

# Functional responses of an apex predator and a mesopredator to an invading ungulate: Dingoes, red foxes and sambar deer in south-east Australia

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**Abstract** Biological invasions by large herbivores involve the establishment of novel interactions with the receiving mammalian carnivore community, but understanding these interactions is difficult due to the large spatiotemporal scales at which such dynamics would occur. We quantified the functional responses of a native apex predator (the dingo (*Canis familiaris*), which includes wild dogs and their hybrids) and a non-native mesopredator (red fox; *Vulpes vulpes*) to an invading non-native ungulate (sambar deer; *Cervus unicolor*) in Australia. We predicted that the apex predator would exhibit a stronger functional response to increasing sambar deer abundance than the mesopredator. We used a state–space model to link two 30-year time series: (i) sambar deer abundance (hunter catch-per-unit-effort); and (ii) percentages of sambar deer in dingo ( $N = 4531$ ) and fox ( $N = 5002$ ) scats. Sambar deer abundance increased over fourfold during 1984–2013. The percentages of sambar deer in dingo and fox scats increased during this 30-year period, from nil in both species in 1984 to 8.2% in dingoes and 0.5% in foxes in 2013. Dingoes exhibited a much stronger functional response to increasing sambar deer abundance than foxes. The prediction that invading deer would be utilized more by the apex predator than by the mesopredator was therefore supported. The increasing abundance of sambar deer during the period 1984–2013 provided an increasingly important food source for dingoes. In contrast, the smaller red fox utilized sambar deer much less. Our study demonstrates that prey enrichment can be an important consequence of large herbivore invasions and that the effect varies predictably with the trophic position of the mammalian carnivores in the receiving community.

**Key words:** biological invasions, diet, predators, prey enrichment, state–space model.

## INTRODUCTION

Large mammalian herbivores have been widely introduced throughout the world, often establishing new populations (Long 2003) that subsequently increase in abundance (Forsyth & Caley 2006). These invasions can have a wide variety of significant negative impacts on native ecosystems (Wardle *et al.* 2001; Côté *et al.* 2004); one hitherto unexplored consequence is the establishment of novel interactions between the large herbivore and the receiving mammalian carnivore community.

The potential interactions will at least partly depend on the body mass and hunting strategies of

the carnivore relative to the body mass and antipredator behaviours of the large herbivore (Sinclair *et al.* 2003). Ungulates are the primary prey of mammalian apex predators in many parts of the world, and predator density is usually positively related to ungulate biomass (Ripple *et al.* 2014; Hatton *et al.* 2015). Whereas apex predators can kill ungulates, smaller mesopredators often utilize ungulates as carrion (Paquet 1992; Wilmers *et al.* 2003; Prugh *et al.* 2009). The relationship between the consumption of prey by a predator and prey abundance is described by the functional response (Solomon 1949; Holling 1959). In multiprey systems, predators may only eat an invading species when it becomes relatively abundant (i.e. a type III functional response; Pech *et al.* 1992; Messier 1994). Quantifying the functional response is

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critical in understanding predator–prey dynamics, but it is difficult to estimate in apex predator – ungulate prey systems (Marshall & Boutin 1999). More generally, understanding interactions between ungulates and carnivores is difficult due to the large spatial scales utilized by these taxa (Tucker *et al.* 2014) and the long timescales at which dynamics operate (e.g. invading ungulates may take many decades to attain peak abundances; Forsyth & Caley 2006).

The diets of mammalian predators are commonly determined by analysing their scat contents (Klare *et al.* 2011; Newsome *et al.* 2016), and the abundances of ungulates are often indexed using harvest statistics (Van Deelen & Etter 2003; Imperio *et al.* 2010; Iijima *et al.* 2013; Kahlert *et al.* 2015). The functional response could be estimated from temporal changes in the abundance of the ungulate and temporal changes in the frequency of the ungulate in the predator's diet, but to our knowledge, this has not been done. Furthermore, recent advances in computational power mean that uncertainties in both time series (i.e. scat contents and prey abundances) can be properly accounted for in a Bayesian framework using a state–space model (Bolker 2008; Smout *et al.* 2010). In particular, a state–space model enables over-dispersion to be better modelled, potentially important information about the species and their dynamics to be used as informative priors, and properly propagates uncertainty when making predictions.

