Seasonal and daily activity of non-native sambar deer in and around high-elevation peatlands, south-eastern Australia

Sebastien Comte[A,*] [iD], Elaine Thomas[B], Andrew J. Bengsen[A] [iD], Ami Bennett[C] [iD], Naomi E. Davis[C,D] [iD], Sean Freney[A,G], Stephen M. Jackson[A,H] [iD], Matt White[E], David M. Forsyth[A] [iD] and Daniel Brown[F]

For full list of author affiliations and declarations see end of paper

*Correspondence to:
Sebastien Comte
Vertebrate Pest Research Unit,
NSW Department of Primary Industries,
1447 Forest Road, Orange, NSW 2800,
Australia
Email: sebastien.comte@dpi.nsw.gov.au

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Andrea Taylor

ABSTRACT

Context. Of the six species of non-native deer present in Australia, the sambar deer is the largest and has been identified as a major threat to high-elevation peatlands in south-eastern Australia. However, little is known about sambar deer activity in high-elevation peatlands. **Aims.** The aims of this study were to quantify sambar deer activity (including wallowing) seasonally and daily in response to biotic and abiotic variables, and how activity was impacted by ground-based shooting. **Methods.** To estimate sambar deer activity, camera traps were continuously deployed for 4 years in two ~4300-ha areas in Alpine National Park, Victoria, south-eastern Australia. One area was subject to management operations using ground-based shooting to target deer and the other was not. Monthly activity of sambar deer was modelled using biotic (woody vegetation cover), abiotic (snow depth, aspect, slope, distance to water, road and peatland) and management (treatment versus non-treatment) covariates. Additional camera traps were deployed to monitor sambar deer activity at wallows. **Key results.** Sambar deer activity decreased when snow depth increased (between July and September), and was highest in easterly and northerly aspects with dense woody vegetation close to high-elevation peatlands and roads. During our 4-year study, sambar deer activity decreased in the treatment area but increased in the non-treatment area. Sambar deer exhibited a crepuscular diel cycle, with greatest activity around sunset. Only male sambar deer were observed to wallow, with most wallowing occurring in the afternoon during October–June. **Conclusions.** Sambar deer utilised high-elevation peatlands during October–June. Daily activity was crepuscular and was greatest in dense tree cover close to roads. Ground-based shooting reduced sambar deer activity in and around high-elevation peatlands. **Implications.** Control operations targeting sambar deer at high elevations in south-eastern Australia should be conducted during October–June. Outside this period sambar deer appear to use lower-elevation habitats. The effectiveness of ground-based shooting could be improved by focusing this control action around sunset (when sambar deer are most active) and in places with dense vegetation close to roads and high-elevation peatlands.

Keywords: Alpine National Park, biological invasions, camera trap, *Cervus unicolor*, diel cycle, invasive species, population dynamics, ungulates, wallowing.

Introduction

Introduced species can be important drivers of ecological change (Didham *et al.* 2005), and significant resources are spent managing their impacts (Diagne *et al.* 2021). This is particularly the case for deer (Family: Cervidae), which have been widely introduced around the world (Long 2003) and can significantly alter ecosystems, primary industries and human health (Wardle *et al.* 2001; Côté *et al.* 2004). Effective management of introduced species such as deer requires an understanding of their biology and the mechanisms by which their impacts occur (Simberloff *et al.* 2005) along with consideration for the local socio-economic context (Dolman and Wäber 2008). Factors that can be important predictors of deer activity and impacts in temperate ecosystems include aspect,

tree cover, proximity to water and, at high elevations, snow depth (White *et al.* 2009; Allen *et al.* 2015; Coe *et al.* 2018). The presence of anthropogenic structures, such as roads, farmlands and habitations can also affect the activity and impacts of deer (Forman and Deblinger 2000; Menichetti *et al.* 2019; Pfeiffer *et al.* 2020).

Of the six deer species that were deliberately and successfully introduced into Australia, the sambar deer (*Cervus unicolor*[1]) is the largest; adult males and females weigh 220 and 140 kg, respectively (Bentley 1998; Moriarty 2004). Since their introduction in the Australian state of Victoria in 1860, sambar deer have colonised a wide range of habitats in south-eastern Australia, from coastal forest and heathlands to high-elevation treeless plains (Moriarty 2004; Davis *et al.* 2016). 'The reduction in biodiversity of native vegetation by sambar deer' has been listed as a key threatening process under Victoria's *Flora and Fauna Guarantee Act 1988*, including impacts on Alpine Sphagnum Bogs and Associated Fens (hereafter referred to as high-elevation peatlands), a nationally endangered ecological community (Australian Government, *Environment Protection and Biodiversity Conservation Act 1999*). The impacts of sambar deer result from behaviours such as herbivory, antler thrashing, rubbing of trees, wallowing and trampling (Bennett and Coulson 2010; Bilney 2013; Davis *et al.* 2016).

During the last 20 years, ground-based shooting (reviewed in Bengsen *et al.* 2020) has been used to reduce the density and impacts of introduced deer in Australia, including sambar deer (Bennett *et al.* 2015). Implementation of effective ground-based shooting, however, is hampered by a lack of information about the daily and seasonal activities of sambar deer in their non-native range [but see Forsyth *et al.* 2009; Davies *et al.* 2020]. This information is needed to determine at what time(s) of the day and in which month(s) ground-based shooting is likely to be most effective. Ground-based shooting can, in turn, influence the activity of surviving deer spatially and temporally, with deer shifting their activity from diurnal to nocturnal (Ikeda *et al.* 2019) and selecting densely-vegetated habitats (Benhaiem *et al.* 2008; Laguna *et al.* 2021).

