic, M., Ritchie, E.G. & Dickman, C.R. (2012) Top predators as biodiversity regulators: the dingo *Canis lupus dingo* as a case study. *Biological Reviews*, **87**, 390–413.
- Letnic, M., Koch, F., Gordon, C., Crowther, M.S. & Dickman, C.R. (2009) Keystone effects of an alien top-predator stem extinctions of native mammals. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 3249–3256.
- Letnic, M., Greenville, A., Denny, E., Dickman, C.R., Tischler, M., Gordon, C. & Koch, F. (2011) Does a top predator suppress the abundance of an invasive mesopredator at a continental scale? *Global Ecology and Biogeography*, **20**, 343–353.
- Mahon, P.S., Bates, P.B. & Dickman, C.R. (1998) Population indices for wild carnivores: a critical study in sand-dune habitat, south-western Queensland. *Wildlife Research*, **25**, 217.
- Parkes, J.P., Robley, A., Forsyth, D.M. & Choquenot, D. (2006) In my opinion: adaptive management experiments in vertebrate pest control in New Zealand and Australia. *Wildlife Society Bulletin*, **34**, 229–236.
- Pople, A.R., Grigg, G.C., Cairns, S.C., Beard, L.A. & Alexander, P. (2000) Trends in the numbers of red kangaroos and emus on either side of the South Australian dingo fence: evidence for predator regulation? *Wildlife Research*, **27**, 269–276.
- Read, J. & Eldridge, S. (2010) An optimised rapid detection technique for simultaneously monitoring activity of rabbits, cats, foxes and dingoes in the rangelands. *The Rangeland Journal*, **32**, 389–394.
- Ritchie, E.G. & Johnson, C.N. (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, **12**, 982–998.
- Ritchie, E.G., Elmhagen, B., Glen, A.S., Letnic, M., Ludwig, G. & McDonald, R.A. (2012) Ecosystem restoration with teeth: what role for predators? *Trends in Ecology & Evolution*, **27**, 265–271.
- Robley, A., Gormley, A.M., Forsyth, D.M. & Triggs, B. (2014) Long-term and large-scale control of the introduced red fox increases small native mammal occupancy in Australian forests. *Biological Conservation*, **180**, 262–269.
- Sergio, F., Marchesi, L., Pedrini, P. & Penteriani, V. (2007) Coexistence of a generalist owl with its intraguild predator: distance-sensitive or habitat-mediated avoidance? *Animal Behaviour*, **74**, 1607–1616.
- Stander, P.E. (1998) Spoor counts as indices of large carnivore populations: the relationship between spoor frequency, sampling effort and true density. *Journal of Applied Ecology*, **35**, 378–385.
- Van Dyck, S. & Strahan, R. (2008) *The Mammals of Australia*, 3rd edn. Reed New Holland, Chatswood, NSW.
- Wallach, A.D., Johnson, C.N., Ritchie, E.G. & O'Neill, A.J. (2010) Predator control promotes invasive dominated ecological states. *Ecology Letters*, **13**, 1008–1018.
- Wang, Y. & Fisher, D. (2012) Dingoes affect activity of feral cats, but do not exclude them from the habitat of an endangered macropod. *Wildlife Research*, **39**, 611–620.

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