Many non-native ungulate species have established wild populations in Australia (Forsyth *et al.* 2004), and some have the potential to substantially expand their current geographic ranges (Davis *et al.* 2016). There is particular interest in understanding how invading non-native deer interact with Australia's apex predator, the dingo (*Canis familiaris* (Jackson *et al.* 2017), present for >4000 years; Savolainen *et al.* 2004), and also with a non-native mesopredator, the red fox (*Vulpes vulpes*, present for ~150 years; Saunders *et al.* 1995). Most dingoes are hybrids with wild or domestic dogs (Stephens *et al.* 2015), and their adult body mass (~16 kg; Fleming *et al.* 2001) typically exceeds the threshold of 15 kg that distinguishes apex predators from mesopredators (Prugh *et al.* 2009). Dingoes can hunt cooperatively to kill large prey such as adult male red kangaroos (*Oshphranter rufus*) up to 90 kg (Thomson 1992), whereas the smaller red fox (6 kg; hereafter 'fox') is a solitary hunter (Macdonald 1983; Saunders *et al.* 1995). Large- and medium-sized mammals constitute a greater proportion of the dingo diet than that of the fox diet (Saunders *et al.* 1995; Fleming *et al.* 2001; Davis *et al.* 2015), and it has been hypothesized that the invasion of Australia by deer has increased the food supply for dingoes (i.e. 'prey enrichment'; sensu Roemer *et al.* 2002; Davis *et al.* 2016). Furthermore,

dingoes could also potentially reduce deer abundances through predation, particularly of neonates (i.e. 'biocontrol'; Letnic *et al.* 2012; Dickman *et al.* 2014).

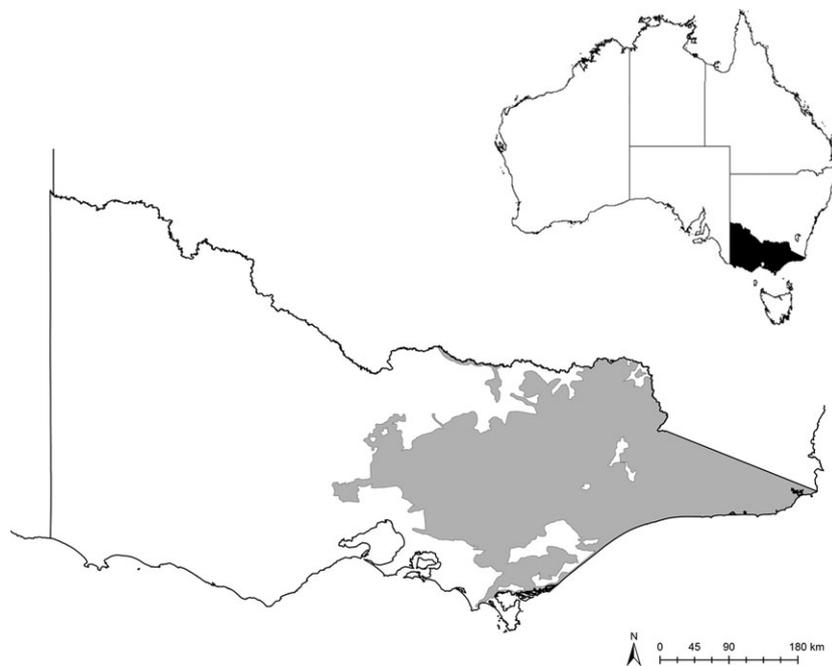
The sambar deer (*Cervus unicolor*) is the largest deer species in Australia (males can weigh up to 250 kg and females up to 150 kg; Bentley 1998). Native to India, Sri Lanka and south-east Asia (Leslie 2011), sambar deer were introduced to south-east Australia during the 1860s and have subsequently colonized large areas in Victoria and New South Wales (Davis *et al.* 2016), where there are concerns about their impacts on plant communities (Forsyth & Davis 2011). In their native range, sambar deer are an important prey of the cooperative hunting dhole (*Cuon alpinus*; 15–17 kg) (Hayward *et al.* 2014), which preferentially kill calves (Venkataraman *et al.* 1995). There is evidence of sambar deer calves being killed by dingoes, but whether dingoes kill healthy adults is unknown (Bentley 1998). However, given that similar-sized canids elsewhere in the world kill large ungulates (e.g. Pierce *et al.* 2000; Hayward *et al.* 2006), it is likely that dingoes can kill adult sambar deer. There are no records of foxes killing sambar. Hunting sambar deer is a popular recreational activity in south-east Australia (Bentley 1998; Moloney & Turnbull 2013), and carcasses do not have to be removed by hunters; hence, recreational hunting can provide food for dingoes and foxes (Forsyth *et al.* 2014).

