This is a peer reviewed version of the following article: S. Sotorra, D. Blair, W. Blanchard, D. Lindenmayer; Modelling the factors influencing Sambar Deer (*Rusa unicolor*) occurrence in the wet eucalypt forests of south-eastern Australia. *Australian Zoologist* 1 January 2021; 41 (2): 241–253. doi: <u>https://doi.org/10.7882/AZ.2020.040</u>; which has been published in final form at <u>https://doi.org/10.7882/AZ.2020.040</u>

Modelling the factors influencing Sambar Deer (*Rusa unicolor*) occurrence in the wet eucalypt forests of south-eastern Australia

S. Sotorra^{1,2}, D. Blair,^{1,3+}, W. Blanchard¹, and D. Lindenmayer^{1,3}

¹Fenner School of Environment & Society, The Australian National University, Canberra ACT, 2601

²University of Bourgogne Franche-Comté, UMR CNRS 6249 Chrono-Environment 16, route de Gray, F-25030 BESANCON Cedex, France

³National Environment Science Program, Threatened Species Recovery Hub, Fenner School of Environment & Society, The Australian National University, Canberra ACT, 2601.

⁺Deceased

Corresponding author: david.lindenmayer@anu.edu.au

Running Head: Sambar Deer in Victorian ash forests

Abstract

Many invasive species have had negative effects on the Australian environment, including the introduced Sambar Deer (*Rusa unicolor*). However, there is a paucity of information on the factors influencing the fine scale distribution and abundance patterns of Sambar Deer in south-eastern Australia. We present the results of a field survey of Sambar Deer in the Critically Endangered Mountain Ash (*Eucalyptus regnans*) forests of the Central Highlands, Victoria. Our key question was: What factors influence detections of Sambar deer (based on scat counts) within the Mountain Ash forests of the Victorian Central Highlands? We surveyed 86 long-term field sites and detected a total of 245 groups of Sambar Deer pellets on 42% of these sites. Negative binomial regression modelling identified three factors associated with the occurrence of deer pellets. We recorded more pellets: (1) in 30 and 80 year old forest that remained unburned in fires that occurred in 2009, (2) on sites within closed National Parks relative to sites in State Forest, and (3) close to streams.

Key words: introduced herbivore, Mountain ash forest, faecal pellet index

Introduction

The Australian environment and Australian biodiversity have been affected by a wide range of exotic animals (Woinarski et al. 2015). These include large introduced herbivores (Braysher 2017; West 2018) such as horses (*Equus caballus*) (Cherubin et al. 2019; Driscoll et al. 2019), camels (*Camelus dromedaries*) (Hart and Edwards 2016), goats (*Capra hircus*) (Masters et al. 2018), and buffalo (*Bubalus bubalis*). Six species of deer also have become established in Australia (Braysher 2017).

Relatively little is known about the factors influencing the abundance and impacts of exotic deer in many parts of south-eastern Australia (Potts et al. 2015; Davis et al. 2016). This includes the Sambar Deer (*Rusa unicolor*) which is considered to be among the most successful invasive mammals worldwide (Davis et al. 2016). However, there is some evidence that the range of Sambar Deer is expanding and its abundance is increasing in south-eastern Australia (Moriarty 2004; Peel et al. 2005; Gormley et al. 2011). Indeed, Sambar Deer is present in a wide range of environments and predictions from modelling suggest the Sambar Deer could occupy nearly half of the Australian continent (Davis et al. 2016). Therefore, a better understanding of the factors influencing the occurrence of the species is critical, especially for developing effective and targeted management actions (Braysher 2017).

Here we report the results of a stratified field survey of Sambar Deer occurrence in the Mountain Ash (*Eucalyptus regnans*) forests of the Central Highlands of Victoria. Sambar Deer is the only deer species in our study area (DELWP 2019) and has been known to occur in the region for several decades (Houston 2003; Bennett 2008; Di Stefano et al. 2009). The overarching question which motivated our study was: What factors influence detections of

Sambar Deer (based on scats) within the Mountain Ash forests of the Victorian Central Highlands? As part of addressing this question, we tested four predictions.

Prediction 1. Forest age effects. We predicted that detections of the Sambar Deer would be greatest in older forest as such stands generally have an open structure (Ashton 1981; Aulak and Babinska-Werka 1990), facilitating movement and access to food resources. Work on Roe Deer (*Capreolus capreolus*) in Poland suggested that animals were more likely to be recorded in open, old growth forests. An alternative prediction was that detections of animals would be higher in young forest. This is because such areas which support dense vegetation cover which both provides shelter from human disturbances such as hunting and abundant young palatable foliage for browsing at accessible height (see Bennett and Gumal 2001; Bowman et al. 2010).

Prediction 2. <u>Land tenure effects</u>. We predicted there would more detections of Sambar Deer in closed water catchments and National Parks where no hunting occurs and there is limited human access. An alternative prediction was there would be more detections in wood production forests where timber harvesting has fragmented the forest including a more extensive road network for movement and landscapes have more edges which may provide suitable combinations of cover and foraging habitat. Studies in the USA have shown that the occurrence of White-tailed Deer is strongly associated with edges (Williamson and Hirth 1985; Shen et al. 2016).

Prediction 3. <u>Slope effects</u>. We predicted there would be more detections of Sambar Deer on flatter sites. This was because of the energetic costs for animal movement on steep slopes (Taylor et al. 1972). Studies of Mule deer (*Odocoileus hemionus*) have found that steepness

affects movement and habitat selection (Parker et al. 1984; Lendrum et al. 2012). However, a recent study in Victoria found no effect of slope on the occurrence of Sambar Deer (Gormley et al. 2011).