In their native range, which spans from sea level in the Philippines to >3500 m in the Himalayas (Green 1987; Whitehead 1993), sambar deer activity is strongly positively associated with wet forest gullies adjacent to flat grasslands (Simcharoen *et al.* 2014; Yen *et al.* 2019). In low-elevation catchments in south-eastern Australia, aspect, distance to water and elevation were important predictors of the relative abundance of sambar deer (Forsyth *et al.* 2009). Sambar deer are considered non-migratory in their native range, but in mountainous regions they move to higher elevations during the warmer months (Green 1987; Yen *et al.* 2019). Sambar deer are crepuscular, typically resting in dense forest during the day and moving into open areas to feed at dusk and then returning to cover at dawn (Kawanishi and Sunquist 2004; Matsubayashi *et al.* 2007; Brodie and Brockelman 2009). The seasonal and daily activity of sambar deer in Australia have been little investigated, although Davies *et al.* (2020) reported a crepuscular daily activity pattern in Baw Baw National Park (Victoria) during spring and early summer. In contrast to deer species indigenous to temperate regions [e.g. fallow deer (*Dama dama*) and red deer (*Cervus elaphus*)], tropical species such as sambar deer have low reproductive seasonality. Although sambar deer males with hard antlers, and females with newly-born calves, can be observed throughout the year, in Australia, a peak of rutting activity and birthing has been observed during winter (Bentley 1998; Harrison 2010; Asher 2011; Watter *et al.* 2020). Most wallowing is thought to be done by adult male sambar deer when rutting (Chalmers 2018), but otherwise little is known of the wallowing activity of sambar deer in Australia.

The objective of this study was to answer five key questions about sambar deer activity in and around high-elevation peatlands in south-eastern Australia: (1) does the strong seasonality of the high-elevation environment influence the monthly activity of sambar deer? (2) does sambar deer activity increase with increasing tree cover and increasing proximity to watercourses? (3) does sambar deer activity peak at dusk and dawn? (4) are there sex–age class differences in wallowing activity by sambar deer? and (5) does ground-based shooting reduce sambar deer activity?

Material and methods

Study areas

We conducted our study at two high-elevation areas on the Bogong High Plains (BHP), within Alpine National Park, Victoria, south-eastern Australia (36.87°S, 147.28°E; Fig. 1). These two areas were a subset of eight areas included in a management program organised by Parks Victoria assessing the effects of ground-based shooting on the impacts of sambar deer on high-elevation peatlands. The original design proposed that all eight study areas have camera traps (Davis *et al.* 2015*a*, 2015*b*), but for financial reasons they were only placed in two areas. The treatment (ground-based shooting) was allocated to one of the two areas by a coin toss; the other is hereafter referred to as the non-treatment area. The mean elevations of the treatment (4422 ha) and non-treatment (4201 ha) areas were 1417 and 1561 m, respectively. Both areas receive a mean of 1302 mm of rainfall annually, with low monthly variation (range: 92.7–139.3 mm). Mean monthly minimum and maximum temperatures range from 8.3 to 16.9°C in February to −3.2 and 0.9°C in July (Australian Bureau of Meteorology, Falls

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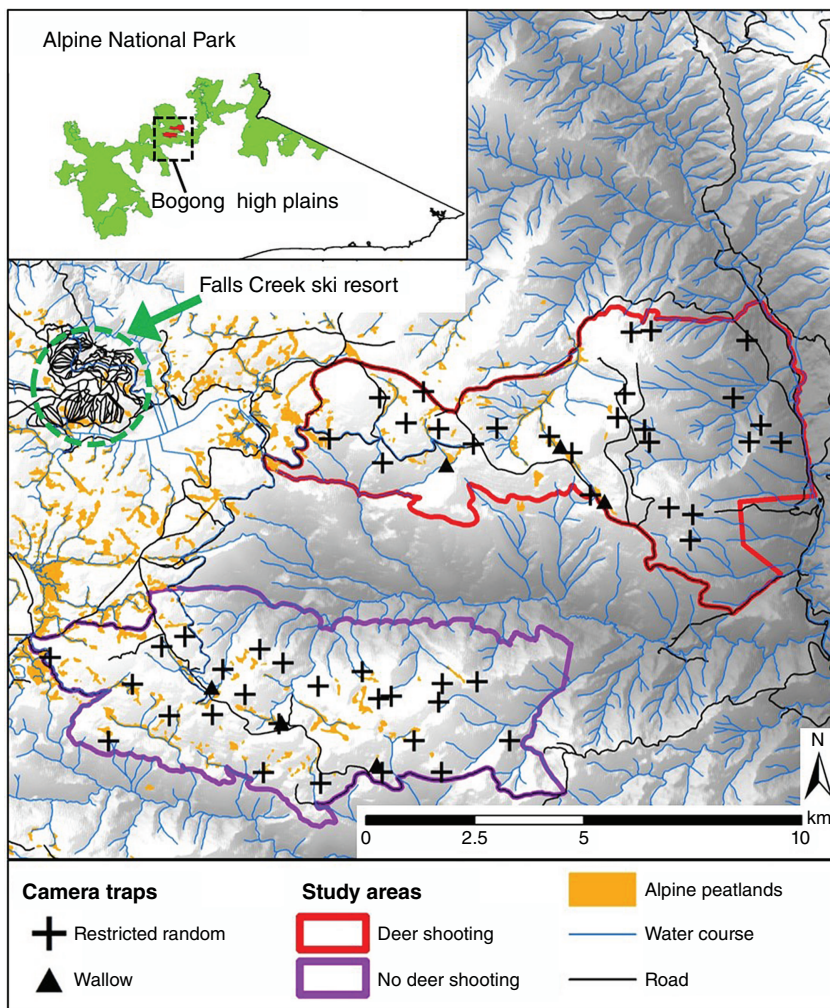[1]Mammal taxonomy follows Jackson and Groves (2015).

Fig. 1. Locations of the treatment (red) and non-treatment (purple) areas, and of the camera traps deployed within them between April 2015 and April 2019. The inset map shows the two study areas (red) within Alpine National Park (green), Victoria, south-eastern Australia.

Creek weather station, http://www.bom.gov.au). Snow typically accumulates on the ground from June to October, with a maximum mean monthly snow depth of 136 cm (2014–2019, Daily Snow Depth Records Falls Creek, Department of Environment, Land, Water & Planning, https://discover.data.vic.gov.au).