We predict that because the apex predator (dingo) will kill and scavenge the invading sambar deer, they will exhibit a stronger functional response to an increasing sambar deer population than the mesopredator (fox) that has access to sambar deer only as scavengers. To test this prediction, we use two concurrent 30-year time series: one of sambar deer relative abundance (hunter catch-per-unit-effort) and the other of dingo and fox scat contents. Our state–space model enables a type III functional response to be fitted for dingoes and foxes. Our results show a stronger functional response by dingoes than foxes to the increasing sambar deer population, indicating that large herbivore invasions can enrich the prey of the receiving mammalian carnivore community in a way that varies predictably with the trophic position of the carnivore.

## METHODS

### Study area and species

Our study area was 66 300 km<sup>2</sup> in south-east Australia, spanning latitudes –35.8159 to –38.8547 and longitudes 144.3020–149.9726 (Fig. 1). Dingoes (including wild dogs and their hybrids; Stephens *et al.* 2015) and foxes were present throughout the study area prior to the arrival of sambar deer (Menkhorst 1995; West 2008). The sambar deer population was established from multiple releases



**Fig. 1.** Our study area (shaded grey) within the State of Victoria (shaded black), south-east Australia.

around the city of Melbourne during the period 1863–1873 and has subsequently colonized eastward (Bentley 1998). By 1984, when our study began, sambar deer were common throughout the study area, except in the far east where they were patchily distributed (Slee 1985; Bentley 1998). Within the study area, all three species live in ecosystems ranging from coastal forest to montane forest and alpine heathland (Saunders *et al.* 1995; Bentley 1998; Fleming *et al.* 2001).

## Data sources

### *Sambar deer abundance*

The Australian Deer Association conducted an annual mail survey from 1984 to 1994 of sambar deer hunting effort and harvest by its Victorian members (White *et al.* 1991). Sambar deer hunters must purchase an annual licence from the Victorian State Government (VSG). From 1995 to 2008, the VSG conducted an annual postal survey of a random sample of 1000 licensed deer hunters, quantifying their hunting effort and harvest during the preceding year. From 2009 to 2013, the VSG conducted telephone surveys of a random sample of 200 licensed hunters every 2 months (Moloney & Turnbull 2013). Respondents were asked to report the number of days hunted and the number of sambar deer harvested. The annual sambar deer hunting effort and harvest data collected in these surveys was expressed as the number of sambar deer harvested per hunter day, a catch-per-unit-effort (CPUE) index of abundance. Hunter CPUE indices have been shown to be positively correlated with ungulate density (Van Deelen & Etter 2003; Imperio *et al.* 2010; Iijima *et al.* 2013; Kahlert *et al.* 2015); that is, increasing CPUE indicates increasing deer abundance.

### *Dingo and fox scat contents*

Davis *et al.* (2015) collated the contents of dingo and fox scats collected throughout Victoria. There were 4531 dingo scats and 5002 fox scats collected within our study area during the period 1984–2013. Scats were air-dried or frozen and then stored until they were oven-dried (48 h at 90°C) prior to analysis. Analysts then washed and sieved scat contents to extract indigestible remains for examination. Scat contents were determined using macroscopic and microscopic features of indigestible remains, particularly morphometric features of hair, bones and teeth (Davis *et al.* 2015). The characteristic guard hairs of mammal species were identified based on general appearance, cross-sectional shape and size, relative widths of medulla and cortex, cuticular scale pattern and structure of medulla (Brunner & Wallis 1986). Hairs of closely related mammals can be similar (Brunner & Wallis 1986). Of the mammals present in Victoria, only deer and goats have a distinctive honeycomb lattice medulla pattern and deer hair can be differentiated from that of goats based on their shape in cross section (B. Triggs, pers. comm., 2017). The hairs of some deer species are similar, but sambar deer hair is distinguished primarily by its length (~40 mm longer than that of any other deer species present in Victoria), resulting in an estimated error rate of <15% for identification of sambar deer hair (B. Triggs, pers. comm.).