Prediction 4. <u>Distance to water effects</u>. We predicted Sambar Deer detections would be greatest on sites close to streams because of generally higher biomass (and therefore more food resources) in such places. An alternative prediction was that the Sambar Deer would avoid streamside areas because the rainforest vegetation that characterizes these areas (Lindenmayer et al. 2015) may support largely unpalatable plant species (e.g. Tree ferns, *Dicksonia antarctica* and *Cyathea australis*). Studies of other deer species have found that proximity to water has important effects on occurrence, such as investigations of Mule Deer (*Odocoileus hemionus*) and White-tailed Deer (*Odocoileus virginianus*) in Texas, USA (Brunjes et al. 2006) and Red Deer (*Cervus elaphus*) in China (Liu et al. 2004).

An understanding of the key factors influencing the distribution and abundance of a species is a fundamental part of ecology (Elton 1927; Krebs 2009) and crucial for the effective control of invasive species (Braysher 2017). In the case of deer, studies from places where particular species are native have shown that large populations can: (1) have significant negative effects on vegetation cover and plant species composition (Tanentzap et al. 2011; Gerhardt et al. 2013), (2) lead to economic losses in agricultural crops and forest plantations (Corgatelli et al. 2019) and, (3) become vectors of disease that can be transmitted to livestock (Hars et al. 2006). In Australia, there have been concerns about contamination of drinking water by pathogens in the pellets left by the Sambar Deer, including in the Upper Yarra Catchment which is located in the Central Highlands of Victoria and is a key part of the water supply system for the city of Melbourne (Bennett 2008).

Background: The biology of Sambar Deer

The Sambar Deer was introduced to Australia in the 1860s from the Philippines and Sri Lanka (Bentley 1998) for recreational hunting. The species is essentially a non-social animal (Bentley 1998) and a browser or mixed feeder (Burke 1982; Davis et al. 2016). Sambar Deer is the largest deer species in Australia and adults weigh 100-340 kg and are up to 1.3m at shoulder height (Bentley 2008). Adult Sambar Deer have no native predators in Victoria, although young animals may be prey for dingoes and wild dogs (Forsyth et al. 2018). Human hunting and systematic culling is the primary control mechanism for adult animals.

Protection and hunting status

In the countries where Sambar Deer is native, the species is listed as Vulnerable (VU) by the IUCN (Timmins et al. 2015). It is considered to be a pest in Australia (Invasive Plants and Animals Committee 2016). Management of Sambar Deer within Australia varies between jurisdictions with varying legislation across different states. In Victoria, three main regulations apply. The *Wildlife Act (1975)* gives protected status to all deer as wildlife. Since 2008, the *Flora and Fauna Guarantee Act (1988)* has listed Sambar Deer as a 'potentially threatening process' to the biodiversity of native vegetation in Victoria, mainly due to rubbing on trees, browsing on threatened shrub species, and dispersal of weeds (DELWP 2016). Victoria's *Wildlife (Game) Regulations (2012)* declared Sambar Deer to be a game species, allowing it to be hunted year round and with unlimited bag limits in specific areas. Recreational hunting is prohibited in protected areas such as the closed water catchments of the Yarra Ranges National Park. Individual deer that damage public land can be destroyed under an 'Authority to Control Wildlife' permit. Individual animals causing damage on private property can be destroyed without a permit (under specific conditions). Recreational

hunting of Sambar Deer has increased dramatically in Victoria (Moloney and Turnbull 2013). In 2009-2010, 32,280 Sambar Deer were shot. This increased to 84,840 animals in 2016-2017.

Methods

Study area

We conducted this study in the Mountain Ash forests of the Central Highlands of Victoria, in south-eastern Australia (Figure 1). Mountain Ash forest covers approximately 162,000 ha in our study region (Lindenmayer et al. 2013) and occurs in areas between 500m and 1100m in elevation. Mountain Ash forests are dominated by tall eucalypt overstorey trees, scattered midstorey trees, shrubs, a large range of ferns, a moist ground layer and fertile loamy soils (Costermans 2009; Blair et al. 2016). The Mountain Ash ecosystem is classified as Critically Endangered under the IUCN Red List Ecosystem criterion (Burns et al. 2015).

The climate of the Central Highlands region is classified as temperate with generally mild summers with periodic high temperatures and extreme fire weather. The main form of natural disturbance in the study area is wildfire and the primary kind of human disturbance is clearfell logging (Lindenmayer et al. 2013). Wildfires can burn at high severity and intensity and historically have burnt large areas of the Central Highlands region. In 1939, approximately 79% of the Mountain Ash forest in the Central Highlands of Victoria was burnt (Gill 1981). In 2009, approximately 50% of the forest was burnt (Lindenmayer et al. 2019).

We surveyed sites within the Maroondah and O'Shannassy water catchments which are part of the Yarra Ranges National Park. These water catchments supply drinking water to

Melbourne and environs (Viggers et al. 2013) and are closed to the public and to timber harvesting. Amateur hunting does not occur within the closed catchments and professional culling of deer populations has not been conducted within them for more than ten years (Mario Malovic, Melbourne Water, pers. comm., 2019). We also surveyed sites in the Toolangi, Marysville and Powelltown State Forests where hunting is permitted and human access for logging, walking and other activities is allowed.

Survey design

To estimate the occurrence of Sambar Deer, we assessed animal presence using the detection of pellets. Our field method was adapted from the Faecal Pellet Index (FPI) (Forsyth 2005) and is used by Parks Victoria (Parks Victoria 2005). The Faecal Pellet Index approach has been shown to be strongly positively and linearly correlated with deer density (Forsyth 2005). Deer pellet counts are frequently used as an index of deer abundance in many other parts of the world, including Europe, North America and New Zealand (Rowland et al. 1984; Forsyth et al. 2010; Torres et al. 2015). This is a non-intrusive, repeatable method and does not modify the ecological properties of sites.

We surveyed 86 field sites between March and May 2019 (Figure 1). Each site measured 100m x 100m in size with a central transect running perpendicular to the front edge of the site (Figure 2).