The study areas consist of mostly flat to undulating terrain with a mosaic of subalpine woodland dominated by snow gums (*Eucalyptus pauciflora*) and treeless plain including alpine sphagnum bogs and associated fens (dominated by *Sphagnum subsecundum* and *S. cristatum*). The steeper slopes along water-formed gullies are mostly covered by montane wet forests (dominated by alpine ash *E. delegatensis*) with dense understorey (Conn 1993). In addition to their high biodiversity values, these plant communities regulate and filter water flows to major river systems that benefit agriculture, hydroelectricity and drinking water supply. Other medium- or large-herbivores present in the study area, in addition to sambar deer, are the native swamp wallaby (*Wallabia bicolor*) and bare-nosed wombat (*Vombatus ursinus*). The management program was designed to be outside

of the main distribution of feral horses (*Equus caballus*; Cairns and Robertson 2014), but some horses were present in both study areas.

Camera trapping

In each study area, 25 camera traps were continuously deployed between April 2015 and April 2019. Two camera trap models were used for the first month of monitoring: the Reconyx PC900 and the Reconyx HC500 (Reconyx Inc., Holmen, Wisconsin, USA). From May 2015 to April 2019, all camera traps (except for one model PC900) were replaced by the Reconyx HC600 model. All camera traps were visited every 6 months to replace the batteries and Secure Digital (SD) cards. Camera locations were selected using restricted random sampling. Each study area was divided into 160-ha hexagonal cells, within which a random point was generated as the camera trap location (Fig. 1). To maximise detection, camera traps were located at the nearest wildlife trail to the random sampling coordinates (within 50 m radius). The average distance between cameras

was 617 m (range: 120–1338 m) and 850 m (range: 103–1982 m) in the treatment and non-treatment areas, respectively, and 6560 m (range: 4811–9913 m) between the two areas. To standardise detection probabilities, all cameras were mounted 130–150 cm above ground on a tree facing south (to avoid direct sunlight) and with the detection sensor aimed at a linear distance of 6 m from the camera. Vegetation was trimmed within the detection zone (i.e. 6 m in front of each camera trap and 40° either side of the central line of sight) to prevent false triggers from moving grass and branches. Camera traps were not baited or lured. To maximise the detection and accurate identification of deer, cameras were set to 'high sensitivity', 'three images per movement' and 'rapidfire' with no delay between trigger events.

In addition, three camera traps (Reconyx HC600) were subjectively located within each study area to continuously monitor active wallows in high-elevation peatlands between April 2015 and April 2019 (Fig. 1). These cameras were mounted on a metal stake 200 cm above ground and 200 cm from the edge of the wallow, facing the centre of the wallow. The camera settings were the same as those described above. The objective of these cameras was to quantify wallowing activity by sambar deer (see Question 4), as none of the other 50 cameras described above overlooked wallows.

Image processing

Data were obtained by downloading images from the SD cards onto a computer and manually assigning a defined set of metadata tags to each image, where relevant, using the software ExifPro v2.1 (Kowalski and Kowalski 2013).

Images were grouped into independent detection events separated by ≥10 min and the same metadata were assigned to all images within one detection event, with the timestamp of the first image used for all images in that event. The same two experienced observers tagged all images. These detection events were considered a representative sample of the true sambar deer activity distribution in the study areas (Linkie and Ridout 2011). The metadata included the species detected and the number of individuals detected during each event. For sambar deer, individuals were additionally assigned to two sex–age classes: males and females-juveniles (including calves, Fig. 2). All individuals with visible antlers or pedicles were tagged as males. Individuals were classified as females based on their body size and the absence of antlers or external genitalia. The presence of a calf or a juvenile close to the animal was also used to assign adult antlerless individuals as females. All individuals with small body size, calves and yearlings without spike antlers, were considered as juveniles with no sex assigned. For the cameras monitoring the wallows, the antler stage of all male sambar deer was further described as hard antlers, velvet antlers or no antlers (pedicles visible). Due to the low variability in colour and texture of sambar deer coats, it was not possible to confidently identify individuals.

Given that sambar deer activity is likely to be driven by sunlight, and that sunrise and sunset varied through the year in our study areas, we scaled the timestamps of each detection event into sun time (i.e. sunrise and sunset, every day, were represented by 6:00 and 18:00, respectively) using the function sunTime in the R-package overlap version 0.3.3 (Ridout and Linkie 2009).
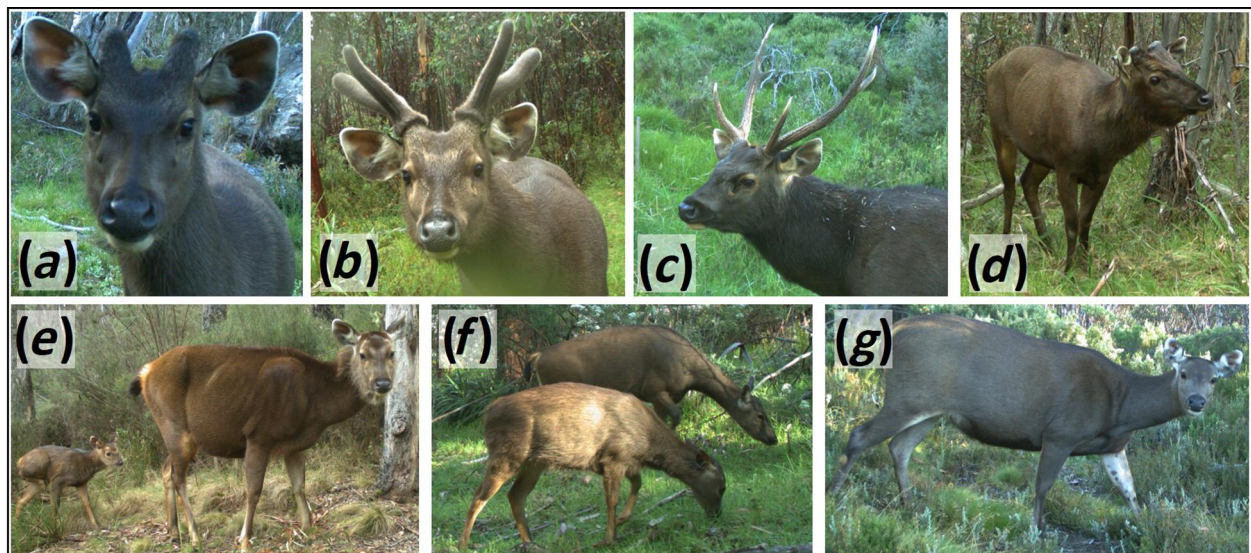

Fig. 2. Sex–age classes of sambar deer photographed by camera traps at two high-elevation study areas in Alpine National Park, Victoria, south-eastern Australia. (*a*) male with velvet spikes; (*b*) adult male with growing velvet antlers; (*c*) adult male with hard antlers; (*d*) adult male with no antler (pedicles visible); (*e*) adult female with calf; (*f*) adult female with juvenile (sex undetermined) in foreground; (*g*) adult female. For the analyses, the classes (*a*) to (*d*) were grouped as males and classes (*e*) to (*g*) were grouped as females-juveniles (including calves).