### **Functional responses of dingoes and foxes to sambar deer abundance**

Sambar deer abundance was modelled using the discrete Ricker form of logistic growth (Ricker 1954):

$$N_{t+1} = N_t e^{r(1-N_t/K)}, \quad (1)$$

where  $N$  is population size,  $r$  is the intrinsic (maximum) exponential growth rate,  $K$  is the carrying capacity, and year is indexed by  $t$ . The Ricker model provides a useful representation of the dynamics of ungulate populations (reviewed in Owen-Smith 2010). The abundances of sambar deer were not directly observed (i.e. sambar deer abundance was a latent variable), but were estimated from the CPUE using a state-space model, an approach that has been widely used for understanding the dynamics of harvested populations (e.g. Schnute 1994; Bolker 2008; Iijima *et al.* 2013). The model was fitted using a Bayesian implementation of the type I autoregressive state-space model, including both process and observation noise (Bolker 2008). The natural logarithm of population size at each time point ( $N_t$ ) was modelled as a discrete time autoregressive model:

$$\log(N_{t+1}) = \log(N_t) + r(1 - N_t/K) + W, \quad (2)$$

where  $W$  is the process noise, distributed normally with variance  $\sigma_W^2$ . This type I autoregressive model has statistical properties identical to the continuous time model evaluated at discrete intervals. The observed CPUE data,  $O_t$ , were modelled as the 'true' state plus observation error:

$$\log(O_t) = \log(N_t) + V. \quad (3)$$

The observation error  $V$  was again normally distributed with variance  $\sigma_V^2$ . Thus, both process noise and observation error in relation to the untransformed population size were distributed log-normally.

The functional response model used  $\mu$  as the rate of deer intake by dingoes or foxes, which is a latent (unobserved) variable. We used a type III functional response (Pech *et al.* 1992) relating intake to deer abundance:

$$\mu = \frac{bN^2}{a^2 + N^2}, \quad (4)$$

where  $b$  is the asymptotic (maximum) intake rate and  $a$  is the population size at which the intake rate reaches half its maximum ( $b/2$ ). Other functional responses could be fitted (e.g. Messier 1994), but these have additional parameters that would be difficult to estimate with the available data (Marshall & Boutin 1999).

If  $p_t$  is the proportion of dingo or fox scats containing deer in year  $t$ , then the binary observation of whether or not a scat contains sambar deer is distributed as Bernoulli ( $p_t$ ):

$$y_i \sim \text{Bern}(p_t). \quad (5)$$

In each year, the number of scats collected is  $S_t$ , so the number containing sambar deer ( $n_t = \sum y_i$ ) will be binomially distributed:

$$n_t \sim \text{Binom}(S_t, p_t). \quad (6)$$

Assuming the rate of sambar deer dietary intake by dingoes is proportional to their rate of encounter (either through predation or scavenging), then we can link the prevalence of sambar deer in dingo and fox scats to  $\mu$  and hence deer abundance:

$$p_t = 1 - e^{-\mu}. \quad (7)$$

The diet data come from multiple studies, introducing extra-binomial variation. We accounted for this variation by including a random effect term implemented on a logit scale. By rearrangement:

$$\text{logit}(p_t) = \log(e^{\mu} - 1) + \tau, \quad (8)$$

where the random effect term is distributed with mean 0 and standard deviation  $\sigma_\tau$ ; that is,  $\tau \sim N(0, \sigma_\tau)$ .

## Model fitting and assessment

The hierarchical model was fitted using OpenBUGS within the R software environment (R Core Team 2014) with the R2OpenBugs R package (Sturtz *et al.* 2005). Convergence of the sampler was assessed visually using Gelman & Rubin's convergence diagnostic ( $R$ ; Gelman & Rubin 1992). Uninformative priors were placed on all parameters except for  $r$  [the intrinsic exponential growth rate of the sambar deer population] (Appendix S1). We used an informative prior for  $r$  (normal with a mean of 0.27 per year and a standard deviation of 0.10) from a published analysis of the dynamics of an increasing sambar deer population in part of the study area during 2007–2011 (Forsyth *et al.* 2012). Three parallel Monte Carlo Markov chains were each run for 30 000 iterations, using diffuse initial values. Convergence was achieved after 10 000 iterations, leaving 20 000 iterations from each chain for inference about the posterior distribution of the parameters.

## Data accessibility

Data associated with this paper have been deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.96c43> (Forsyth *et al.* 2018).

## RESULTS

### Model adequacy

Trace plots for each parameter indicated that the Markov chains were well mixed. All parameters had  $R$  values <1.05, indicating adequate convergence of the chains and reliable samples for posterior inference (Gelman & Rubin 1992).