We selected field sites with a dominant Mountain Ash overstorey and stratified by latitude, longitude, forest age, slope, aspect, logging history, land tenure, and distance to a stream. There were two main categories of sites; long-term forested areas (n=71 sites) and logged sites which were harvested approximately ten years ago (n=15). We assigned sites to one of

six stand age classes. We categorized logged sites by one of four types of logging and management (Table 1).

Our surveys of Sambar Deer pellets on each site consisted of 22 plots (2m radius, 12.56m²) along a central 100m transect. To account for edge effects, we ensured that any given plot was 10m from a road. All plots were at least 4m apart, alternating to the left and right side of a transect, at random distance of 0 to 10m perpendicular to the central transect (Figure 2).

Within each plot, we pushed aside the vegetation (including fern fronds and small branches) to ensure that the entire plot surface could be searched, but without disturbing the litter layer. We recorded Sambar Deer pellets (groups and individual pellets) as being either intact or decayed. An intact pellet was defined as having no recognizable loss of material, regardless of whether the pellet was cracked, partly broken or deformed. The presence of moss or fungus did not affect whether a pellet was considered to be intact or otherwise. We defined a pellet group as intact pellets voided in the same defecation event, and was determined by appearance (i.e., size, shape, and colour) (Baddeley 1985).

Sambar Deer pellets are readily distinguishable from the scats of other mammals occurring in Mountain Ash forests. They are pointed at one end and measure ~ 20 mm in length and 10 mm in width. The scats mostly occur in piles of 10 to 70 pellets.

Measurement of site attributes and covariates

We measured or estimated values for a set of covariates at each site and then used them in the modelling of factors influencing the prevalence of Sambar Deer scats.

Land tenure included sites in either State Forest (SF) managed by the Department of Environment, Land, Water and Planning, or closed catchment areas within the Yarra Ranges National Park (NP), managed jointly by Melbourne Water and Parks Victoria. All sites were on public land. A total of 48 sites were in State Forest and 38 sites were in National Parks and closed water catchments.

Fire severity on the low severity burned sites ('1939 LS') was assessed in the field through direct observation and measurements in the months following the 2009 wildfires. On these sites, the overstorey eucalypt trees remained green while the understorey was scorched or consumed. Unlogged sites had not been disturbed by timber harvesting since the last wildfire.

Logged sites were clearfell harvested followed by a regeneration burn and aerial seeding (of the overstorey eucalypt species) in 2009 or 2010. These sites were not burned by the 2009 wildfires (i.e. they were not salvage logged).

Stand age class corresponded to regeneration events following major wildfires in 2009, 1983, 1939 and before 1900 (old growth). Mountain Ash is an obligate seeder, so forms uniform age cohorts following high severity wildfire. In this way, at the time of the study, the overstorey eucalypts were 10, 46, 80 and 120+ years old, respectively. Sites were selected for having a uniform aged overstorey across the site.

Slope was the slope angle measures in degrees from the midpoint of the transect on a field site. Values for slope varies from zero to 26 degrees.

Distance to the nearest stream was determined using GIS measurements based on GPS locations of the sites. The distance between the start of a site (0m) and nearest major stream as determined using the software Quantum GIS v.3.14, based on the GPS coordinates of the sites surveyed and a vector layer of the streams provided by the Victorian Government. Values for distance to a stream ranged from 45 to 2245 m.

Statistical analysis

We used Bayesian zero-inflated negative binomial regression modelling (Welsh et al. 1996; McCarthy 2007) to quantify the factors influencing the number of Sambar Deer pellet groups observed on each site. We used zero inflated modelling to account for the fact that 53 of 86 field sites did not contain any deer pellets and a negative binomial distribution was used to account for over dispersion relative to the Poisson distribution.

We constructed statistical models with the following covariates: stand age class (see Table 1), land tenure, distance to stream, slope, easting and northing for each site. We considered only linear effects of the continuous variables, as preliminary investigations showed no evidence of non-linear effects. Our full model is given by:

 $LP_i = \text{EastingS}_i + \text{NorthingS}_i + \text{DistanceToStreamS}_i + \text{SlopeS}_i + \text{LandTenure}_i$

+ AgeClass_i

where, LP_i , is the linear predictor for the ith site, we used the log-link function to link the linear predictor to the mean of the zero-inflated negative binomial distribution (McCulloch and Searle 2001).

We employed the leave one out cross validation information criteria (LOOIC (Vehtari et al. 2017) to select the best fitting model from the 64 candidate models (Appendix 1). We

constructed models using the *brms* package in R 3.5.1 (Bürkner 2017). We used default priors in brms, which place an improper flat prior on the regression coefficients, a gamma (0.01, 0.01) prior to the negative binomial shape parameter and a beta (1,1) prior to the zero inflation parameter. We ran four chains for 2000 iterations discarding a burn of 1000, which yielded 4000 samples for posterior inference. We assessed convergence of the Markov Chains via the Gelman and Rubin \hat{R} statistic (Gelman and Rubin 1992) which was less than 1.01 for all parameters, indicating adequate convergence.

Results

Detections of Sambar Deer

We surveyed a total of 86 sites, comprising a total of 1892 (2m-radius) plots. This corresponded to a total of 23 777.6m² of forest that we surveyed. We detected Sambar Deer pellets on 41% of our sites (Table 2).

Most of the decayed pellets that we identified were part of groups of intact pellets. The analysis of resulting data was completed using the sum of all groups without any differentiation between intact and decayed pellets. The average group size was 35.8 pellets/group. This gave an estimate of 3.2 pellets/plot or 0.3 pellet/m². We based our statistical analyses on the number of groups (n=245) and not counts of individual pellets.