Habitat variables

Snow depth was recorded daily at Falls Creek ski resort, <5 km from the two study areas (Fig. 1). These measurements started in June and stopped at the end of the ski season in early October, when snow was often still present on the ground. We assumed an absence of snow between November and May by fixing the snow depth to zero. We then modelled the mean monthly snow depth (cm) across the 4 years of the study (2015–2019) using a General Additive Mixed Model (GAMM) with a Tweedie family to handle the zero-inflated and continuously positive data. To account for the circular nature of the months (i.e. December and January are adjacent), we modelled month as a cyclic cubic spline. We included year as a random effect. We used the same approach to model the monthly minimum and maximum temperatures (degrees Celsius) during our 4-year study with Gaussian family GAMMs (Fig. 3).

We described the topography of the two study areas using four variables measured over a grid of 100 m × 100 m: elevation, slope, aspect and terrain ruggedness. We classified the vegetation structure as the proportions of woody vegetation cover and herbaceous cover for each grid cell. We used the geographic coordinates of each camera to extract covariate values for the matching grid cell. For each camera, we measured the distances to the nearest watercourse, road and peatland. The data sources for these 12 variables are given in Supplementary Table S1. We tested for collinearity within all covariates and kept only one variable from each group of dependent variables (Pearson's correlation coefficient $|r| > 0.7$; Tables 1, S2).

Spatio-temporal activity

We measured sambar deer activity as the number of independent detections for both sex–age classes (males and females-juveniles) on each camera trap during each calendar month (1–12) and year (1–5). We fitted a generalised linear mixed model (GLMM) in a Bayesian framework to estimate the effects of the habitat variables (Table 1) on sambar deer activity with a negative binomial family and a random effect for month:

$$Y_i \sim NB(p_i, r)$$
$$p_i = \frac{r}{r + \lambda_i}$$
$$\log \lambda_i = \sum_j \beta_j X_{ij} + \theta_{month},$$

and

$$\beta_j \sim N(0, 10)$$
$$r \sim U(0, 50)$$
$$\theta_{month} \sim N(0, \sigma_{month})$$
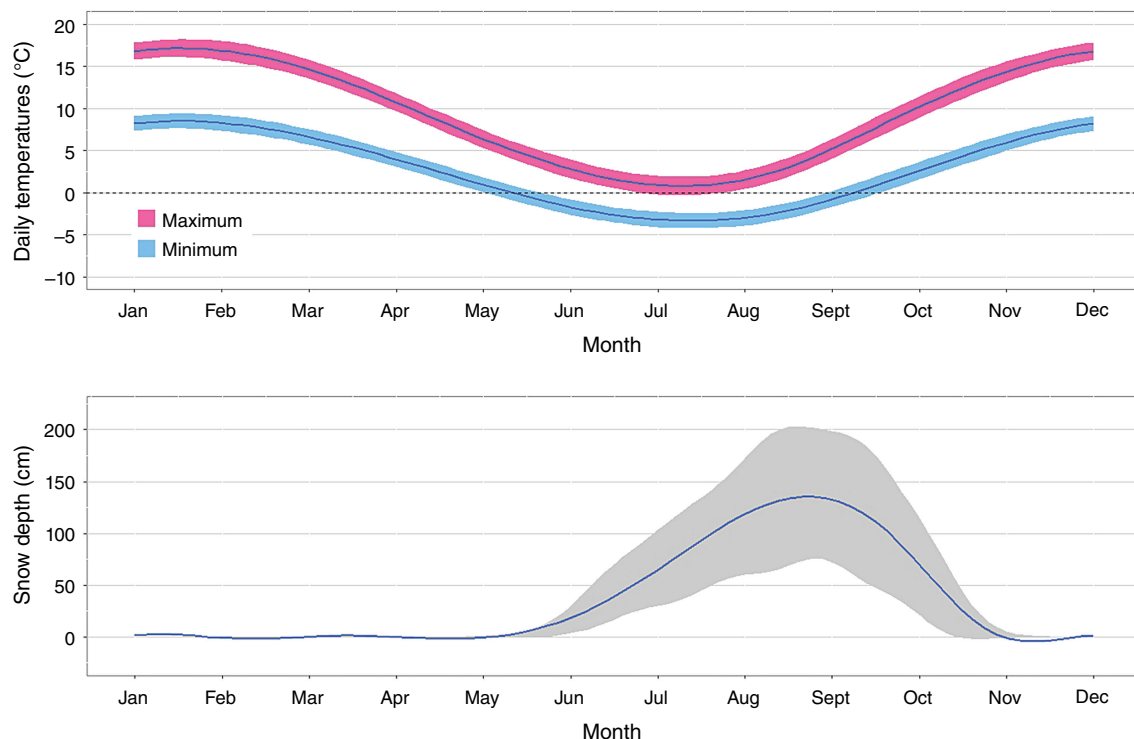$$\sigma_{month} \sim U(0, 20),$$

Fig. 3. Mean daily temperatures and snow depth at Falls Creek ski resort, Victoria, south-eastern Australia, between April 2015 and April 2019. Shaded areas show the 95% confidence intervals around the predicted means (blue lines).

Table 1. Habitat variables included in our model of sambar deer activity in Alpine National Park, Victoria, south-eastern Australia.