### Temporal changes in sambar deer abundance

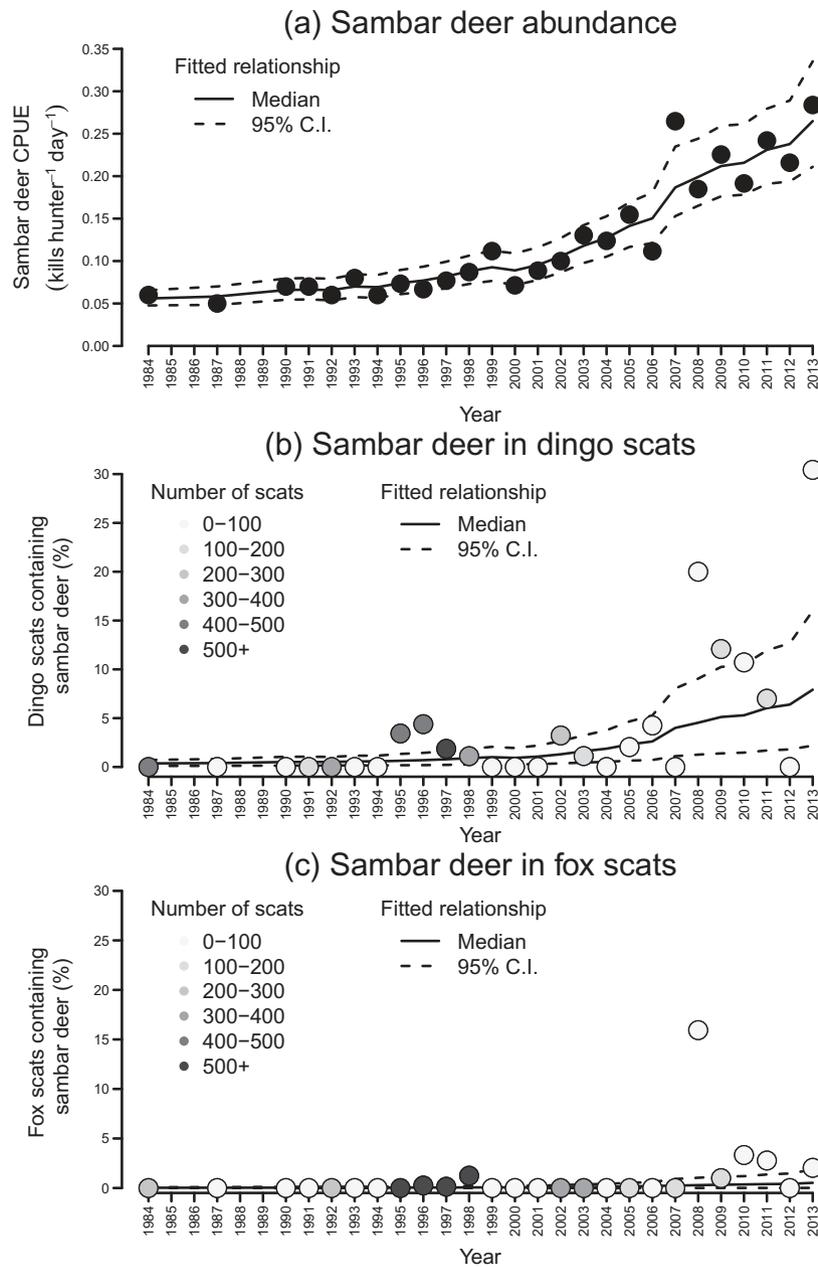
Sambar deer abundance increased during the 30-year study period, from a low of 0.06 (95% credible interval (CI) = 0.05–0.07) sambar deer harvested per hunter day in 1984 to a high of 0.26

(95% CI = 0.21–0.33) in 2013 (Fig. 2a). Abundance increased greatly during the last 8 years of the study (2006–2013). The estimated intrinsic exponential rate of increase ( $r$ ) was 0.047 per year (95% CI = 0.003–0.088 per year; Table 1, Appendix S2, Fig. A1a). There was no evidence that the deer population approached carrying capacity, and there was a uniformly distributed posterior

distribution for this parameter (Appendix S2, Fig. A1b).

**Sambar deer in the diets of dingoes and foxes**

The mean ( $\pm$ SD; range) annual sample sizes of dingo and fox scats were 174 ( $\pm$ 224; 0–1020) and



**Fig. 2.** Changes in sambar deer abundance, and the consumption of sambar deer by dingoes and red foxes, in south-east Australia, 1984–2013. (a) Trajectory for the catch-per-unit-effort (CPUE) sambar deer abundance index. (b) Percentage of dingo scats containing sambar deer. (c) Percentage of fox scats containing sambar deer. All figures show the observed data (circle) and the median (black line) and 95% credible intervals (CIs; dashed line) from the posterior distribution. The 95% CIs for scats relate to the true prevalence and do not include the estimated random effects. For actual scat sample sizes, see Appendix S2, Table A1.