Model of the factors influencing the occurrence of Sambar Deer pellets

We fitted a negative binomial model to accommodate over-dispersion in the data (due to the high number of zeros associated with the absence of Sambar Deer pellets on any plot within a site). The best fitting model for the prevalence of Sambar Deer pellets included three key covariates (Table 3): (1) an age class effect with fewer pellets recorded on unburned 1939

aged forest and 1983 aged forest (Figure 3a), (2) an effect of land tenure with more pellets detected in closed catchments and the Yarra Ranges National Park relative to State Forest (Figure 3b) and, (3) a negative effect of distance to water (stream), more pellets are found closer to the water (Figure 3c).

Discussion

We sought to quantify the factors influencing the occurrence of Sambar Deer pellets, which are a surrogate of the occurrence of the species (Forsyth 2005), in the Mountain Ash forests of the Central Highlands of Victoria. We found three key factors were associated with the prevalence of pellets; land tenure, distance to stream, and the age of the forest. We discuss the possible reasons why these factors were important in further detail in the remainder of this section and conclude with some commentary on the limitations of this study.

Forest age class effects

We found a complex relationship between the occurrence of Sambar Deer pellets and the age of Mountain Ash forest (Table 3 and Figure 3a). Stand age influences the structure of Mountain Ash forests (Lindenmayer et al. 2000) and this may lead to spatial variation in access to food and/or ease of movement by the Sambar Deer. For example, the size and the density of trees, disturbance history and the diversity of the ground understorey varies among different forest age classes (Blair et al. 2016). Greater detection of animals (as reflected in greater pellet counts) in young forests and forests regenerating after the 1939 fires and burned at low severity in 2009 may be explained by the abundance, accessibility and diversity of food resources in these areas. Given that sites logged in 2009 have lower plant species richness relative to forest burned in 2009 at either low or high severity (Blair et al. 2016), if diversity of food resources alone were a significant determinant of Sambar Deer presence, we

would expect logged sites to have fewer deer pellets than either of the 2009 burned forest categories. This was not the case. Fire and logging regeneration also create very dense stands of young eucalypts and *Acacia* spp. trees that may provide shelter and protection for Sambar Deer. Such patterns were not replicated in sites burned at low severity in 2009 where the unburned overstorey prevented a dense cohort of eucalypts and *Acacia* from developing. With greatest pellet numbers in the 2009UB sites, followed by logged sites and 1939LS sites, it appears that a combination of vegetation density and plant diversity may influence the presence of Sambar Deer in Mountain Ash forests. In addition, high severity fire and logging may have direct negative effects on Sambar Deer populations, although the species has been found to recolonize burnt areas within 16–24 months of a fire (Forsyth et al. 2012).

Old growth (OGUB – see definition in Table 1) sites were characterized by moderate levels of deer presence (Fig. 3a) with pellet counts greater than 1983UB and 1939UB sites, but less than recently disturbed sites. This is likely due to both the presence of an open overstorey and land tenure effects. The open overstorey typical of old growth sites is typically associated with greater understorey and midstorey tree diversity than 1983UB and 1939UB sites (Blair et al. 2016). This may provide protective cover for Sambar Deer, in a similar way to the densely stocked eucalypts and *Acacia* spp. trees in young forests. As nearly all old growth stands are in National Parks and closed water catchments, deer presence is likely to be a combined effect of forest structure and the effects of land tenure (which are discussed in the next section).

Land tenure effects

We recorded more Sambar Deer pellets on sites located within the Yarra Ranges National Park and in the closed water catchments (where public access is precluded) (Figure 3b) and there has been no professional culling for at least 10 years. Sambar Deer is considered to be a "shy" species (Harris 1966) and it is likely there were fewer detections in State Forest because of human activities like hunting and logging.

Distance to stream effects

We uncovered evidence of a distance to stream effects with more Sambar Deer pellets recorded on sites close to water (Table 3 and Figure 3c). Sambar Deer are dependent on access to water (McKay and Eisenberg 1974; Dinerstein 1979). Earlier studies in the Upper Yarra Catchment also found that proximity to water was an important factor influencing the occurrence of Sambar Deer, with animals most often detected < 500 metres from water (Forsyth et al. 2009), possibly because of the need to access free-standing water (Simcharoen et al. 2014). Studies of other deer species have found that proximity to water is important, such as those of the Mule Deer (*Odocoileus hemionus*) and White-tailed Deer (*Odocoileus virginianus*) in Texas, USA (Brunjes et al. 2006) and Red Deer (*Cervus elaphus*) in China (Liu et al. 2004).

Limitations of the study

We are aware that our study had several limitations. First, our surveys were based on the detection of pellets and not directly of animals. This may create biases in terms of where pellets are most readily detected. For example, foraging activities by the Superb Lyrebird (*Menura novaehollandiae*) may have influenced detections of Sambar Deer pellets. The Superb Lyrebird is a large ground-foraging species that can perturb up to 200 tonnes of litter annually (Ashton and Bassett 1997). By turning over litter, the Superb Lyrebird may cover deer pellets at a faster rate than if the litter remains undisturbed. This may lead to an underestimate of Sambar Deer presence. Although the Superb Lyrebird is widespread, it does

not occur everywhere in Mountain Ash forests and its impact on detections of Sambar Deer pellets may vary between sites. Bird surveys (conducted in 2016/2017) on the same sites we completed surveys of Sambar Deer pellets produced 219 observations of the Superb Lyrebird (Lindenmayer et al. unpublished data) on 42 of the 71 sites that we sampled (although no logged sites had evidence of disturbance of the litter layer by the Superb Lyrebird).