Variable	Unit	Mean	Minimum	Maximum	Correlation[A]
Elevation	Metres	1490.9	811.9	1737.2	*a*
Slope	Degrees	10.7	2.1	27.6	*b* (kept)
Terrain ruggedness	Index 1–40	15.7	3.3	39.5	*b*
Aspect	Degrees	174.7	26.2	349.9	
Snow depth	Centimetres	33.8	0.0	135.6	*c* (kept)
Min temperature	Celsius	3.0	−3.2	8.3	*c*
Max temperature	Celsius	9.8	0.9	16.9	*c*
Woody vegetation cover	Percentage	89.8	22.0	100.0	*d* (kept)
Herbaceous cover	Percentage	7.6	0.0	66.7	*d*
Distance to watercourses	Metres	201.6	0.3	519.0	
Distance to roads	Metres	569.5	2.8	2174.8	
Distance to peatlands	Metres	682.0	0.5	4097.1	*a* (kept)

For a full description of each variable, see Table S1.
[A]Groups of dependent variables with a Pearson's correlation coefficient $|r| > 0.7$.

where Y_i represents the negative binomial density function of sambar deer activity during 1 month on one camera trap, with p_i the success parameter, r the dispersion parameter, $\beta_j X_{ij}$ the linear predictors, and θ_{month} the random effect of month.

The effect of snow depth (cm) on sambar deer detections was modelled as linear predictors with sex–age-specific intercepts and slopes. The effect of year (2015–2019) on sambar deer detections was modelled as linear predictors with intercepts and slopes for each study area. Slope (0–90°), distances (m) to water, road and peatland, and woody vegetation cover (1–100), were modelled as linear predictors. Aspect is a circular variable (0–360°) and hence it was modelled using a sine function for easterly aspect and a cosine function for the northerly aspect. We added a random effect of month to account for multiple measurements during the same month across the years of the study.

All predictor variables, except for aspect, were centred on their mean to facilitate the mixing of the Monte Carlo Markov chains (MCMC). We ran three chains of 150 000 iterations each, with 5000 adaptation runs and 5000 burn-in runs. We assessed the mixing of the MCMC chains visually and with the Gelman–Rubin diagnostic (*R*; Gelman and Rubin 1992).

The snow depth predictions were made using the R-package mgcv v1.8-31 (Wood 2011; R Core Team 2020). Spatial analyses were performed using the R-packages raster version 3.1-5, rgdal version 1.5-10 and rgeos version 0.5-3 (Bivand and Rundel 2020; Bivand *et al.* 2020; Hijmans 2020). We evaluated the Pearson correlation among covariates using the package Hmisc version 4.4-0 (Harrel 2020). The Bayesian regression analyses were performed using the packages runjags version 2.0.4-6 (Denwood 2016) and coda version 0.19-3 (Plummer *et al.* 2006).

Diel activity

Annual and daily activity patterns are circular and likely to be non-linear. Generalised additive models have been used to describe the diel cycles of deer (Bischof *et al.* 2014). To obtain a sample size sufficient to meaningfully estimate seasonal trends, we pooled detection events by month. For each camera, for each month, we then constructed the response variable as the proportion of detections for every hour of the day (0–23, scaled as sun time 6:00 being sunrise and 18:00 sunset) resulting in a sum of 1 for each camera-month. We retained camera-months with at least three detection events. To account for the circular nature of deer activity, we used a cyclic cubic spline for both hour and month, and included their interaction term in the model using a tensor product interaction. We allowed both terms to have sex–age-specific smoothing functions. We also included camera within each area and within each year as a nested random effect. The model was fitted with a quasi-binomial distribution (to account for overdispersion), with a penalty added to the null space of each smooth term, using the R-package mgcv version 1.8-31.

Wallowing activity

Sambar deer detected at a wallow were not always wallowing. We discarded detections of deer that were walking by the wallow, only grazing outside the wallow or drinking from the wallow. A wallowing event was defined as an individual observed lying down in the wallow, rolling from side to side and rubbing its head or antlers on the adjacent vegetation (Fig. 4).

We first characterised the proportion of images with wallowing each month in the treatment and non-treatment areas using the previously described sex–age classes and the

Fig. 4. Male sambar deer in hard antler wallowing in a high-elevation peatland in Alpine National Park, Victoria, southeastern Australia, 6th of November 2015.

different antler stages. We then compared the circadian distribution of wallowing activity in both areas using non-parametric kernel density estimates calculated with the R-package overlap version 0.3.3 (Ridout and Linkie 2009). We compared the mean and variance of the two distributions using a Mardia–Watson–Wheeler test of homogeneity (Zar 1996) in the R-package circular version 0.4-93 (Agostinelli and Lund 2017).

Results

Data scope

Between April 2015 and April 2019, the 50 camera traps recorded 444 516 images. The theft of five cameras resulted in a 6-month gap in data for each camera location before the camera was replaced. Sambar deer were detected on 8218 independent events (39% in the treatment area with ground-based shooting and 61% in the non-treatment area with no ground-based shooting) for a total of 10 227 deer (mean and maximum group sizes = 1.24 and 8). The detections consisted of 62% adult males, 29% adult females and 9% unsexed juveniles and calves. Sex–age class could not be determined for 1465 detections (14%), and these were excluded from analyses. No deer species other than sambar were detected. A total of 54 feral horses were detected on 24 independent events (maximum group size = 9; 75% of detections in the treatment area). A total of 454 wild dogs/dingoes (*Canis familiaris*) were detected on 322 independent events (maximum group size = 5; 65% of detections in the treatment area). A total of 75 humans were detected on 30 independent events (maximum group size = 10;

35% of detections in the treatment area). Of those, only one deer shooter (involved in the management program) was detected, once on one camera in the treatment area.

Spatio-temporal activity

All covariates included in our model were significantly associated with sambar deer activity (i.e. none of the 95% credible intervals included zero; Table S3), although effect sizes varied greatly (Fig. 5). Sambar deer detections were 1.6 times more likely to be due to males than females-juveniles. As predicted, sambar deer activity in the study area was strongly influenced by seasonal snow accumulation. The number of detections of both males and females-juveniles decreased by approximately 80% when snow depth reached its mean monthly maximum (136 cm). Sambar deer avoided the steepest slopes and selected easterly and northerly aspects. As expected, sambar deer were more active in areas with dense woody vegetation, and were more active closer to roads and peatlands, but away from watercourses (Fig. 5). At the beginning of the study, sambar deer detections were 30% lower in the treatment area (i.e. subject to ground-based shooting) than in the non-treatment area (Table S3). During the 4-year study (across five calendar years) there was a 14% annual decrease in sambar deer activity in the treatment area, but a 7% annual increase in the non-treatment area.