192 ( $\pm 238$ ; 0–787), respectively (Appendix S2, Table A1). Although sample sizes of both dingoes and foxes were large in 1984 ( $\geq 238$ ) and from 1990–1992 ( $\geq 65$ ), the first dingo and fox scats containing sambar deer were recorded in 1995 and 1996, respectively (Fig. 2b,c). Thereafter, the proportion of dingo scats containing sambar deer, although variable, either equalled or greatly exceeded the proportion of fox scats containing sambar deer. Corresponding to the large increase in sambar deer abundance post-2006 (Fig. 2a), the proportions of dingo and fox scats containing sambar deer were highest during the period 2008–2013 (with the exception of 2012, in which only 20 dingo and 73 fox scats were sampled). The modelled estimated percentage of dingo and fox scats containing sambar deer in the last year of the study was 8.2% (95% CI: 2.7–16.4%) and 0.5% (95% CI: 0.01–1.9%), respectively (Fig. 2b,c). The standard deviations for the random effects modelling the extra-binomial variation in the proportion of sambar deer in the diets indicated that there was much greater variation in the proportion of sambar deer in the scats of foxes than in those of dingoes (Table 1; Appendix S2, Fig. A2a,b).

### Functional responses of dingoes and foxes to sambar deer

The parameterization of the functional response of both dingoes and foxes to sambar deer reflects the larger scat sample sizes for both species in periods of low sambar deer abundance (Fig. 3a,b). There was also a strong ridge in the posterior likelihood for the two estimated parameters ( $a$  and  $b$ ) for both dingoes and foxes (Appendix S2, Fig. A3a,b), indicating that these must be considered jointly. Dingoes exhibited a much stronger functional response to increasing sambar deer abundances than foxes, with the proportion of scats containing sambar deer increasing significantly more with increasing sambar deer abundance for dingoes than for foxes (Fig. 3a,b).

There was no evidence that consumption of sambar deer by dingoes was approaching a maximum – that is, reaching satiation (Fig. 3a). However, using combinations of  $a$  and  $b$  from the posterior likelihood, the functional response of dingoes to sambar deer can be extrapolated beyond the maximum sambar deer abundance recorded in our study (0.26 sambar deer per hunter day) (Appendix S2, Fig. A4). This revealed that sambar deer would become the dominant item in dingo scats (i.e.  $>50\%$ ) when the abundance index was 0.80 sambar deer per hunter day (95% CI; 0.55–1.29 sambar deer per hunter day), and that sambar deer would be present in nearly all dingo scats if the sambar deer abundance

index exceeded two sambar deer per hunter day (Appendix S2, Fig. A4).

## DISCUSSION

The abundance of invading non-native sambar deer increased more than fourfold from 1984 to 2013, and there was a concurrent increase in the frequency of sambar deer in dingo and fox scats. As predicted, the apex predator exhibited a much stronger functional response to sambar deer than did the mesopredator. There was, however, no evidence that the maximum intake rate was approached for either carnivore. Our natural experiment indicates that dingoes did not prevent an increase in the abundance of sambar deer; rather, the invasion of sambar deer enriched the food supply of dingoes and, to a much lesser extent, of foxes.