A key knowledge gap concerns the rate of decay rate of Sambar Deer pellets in Mountain Ash forests. The rate of decay has been estimated to be 226 days (Houston 2003) in flat areas (an open grassy area in the Upper Yarra catchment). Despite that area being close to some of our survey sites, vegetation and soil characteristics vary spatially and this also may affect rates of decomposition. Rainfall is another factor that may affect the longevity of pellets, as shown in a study in the lowland bamboo forest of Thailand, where 67% of pellet groups were identifiable after 270 days during the dry season, while only 30% of pellet groups were identifiable during the wet season (Wiles 1980). We completed all surveys during the same season (March to May 2019) to minimize the impacts of season. However, the rate at which faecal pellets decay also can vary depending on weather, soils, and vegetation types (Van Etten and Bennett 1965). Finally, we did not attempt to quantify diet and foliage preferences in the Sambar Deer and studies would require different approaches than employed here such as the establishment of exclusion plots (e.g. see Bennett and Coulson 2008; Mulvaney et al. 2017).

Conclusions

We found that three factors influenced the occurrence of the Sambar Deer in the Mountain Ash forests of the Central Highlands of Victoria. Stand age can influence the structure of the forest and this may, in turn, lead to spatial variation in variety of, and access to, food, ease of movement, and the ability to hide. There was a marked land tenure effect with the occurrence of Sambar Deer being higher in the Yarra Ranges National Park and closed water catchments than in State Forests. Greater human access including hunting in State Forests may account for this result. The third key factor associated with the prevalence of Sambar Deer pellets was the distance to nearest streams, where animals can access water.

Acknowledgements

We thank Professor Patrick Giraudoux, Lachlan McBurney, and the National Environmental Science Program (Threatened Species Recovery Hub) for indirect support that enabled this study to be completed. We benefited greatly from input from other scientists including Elle Bowd and Dr Amy Bennett. Tabitha Boyer and Claire Shepherd provided editorial assistance on this manuscript. The long-term sites which were part of the surveys for this study have been maintained through the support of the Victorian Government (Parks Victoria and Department of Environment, Land, Water and Planning). Comments by two anonymous referees and Dr Dan Lunney greatly improved an earlier version of this paper. We dedicate this paper to the memory of Dr David Blair who died in tragic circumstances not long after this study was completed.

References

Ashton, D. H., 1981. Fire in tall open forests (wet sclerophyll forests). Pp. 339-366 *in* Fire and the Australian Biota ed by A. M. Gill, R. H. Groves and I. R. Noble. Australian Academy of Science, Canberra.

Ashton, D. H. and Bassett, O. D., 1997. The effects of foraging by the Superb Lyrebird (*Menura novaehollandiae*) in Eucalyptus regnans forests at Beenak, Victoria. *Australian Journal of Ecology* 22: 383-394.

Aulak, W. and Babinska-Werka, J., 1990. Preference of different habitats and age classes of forest by roe deer. *Acta Theriologica* **35**: 289-298.

Baddeley, C. J., 1985. *Assessments of Wild Animal Abundance*. Protection Forestry Division, Forest Research Institute, Christchurch, New Zealand.

Bennett, A., 2008. The impacts of sambar (Cervus unicolor) in the Yarra Ranges National Park. PhD Thesis. Department of Zoology, University of Melbourne.

Bennett, A. and Coulson, G., 2008. Evaluation of an exclusion plot design for determining the impacts of native and exotic herbivores on forest understoreys. *Australian Mammalogy*30: 83-87. http://dx.doi.org/10.1071/AM08010

Bennett, E. L. and Gumal, M. T., 2001. The interrelationships of commercial logging hunting and wildlife in Sarawak: Recommendations for forest management. Pp. 359-374 *in* The Cutting Edge: Conserving Wildlife in Logged Tropical Forests ed by R. A. Fimbel, A. Grajal and J. G. Robinson. Columbia University Press, New York, USA.

Bentley, A., 1998. An Introduction to the Deer of Australia: with special reference to *Victoria*. Australian Deer Research Foundation, Croydon, Victoria.

Bentley, A., 2008. Sambar deer. Pp. 505-506 *in* The Mammals of Australia (Third Edition) ed by S. Van Dyck and R. Strahan. New Holland Publishers, Sydney.

Blair, D., McBurney, L., W., B., Banks, S. and Lindenmayer, D. B., 2016. Disturbance gradient shows logging affects plant functional groups more than fire. *Ecological Applications* 26: 2280-2301. http://dx.doi.org/10.1002/eap.1369

Bowman, J., Ray, J., Magoun, A., Johnson, D. and Dawson, N., 2010. Roads, logging, and the large-mammal community of an eastern Canadian boreal forest. *Canadian Journal of*

Zoology 88: 454-467. http://dx.doi.org/10.1139/z10-019

Braysher, M., 2017. *Managing Australia's Pest Animals. A Guide to Strategic Planning and Effective Management.* CSIRO Publishing, Melbourne.

Brunjes, K. J., Ballard, W. B., Humphrey, M. H., Harwell, F., McIntyre, N. E.,

Krausman, P. R. and Wallace, M. C., 2006. Habitat use by sympatric Mule and White-

Tailed Deer in Texas. The Journal of Wildlife Management 70: 1351-1359.

http://dx.doi.org/10.2193/0022-541X(2006)70%5B1351:HUBSMA%5D2.0.CO;2

Burke, P., 1982. Food plants utilised by sambar deer. Australian Deer 7: 7-12.

Bürkner, P.-C., 2017. brms: An R Package for Bayesian Multilevel Models Using Stan.

Journal of Statistical Software 80: 1-28. http://dx.doi.org/10.18637/jss.v080.i01

Burns, E. L., Lindenmayer, D. B., Stein, J., Blanchard, W., McBurney, L., Blair, D. and

Banks, S. C., 2015. Ecosystem assessment of mountain ash forest in the Central Highlands of Victoria, south-eastern Australia. *Austral Ecology* **40:** 386-399.

http://dx.doi.org/10.1111/aec.12200

Cherubin, R. C., Venn, S. E., Driscoll, D. A., Doherty, T. S. and Ritchie, E. G., 2019. Feral horse impacts on threatened plants and animals in sub-alpine and montane environments in Victoria, Australia. *Ecological Management & Restoration* 20: 47-56. http://dx.doi.org/10.1111/emr.12352 Corgatelli, G., Mattiello, S., Colombini, S. and Crovetto, G. M., 2019. Impact of red deer (*Cervus elaphus*) on forage crops in a protected area. *Agricultural Systems* 169: 41-48. http://dx.doi.org/10.1016/j.agsy.2018.11.009

Costermans, L., 2009. *Native Trees and Shrubs of South-eastern Australia: Covering Areas of New South Wales, Victoria and South Australia.* CSIRO, Australia.