Diel activity

We recorded detections of sambar deer on 1153 camera-days (721 for males and 432 for females-juveniles), representing 23% of the total survey effort. The GAMM revealed a
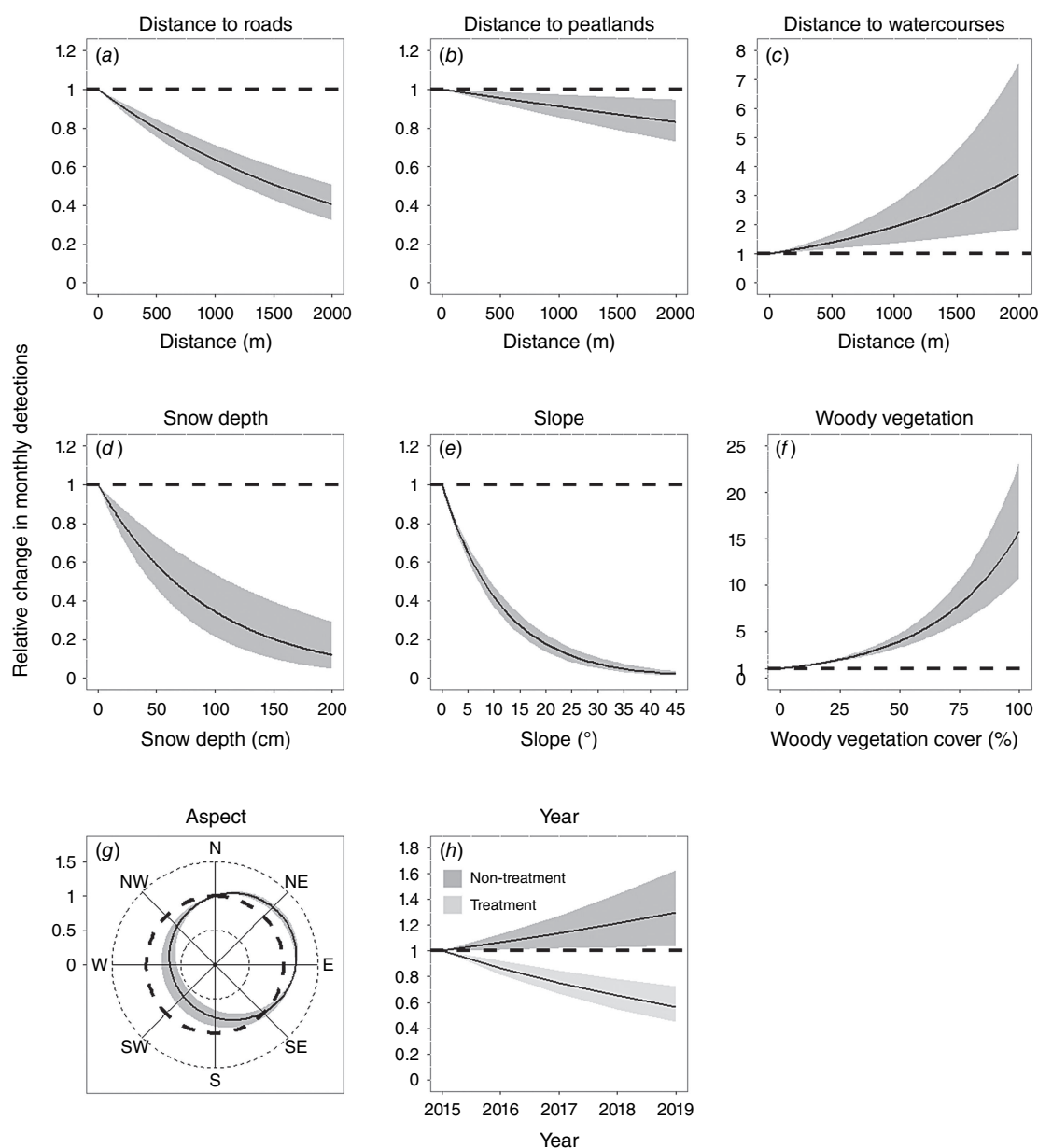
Fig. 5. Relative change in monthly sambar deer detections associated with each environmental covariate (*a*–*h*) in Alpine National Park, Victoria, south-eastern Australia. Black lines show the predicted mean and the shaded areas the 95% credible intervals. Because the effect of snow depth was equivalent for both sex–age classes (Table S3), we only show the relative change for males (*d*).

significant interaction between the hour of the day and month for both sex–age classes (males: EDF = 77.52, $P = <0.01$; females-juveniles: EDF = 82.79, $P = <0.01$; variance explained = 12.4%; see Table S4 for full model output). Sambar deer activity was mainly crepuscular, with most activity occurring just before sunset and, to a lesser extent, around sunrise (Fig. 6). The diel cycle differed in the winter months (July–September), with activity peaking during daylight, later in the morning for females-juveniles, and earlier in the afternoon for males. This shift

in peak activity period coincided with the presence of snow in the study areas (Fig. 3).