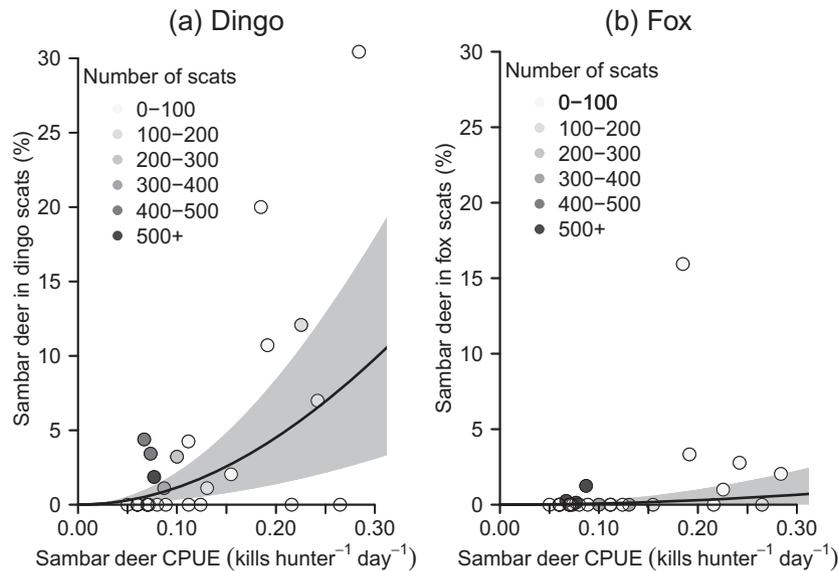
The extent to which dingoes kill rather than scavenge sambar deer is unknown, but our results suggest that dingoes are unable to prevent an increase in the abundance of this large herbivore (i.e. exhibit regulation). Rather, fire and human hunting may be more important determinants of sambar deer abundance. Severe fire kills sambar deer (Forsyth *et al.* 2012), but subsequent vegetation succession is thought to facilitate higher sambar deer abundances (Bentley 1998). Sambar deer hunting is a popular recreational activity in Victoria, with tens of thousands harvested annually within our study area (Moloney & Turnbull 2013). Nevertheless, the fourfold increase in sambar deer abundance and the lack of evidence that the population has approached carrying capacity indicate that neither of these mechanisms prevent growth in sambar deer abundance over the range of densities observed. These factors could, however, eventually limit the densities of sambar deer observed within this study area. Given the large mass of adult sambar deer and the often steep and remote terrain that they inhabit, many hunter-killed carcasses remain *in situ* and hence available to dingoes and foxes to scavenge (Forsyth *et al.* 2014).

One explanation for the substantially lower use of invading sambar deer by foxes than by dingoes is suppression of the mesopredator by the apex predator, either directly by interspecific killing or indirectly by behavioural avoidance (Palomares & Caro 1999; Ritchie & Johnson 2009; Newsome & Ripple 2015). Dingoes can kill foxes (Moseby *et al.* 2012), and there is evidence of foxes avoiding sites used by dingoes in south-east Australia (Mitchell & Banks 2005; Johnson & VanDerWal 2009). Monitoring of hunter-shot sambar deer carcasses with cameras reveals that fox visits are inversely proportional to dingo visits (Forsyth *et al.* 2014). Furthermore, dingoes visit carcasses mostly at dusk and dawn, whereas

**Table 1.** Summary statistics for the posterior distributions of the model parameters

Parameter	Description	Median	SD	Lower 95% CI	Upper 95% CI
$r$	Intrinsic rate of increase in sambar deer population	0.047	0.021	0.003	0.088
$K$	Carrying capacity of sambar deer population	50.2	28.7	2.8	97.5
$\sigma_V$	Standard deviation of observation uncertainty for sambar deer population	0.17	0.03	0.11	0.25
$\sigma_W$	Standard deviation of process uncertainty for sambar deer population	0.11	0.05	0.05	0.23
$a_D$	Type III functional response parameter for dingoes	636.2	258.0	97.0	983.7
$b_D$	Type III functional response parameter for dingoes	22.2	9.8	8.9	45.1
$a_F$	Type III functional response parameter for foxes	626.2	267.1	87.9	986.0
$b_F$	Type III functional response parameter for foxes	100.7	142.5	33.7	615.3
$\sigma_{rD}$	Standard deviation of random effect for sambar deer proportion in dingo diet	1.29	0.49	0.69	2.54
$\sigma_{rF}$	Standard deviation of random effect for sambar deer proportion in fox diet	2.30	1.15	1.15	5.53

CI, credible interval.



**Fig. 3.** Functional responses of (a) dingo and (b) red fox to sambar deer abundance (measured in catch-per-unit-effort (CPUE)). The solid lines are the medians of the modelled relationships, and the shaded regions are the 95% credible intervals for the modelled relationships. For actual scat sample sizes, see Appendix S2, Table A1.

most fox visits are after dusk and before dawn (Forsyth *et al.* 2014). Hence, spatial and temporal patterns of sambar deer carcass use are consistent with the hypothesis that foxes avoid dingoes.

The mean body mass of dingoes is >20% greater in south-east Australia than it was 40 years ago, most likely due to interbreeding with wild or domestic dogs (Claridge *et al.* 2014). Indeed, pure dingoes are now extremely rare in south-east Australia (1% of sampled animals; Stephens *et al.* 2015). A larger body mass would enable dingoes to kill increasingly larger prey, like sambar deer, and to make better use of them as carrion, through stronger bone-crunching

and tearing abilities, and larger bite masses. Additional increases in sambar deer abundance could further advantage larger dingo phenotypes. The hunting behaviours of dingoes are poorly documented (Fleming *et al.* 2001), but the social and morphological similarities of dhole and dingo suggest that the latter could learn to cooperatively hunt to kill adult sambar deer, possibly without the need for larger body mass. Dingoes have been subject to lethal control in large parts of our study area during the period 1984–2013, with pack sizes almost certainly being lower than pack sizes in the absence of control (Fleming *et al.* 2001). A smaller pack size reduces

the ability of dingoes to cooperatively kill large mammals (Dickman *et al.* 2014), and it has been suggested that dingoes could be a more effective predator of invasive ungulates if not controlled (Wallach *et al.* 2010). The tactics used by dingoes to hunt sambar deer, and other non-native ungulates in Australia, deserve study.