Davis, N., Bennett, A., Forsyth, D., Bowman, D., Lefroy, E., W. Wood, S., Woolnough, A., West, P., Hampton, J. and N. Johnson, C., 2016. A systematic review of the impacts and management of introduced deer (family Cervidae) in Australia. *Wildlife Research* 43: 515. http://dx.doi.org/10.1071/WR16148

DELWP. 2016. Flora and Fauna Guarantee Act 1988 Process List, December 2016.

Victorian Government Department of Environment, Land, Water and Planning, Melbourne.

DELWP, 2019. Victorian Biodiversity Atlas. Victorian Government Department of

Environment, Land, Water and Planning.

https://www.environment.vic.gov.au/biodiversity/victorian-biodiversity-atlas. 13 May 2019.

Di Stefano, J., Butler, K., Sebire, I. and Fagg, P., 2009. Mammalian browsing impact on regenerating Eucalyptus seedlings in a large commercially managed native forest estate. *New Forests* **37:** 197-211. http://dx.doi.org/10.1007/s11056-008-9117-4

Dinerstein, E., 1979. An ecological survey of the Royal Karnali-Bardia Wildlife Reserve, Nepal. Part II: Habitat/animal interactions. *Biological Conservation* **16:** 265-300. http://dx.doi.org/10.1016/0006-3207(79)90055-7

Driscoll, D. A., Worboys, G. L., Allan, H., Banks, S. C., Beeton, N. J., Cherubin, R. C., et al., 2019. Impacts of feral horses in the Australian Alps and evidence-based solutions. *Ecological Management & Restoration* 20: 63-72. http://dx.doi.org/10.1111/emr.12357

Elton, C. S., 1927. Animal Ecology. Sidgwick and Jackson, London.

Forsyth, D., J. Barker, R., Morriss, G. and P. Scroggie, M., 2010. Modeling the

relationship between fecal pellet indices and deer density. The Journal of Wildlife

Management 71: 964-970. http://dx.doi.org/10.2193/2005-695

Forsyth, D. M. 2005. *Protocol for estimating changes in the relative abundance of deer in New Zealand forests using the Faecal Pellet Index (FPI).* Landcare Research Contract Report No LC0506/027. Department of Conservation, Wellington, New Zealand.

Forsyth, D. M., McLeod, S. R., Scroggie, M. P. and White, M. D., 2009. Modelling the abundance of wildlife using field surveys and GIS: non-native sambar deer (Cervus unicolor) in the Yarra Ranges, south-eastern Australia. *Wildlife Research* **36**: 231-241.

http://dx.doi.org/10.1071/WR08075

Forsyth, D. M., Gormley, A. M., Woodford, L. and Fitzgerald, T., 2012. Effects of largescale high-severity fire on occupancy and abundances of an invasive large mammal in southeastern Australia. *Wildlife Research* **39:** 555-564. http://dx.doi.org/10.1071/WR12033

Forsyth, D. M., Caley, P., Davis, N. E., Latham, A. D. M., Woolnough, A. P., Woodford,

L. P., Stamation, K. A., Moloney, P. D. and Pascoe, C., 2018. Functional responses of an apex predator and a mesopredator to an invading ungulate: dingoes, red foxes and sambar deer in south-east Australia. *Austral Ecology* **43**: 375-384.

http://dx.doi.org/10.1111/aec.12575

Gelman, A. and Rubin, D. B., 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 7: 457-472. http://dx.doi.org/10.1214/ss/1177011136

Gerhardt, P., Arnold, J. M., Hackländer, K. and Hochbichler, E., 2013. Determinants of deer impact in European forests – A systematic literature analysis. *Forest Ecology and Management* 310: 173-186. http://dx.doi.org/10.1016/j.foreco.2013.08.030

Gill, A. M., 1981. Post settlement fire history in Victorian landscapes. Pp. 77-106 *in* Fire and the Australian Biota ed by A. M. Gill, R. H. Groves and I. R. Noble. Australian Academy of Sciences, Canberra.

Gormley, A. M., Forsyth, D. M., Griffioen, P., Lindeman, M., Ramsey, D. S. L.,

Scroggie, M. P. and Woodford, L., 2011. Using presence-only and presence-absence data to estimate the current and potential distributions of established invasive species. *Journal of Applied Ecology* 48: 25-34. http://dx.doi.org/10.1111/j.1365-2664.2010.01911.x

Harris, L. H., 1966. *Hunting Sambar Deer*. New Zealand Forest Service, Wellington, New Zealand.

Hars, J., Boschiroli, M.-L., Duvauchelle, A. and Garin-Bastuji, B., 2006. La tuberculose à Mycobacterium bovis chez le cerf et le sanglier en France. Émergence et risque pour l'élevage bovin. *Bulletin de l'Académie vétérinaire de France* 159: 393-401.

10.4267/2042/58198

Hart, Q. and Edwards, G., 2016. Outcomes of the Australian feral camel management project and the future of feral camel management in Australia. *The Rangeland Journal* 38: 201-206. http://dx.doi.org/10.1071/RJ15087

Houston, E., 2003. *The use of faecal counts to estimate sambar deer (Cervus unicolor) population abundance in Victoria*. BSc Honours Thesis. Monash University, Clayton, Victoria.