Wallowing activity

Of the six cameras deployed on wallows in April 2015, one camera was stolen in May 2015 and not replaced (so no images were available for that wallow), two cameras recorded images until November 2016 when one was stolen and the other was removed. Three cameras recorded activity
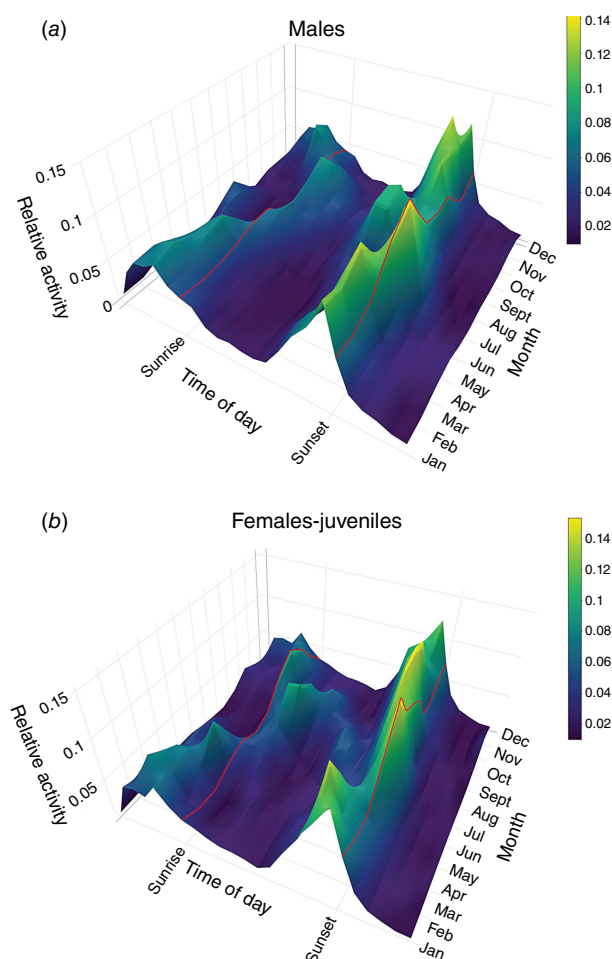
(a) Males

(b) Females-juveniles

Fig. 6. Diel activity of male (*a*) and female-juvenile (*b*) sambar deer in Alpine National Park, Victoria, south-eastern Australia. The time of day is scaled to sunrise (6:00) and sunset (18:00), indicated by red lines.

until the end of the study in April 2019. Between April 2015 and April 2019, we recorded 101 222 images during 5576 camera trap nights at five wallows. A total of 1049 independent detections were recorded for a total of 2047 sambar deer, making sambar deer the most common large mammal species detected at the wallows. Feral horses (*n* = 27 detections) were detected during the last 4 months of the study at a single wallow while grazing, drinking and wallowing. Humans were detected riding horses on seven occasions in and around two wallows. Other species detected at the wallows were bare-nosed wombat (*n* = 7 detections on two cameras, always in darkness), swamp wallaby (*n* = 7 detections on one camera always during daylight), red fox (*Vulpes vulpes*, *n* = 55 detections), wild dog/dingo (*Canis familiaris*, *n* = 16 detections) and feral cat (*Felis catus*, *n* = 8 detections). The European hare (*Lepus europaeus*) was commonly detected at wallows in winter when snow was present. None of these taxa were detected in a wallow; rather, they were walking outside, or drinking from, the wallow.
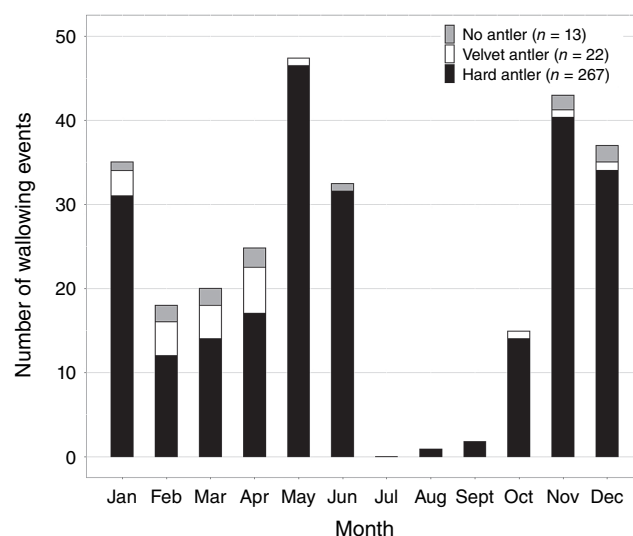

Fig. 7. Monthly wallowing activity (summed between April 2015 and April 2019) of male sambar deer at different stages of antler development in Alpine National Park, Victoria, south-eastern Australia. The legend includes the number of wallowing events recorded (*n*).

A total of 302 out of 1049 detections (29%) showed deer wallowing (i.e. lying in the mud, rolling on their sides or rubbing their head; Fig. 4). All wallowing by sambar deer was by males, with only one juvenile that could not be sexed. Wallowing by sambar deer on Bogong High Plains occurred in two seasonal peaks, one between April and June, and the second between November and January (Fig. 7). Wallowing almost never occurred between July and September, when there was deep snow cover and low sambar deer activity. There was no difference in wallowing activity during the day between male sambar deer in hard antler (*n* = 267) and combined velvet or no antlers (*n* = 22 and *n* = 13, respectively; Mardia–Watson–Wheeler test: $W = 2.359$, $P = 0.307$). Wallowing activity was higher in the treatment area (Table 2), but robust comparison between the two areas is limited by the small number of cameras that monitored wallows. Yet, the daily pattern of wallowing activity was significantly different in the treatment area compared to the non-treatment area. Wallowing peaked around sunset at both areas, but was more widely distributed throughout the afternoon at the non-treatment area (Mardia–Watson–Wheeler test: $W = 7.036$, $P = 0.030$; Fig. 8).

Discussion

The seasonal and daily activity of sambar deer, including wallowing, has not previously been investigated in high-elevation environments with strong seasonality, such as occur in Alpine National Park in south-eastern Australia. In contrast to previous studies of this species in tropical and low-elevation temperate environments, our 4-year study

Table 2. Detections of sambar deer wallowing in two high-elevation areas in Alpine National Park, Victoria, south-eastern Australia, between April 2015 and April 2019.