Sambar deer abundance will continue to increase in the study area (Fig. 2a). Our functional response model predicts that sambar deer would become the dominant item in dingo scats when sambar deer abundance more than triples beyond the maximum abundance observed in the last year of the study. It is, however, unclear whether sambar deer could increase to such a high abundance in the study area before density dependence (Forsyth & Caley 2006; Bonenfant *et al.* 2009) begins to regulate the population. Also, as noted above, to become a specialist predator of sambar deer, dingoes would likely need to adopt the cooperative hunting tactics used by the similar-sized dhole to kill sambar deer in their native range (Venkataraman *et al.* 1995; Hayward *et al.* 2014).

The largest intrinsic rate of increase ( $r$ ) observed for sambar deer in south-east Australia (Forsyth *et al.* 2012) was used as an informed prior in our population model for this species. The 95% credible interval for our posterior estimate of  $r$  (0.00–0.09) was, however, well below the prior value of 0.27. The prior value was for a population not subject to hunting in a small part (25 km<sup>2</sup>) of our 66 300 km<sup>2</sup> study area and monitored annually for five years. In contrast, much of our larger study area was subject to recreational hunting and severe wildfires during our 30-year study period (Bentley 1998; Forsyth *et al.* 2012). Also, our study area was invaded by sambar deer in a generally eastward direction (Bentley 1998), which would have generated spatiotemporal variation in the irruptive dynamic (Forsyth & Caley 2006) and hence the intrinsic rate of increase.

We assumed that changes in the number of sambar deer harvested per hunter day were proportional to changes in sambar deer abundance (i.e. a type I functional response of hunters to deer). The functional response of hunters to deer could be affected by the conscious and subconscious behaviours of hunters. For example, when deer abundance is low, hunters could exercise restraint to minimize their impact on the population, and when deer abundance is high, hunter harvests could saturate (Kahlert *et al.* 2015). These behaviours could generate type II or III functional responses. There are no suitable data with which to verify the form of the relationship between sambar deer harvested per hunter day and sambar deer abundance in our study area, but analyses of the relationship between hunter CPUE statistics and deer abundances overseas mostly indicate a type I

functional response (Van Deelen & Etter 2003; Imperio *et al.* 2010; Iijima *et al.* 2013; Kahlert *et al.* 2015). The more than fourfold increase in sambar deer harvested per hunter day during 1984–2013 therefore likely reflects a similarly large increase in sambar deer abundance within our study area.

The dingo and fox scat data used to parameterize our model are from an amalgam of studies, and there would have been spatial variation in sambar deer abundance within the study area within any given year. Dingo and fox abundances would also have varied with habitat suitability and local control efforts. A type III model adequately describes the dingo functional response to sambar deer, but there are convergence issues when that model is fitted to the fox data. Other functional response forms could have been fitted to the dingo data, but discriminating between the different shapes of functional responses is problematic if the sample size is limited and the system under investigation is highly variable. For example, Marshal and Boutin's (1999) simulations suggest that sample sizes of >300 are required for distinguishing between type II and type III responses with a power of 0.80. This sample size would be extremely difficult to achieve in a mammalian predator–prey system such as the one we investigated.

There is much interest in understanding and managing the impacts of invading non-native large mammalian herbivores on receiving ecosystems (Côté *et al.* 2004), but the concept of prey enrichment has received little attention. Our results indicate that large herbivore invasions enrich the prey of the receiving mammalian carnivore community in a way that varies predictably with the trophic position of the carnivore, with stronger functional responses seen in apex predators than in mesopredators (*sensu* Prugh *et al.* 2009). The body mass and hunting behaviour of the predator relative to the body mass and antipredator behaviours of the large herbivore will be particularly important for predicting how invading herbivores will interact with the receiving mammalian carnivore community (Mech & Peterson 2003; Sinclair *et al.* 2003).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Appendix S1.** Priors used in our models.

**Appendix S2.** Sample sizes and posterior distributions.