Invasive Plants and Animals Committee. 2016. Australian Pest Animal Strategy 2017 to 2027. Australian Government Department of Agriculture and Water Resources, Canberra.
Krebs, C. J., 2009. Ecology: The Experimental Analysis of Distribution and Abundance.
Pearson, New York. Sixth Edition.

Lendrum, P. E., Anderson Jr., C. R., Long, R. A., Kie, J. G. and Bowyer, R. T., 2012. Habitat selection by mule deer during migration: effects of landscape structure and naturalgas development. *Ecosphere* **3**: Art. 82. http://dx.doi.org/10.1890/ES12-00165.1

Lindenmayer, D. B., Cunningham, R. B., Donnelly, C. F. and Franklin, J. F., 2000.

Structural features of old growth Australian montane ash forests. Forest Ecology and

Management 134: 189-204. http://dx.doi.org/10.1016/S0378-1127(99)00257-1

Lindenmayer, D. B., Blair, D., McBurney, L., Banks, S. C., Stein, J. A. R., Hobbs, R. J.,

Likens, G. E. and Franklin, J. F., 2013. Principles and practices for biodiversity conservation and restoration forestry: a 30 year case study on the Victorian montane ash forests and the critically endangered Leadbeater's Possum. *Australian Zoologist* **36**: 441-460. http://dx.doi.org/10.7882/AZ.2013.007

Lindenmayer, D. B., Blair, D. P., McBurney, L. and Banks, S. C., 2015. *Mountain Ash: Fire, Logging and the Future of Victoria's Giant Forests*. CSIRO Publishing, Melbourne.

Lindenmayer, D. B., Blair, D., McBurney, L., Banks, S. and Bowd, E., 2019. Ten years on – a decade of intensive biodiversity research after the 2009 Black Saturday fires in Victoria's Mountain Ash forest. *Australian Zoologist* in press:

Liu, Z., Cao, L., Zhai, H., Hu, T. and Wang, X., 2004. Winter habitat selection by Red Deer (*Cervus elaphus alxaicus*) in Helan Mountain, China. *Zoological Research* 25: 403-409.

Masters, P., Markopoulos, N., Florance, B. and Southgate, R., 2018. The eradication of fallow deer (*Dama dama*) and feral goats (*Capra hircus*) from Kangaroo Island, South Australia. *Australasian Journal of Environmental Management* 25: 86-98.

http://dx.doi.org/10.1080/14486563.2017.1417166

McCarthy, M. A., 2007. *Bayesian Methods for Ecology*. Cambridge University Press, Cambridge, England.

McCulloch, C. E. and Searle, S. R., 2001. *Generalized Linear and Mixed Models*. John Wiley and Sons, New York.

McKay, G. and Eisenberg, J. 1974. *Movement patterns and habitat utilization of ungulates in Ceylon.* Pages 708-721 in V. Geist and F. Walther, editors. The Behaviour of Ungulates and its relation to management. International Union for Conservation of Nature and Natural Resources, The University of Calgary, Alberta, Canada.

Moloney, P. D. and Turnbull, J. D. 2013. *Estimates of harvest for deer, duck and quail in Victoria: results from surveys of Victorian game licence holders in 2013.* Arthur Rylah Institute for Environmental Research, and Victorian Government Department of Environment and Primary Industries, Heidelberg, Victoria.

Moriarty, A., 2004. The liberation, distribution, abundance and management of wild deer in Australia. *Wildlife Research* **31:** 291-299. http://dx.doi.org/10.1071/WR02100

Mulvaney, J., Seddon, J. and Orgill, O. 2017. *Monitoring Impacts of Sambar Deer (Rusa unicolour) on Forests in the Cotter Catchment, ACT. Monitoring design and initial findings. Technical Report.* Environment, Planning and Sustainable Development Directorate, ACT Government, Canberra.

Parker, K. L., Robbins, C. T. and Hanley, T. A., 1984. Energy expenditures for locomotion by mule deer and elk. *The Journal of Wildlife Management* **49:** 474-488. http://dx.doi.org/10.2307/3801180

Parks Victoria, 2005. *Threat monitoring protocol: deer (Family: Cervidae)*. Parks Victoria, Melbourne, Australia.

Peel, B., Bilney, R. J. and Bilney, R. J., 2005. Observations of the ecological impacts of Sambar Cervus unicolor in East Gippsland, Victoria, with reference to destruction of rainforest communities. *The Victorian Naturalist* **122:** 189-200.

Potts, J. M., Beeton, N. J., Bowman, D. M. J. S., Williamson, G. J., Lefroy, E. C. and

Johnson, C. N., 2015. Predicting the future range and abundance of fallow deer in Tasmania, Australia. *Wildlife Research* 4: 633-640. http://dx.doi.org/10.1071/WR13206

Rowland, M. M., White, G. C. and Karlen, E. M., 1984. Use pellet-groups to measure trends in deer and elk populations? . *Wildlife Society Bulletin* 12: 147-155.

Shen, X., Bourg, N. A., McShea, W. J. and Turner, B. L., 2016. Long-term effects of white-tailed deer exclusion on the invasion of exotic plants: A case study in a mid-atlantic temperate forest. *PLOS One* 11: e0151825. http://dx.doi.org/10.1371/journal.pone.0151825

Simcharoen, A., Tommaso, S., Gale, G. A., Roche, E., Chimchome, V. and Smith, J. L.

D., 2014. Ecological factors that influence sambar (Rusa unicolor) distribution and abundance in western Thailand: implications for tiger conservation. *Raffles Bulletin of Zoology* **62:** 100-106.

Tanentzap, A. J., Bazely, D. R., Koh, S., Timciska, M., Haggith, E. G., Carleton, T. J. and Coomes, D. A., 2011. Seeing the forest for the deer: Do reductions in deer-disturbance lead to forest recovery? *Biological Conservation* 144: 376-382.

http://dx.doi.org/10.1016/j.biocon.2010.09.015

Taylor, C. R., Caldwell, S. L. and Rowntree, V. J., 1972. Running up and down hills: some consequences of size. *Science* 178: 1096-1097.

http://dx.doi.org/10.1126/science.178.4065.1096

Timmins, R., Kawanishi, K., Giman, B., Lynam, A., Chan, A., Steinmetz, R., Sagar Baral, H. and Samba Kumar, N. 2015. *Rusa unicolor (errata version published in 2015), The IUCN Red List of Threatened Species 2015: e.T41790A85628124*. IUCN, Available at https://www.iucnredlist.org/species/41790/85628124. Torres, R. T., Valente, A. M., Marques, T. A. and Fonseca, C., 2015. Estimating red deer abundance using the pellet-based distance sampling method. *Journal of Forest Science* 61: 422-430. https://doi.org/10.17221/52/2015-JFS

Van Etten, R. C. and Bennett, C. L., 1965. Some sources of error in using pellet-group counts for censusing deer. *The Journal of Wildlife Management* 29: 723-729.

http://dx.doi.org/10.2307/3798548

Vehtari, A., Gelman, A. and J., G., 2017. Practical Bayesian model evaluation using leaveone-out cross-validation and WAIC. *Statistics and Computing* 27: 1413-1432. http://dx.doi.org/10.1007/s11222-016-9696-4

Victorian Government. 2012. Wildlife (Game) Regulations 2012. S.R. No. 99/2012. Wildlife Act 1975, Australia.

Viggers, J. I., Weaver, H. J. and Lindenmayer, D. B., 2013. *Melbourne's Water Catchments. Perspectives on a World Class Water Supply*. CSIRO Publishing, Melbourne.

Welsh, A. H., Cunningham, R. B., Donnelly, C. F. and Lindenmayer, D. B., 1996.
Modelling the abundance of rare species: statistical models for counts with extra zeros. *Ecological Modelling* 88: 297-308. http://dx.doi.org/10.1016/0304-3800(95)00113-1

West, P., 2018. *Guide to Introduced Pest Animals of Australia*. CSIRO Publishing, Melbourne.

Wiles, G. J., 1980. Faeces deterioration rates of four wild ungulates in Thailand. *Natural History Bulletin of the Siam Society* 28: 121-134.

Williamson, S. J. and Hirth, D. J., 1985. An evaluation of edge use by white-tailed deer. *Wildlife Society Bulletin* 13: 252-257.

Woinarski, J. C., Burbidge, A. A. and Harrison, P. L., 2015. Ongoing unraveling of a continental fauna: Decline and extinction of Australian mammals since European settlement.

Proceedings of the National Academy of Sciences of the USA 112: 4531-4540.

http://dx.doi.org/10.1073/pnas.1417301112

Table 1. Summary description of forest age classes surveyed for the presence of SambarDeer pellets.

| Class | Description | |
|-------------|--|----------|
| | | of sites |
| 2009 UB | Unlogged forest that has remained unburnt (UB) since regenerating | 15 |
| | after high severity wildfire in 2009 | |
| 1939 LS | Unlogged forest that regenerated after wildfire in 1939, burnt a | 15 |
| | second time by low severity (LS) wildfires in 2009 | |
| 1939 UB | Unlogged forest that has remained unburnt since regenerating after | 17 |
| | wildfire in 1939 | |
| 1983 UB | Unlogged forest that has remained unburnt since regenerating after | 12 |
| | wildfire in 1983 | |
| OG UB | Unlogged forest that has remained unburnt since regenerating after | 12 |
| | high severity wildfire prior to 1900 | |
| Clearfelled | Forest that was regenerated in 2009 after clearfell logging | 15 |

Table 2. General results of Sambar Deer pellet monitoring in the Mountain Ash Forests of theCentral Highlands of Victoria

| | Sites | Plots (2m-radius) | |
|-------------------------|-------------------------|----------------------------|--|
| Total | 86 | 1892 | |
| Presence of deer | 35 | 148 | |
| | (41%) | (8%) | |
| Total groups of pellets | 245 | 245 | |
| | (Range: 0-27 per site) | (Range 0-7 per plot) | |
| Total pellets | 5964 | 5964 | |
| | (Range: 0-869 per site) | (Range: 0 to 219 per plot) | |

Table 3. Estimates and confidence intervals for a statistical model of the relationships between presence of Sambar Deer pellets and key explanatory variables. Note that the intercept represents a Land Tenure = State forest and Age Class = 199 LS. Note estimates and 95% credible intervals are presented on the log scale (linear predictor scale) and that (S) represents a continuous variable that has been standardized.

| Variable | Estimate | lower 95% credible | upper 95% | |
|------------------------|----------|--------------------|-------------------|--|
| v al lable | Estimate | interval | credible interval | |
| Intercept | 1.09 | 0.02 | 2.20 | |
| Easting (S) | 0.52 | -0.02 | 1.01 | |
| Distance to Stream (S) | -0.45 | -1.02 | 0.07 | |
| Land Tenure NP | 1.14 | 0.09 | 2.33 | |
| Age Class 1939UB | -3.38 | -5.16 | -1.80 | |
| Age Class 1983UB | -3.12 | -5.01 | -1.39 | |
| Age Class 2009UB | -0.08 | -1.11 | 1.02 | |
| Age Class CF | 1.45 | -0.32 | 3.05 | |
| Age Class OGUB | -1.72 | -3.34 | -0.06 | |

Figure legends

Figure 1. Location of the study area and research sites in the Central Highlands of Victoria, south-eastern Australia.

Figure 2. Site design, transects and plots layout used to survey for Sambar Deer Pellets in the Mountain Ash forests of the Central Highlands of Victoria.

Figure 3. Relationships between the abundance of Sambar Deer pellets and: (A) forest age, (B) land tenure, and (C) distance to a stream. Forest age classes are described in Table 1.