Year	Treatment area		Non-treatment area		
	Wallow 2	Wallow 3	Wallow 11	Wallow 12	Wallow 13
2015	4	43	1	16	2
2016	12	79	1	24	3
2017	–	31	–	33	3
2018	–	27	–	11	2
2019	–	3	–	4	3
Total	16	183	2	88	13

Cameras on wallows 2 and 11 were stolen or removed in November 2016.
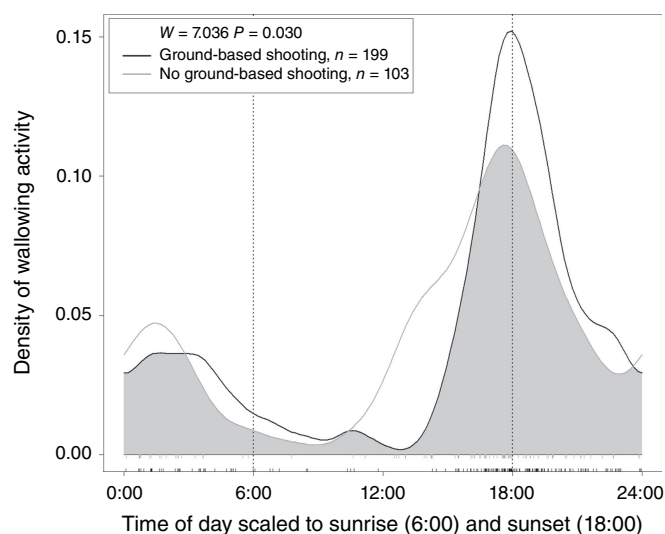
Fig. 8. Daily wallowing activity of sambar deer in an area subject to ground-based shooting and an area not subject to ground-based shooting in Alpine National Park, Victoria, south-eastern Australia. The legend includes the number of wallowing events recorded (*n*) and the results of the Mardia–Watson–Wheeler test (*W* and *P*) between the two areas.

revealed a strong decrease in sambar deer activity in our two study areas during July–September, when snow was present on the ground. As expected, sambar deer activity was greatest within dense woody vegetation but was also higher close to roads and high-elevation peatlands and away from water-courses. Sambar deer showed strong crepuscular activity, with peak activity near sunset. During winter there was a shift in daily activity towards more diurnal activity after sunrise or before sunset. Only male sambar deer were observed to wallow, with a seasonal peak immediately before snow was present. Wallowing peaked near sunset, a pattern that was accentuated in the treatment area subject to management operations using ground-based shooting.

Ground-based shooting is commonly used to reduce the impacts of introduced deer in Australia. We found that sambar deer activity decreased in the treatment area relative to

the non-treatment area. Detection rates of deer on camera traps were positively correlated with deer densities estimated using spatial mark–resight models for white-tailed deer (*Odocoileus virginianus*) across 20 sites in the United States (Parsons *et al.* 2017) and for sambar deer across fives sites in eastern Australia (Bengsen *et al.* 2022). We therefore believe that sambar deer activity on camera traps is a reliable index of sambar deer relative abundance in our study areas. In the non-treatment area, the observed increase in sambar deer activity is consistent with a long-term increase in sambar deer abundance in eastern Victoria, as indexed by hunter's catch-per-unit-effort (Forsyth *et al.* 2018; Moloney *et al.* 2022). Since recreational hunting was prohibited in both study areas, the most likely cause of reduced sambar deer activity in the treatment area was the ground-based shooting implemented there but not in the non-treatment area. During the management operations, 164 sambar deer were removed from the treatment area by ground-based shooting (Parks Victoria, unpubl. data), which could also have led to surviving deer avoiding that area. Human hunting activities can alter the perceived risk for prey, creating a 'landscape of fear' (Laundre *et al.* 2010), which can result in changes in activity or avoidance of risky areas (Benhaiem *et al.* 2008; Cromsigt *et al.* 2013; Le Saout *et al.* 2014). Analysis of the sambar deer catch and effort data recorded by the ground-based shooters, as well as before-after monitoring of deer impacts, will be reported in a subsequent paper and will help understand the effectiveness of ground-based shooting as a management tool for reducing sambar deer impacts in high-elevation areas of south-eastern Australia.

Our results support the general findings that sambar deer prefer dense woody vegetation cover as protection against predators (including humans) and shelter against wind and cold temperatures (Yamada *et al.* 2003; Gormley *et al.* 2011; Sotorra *et al.* 2021). The lower activity of sambar deer close to watercourses in our study may reflect the high availability of surface water (e.g. natural pools, wallows) within the high-elevation peatlands. The higher activity of sambar deer along roads suggest that those linear structures may act as movement corridors across the landscape as was observed in Baw

Baw National Park (Davies *et al.* 2020), an area with a similar road network (i.e. mostly unsealed) and pattern of use by traffic (i.e. seasonal road closures in winter).

Sambar deer were largely absent from our two study areas during July–September, when snow was accumulating on the ground (maximum mean monthly snow depth = 136 cm). The accumulation of snow increases the energetic cost of moving and reduces access to food (White *et al.* 2009). Red deer in the Italian Alps showed vertical movements towards lower elevations associated with seasonal snow accumulation of 20–60 cm (Luccarini *et al.* 2006). In China, native sambar deer living in a mixed coniferous and deciduous forest reserve (elevation range 1600–3200 m) showed a reduced detection rate on camera traps and a stronger use of sheltered areas during the colder months of the year (Zhang *et al.* 2017). The sambar deer that utilised our study areas in spring, summer and autumn presumably moved to lower elevations during winter, as anecdotally reported in Bentley (1998). GPS-collared sambar deer in Taiwan showed strong seasonal movement patterns, moving from high to low elevations during the cold season and back to high elevations during the hot–wet season (Yen *et al.* 2019). Attaching GPS collars to sambar deer present in the high-elevation peatlands of Alpine National Park during summer–autumn would reveal where they move to during winter.

As expected, sambar deer activity in our two study areas was crepuscular, a pattern largely observed for ungulates balancing the risk of human contact during the day (Gaynor *et al.* 2018; Pal *et al.* 2020) and the risk of predation during the night (Kie 1999; Sih *et al.* 2000). In China, sambar deer shifted their activity from multiple daily peaks (low human activity) to one major activity peak at dusk (high human activity), suggesting flexibility in their diel activity (Zhang *et al.* 2017). A similar influence of human presence on sambar deer activity was observed in Bandipur, in southern India, where activity during the day only occurred in the least disturbed areas (Johnsingh 1983). As our study was conducted in a national park, human activities shown to influence deer activity elsewhere [e.g. livestock grazing (Stewart *et al.* 2002) and off-road vehicles (Wisdom *et al.* 2004)] were limited with the exception of the ground-based shooting conducted in the treatment area. Yet, when moving away from the study areas during the winter months, sambar deer likely experienced interactions with humans closer to adjacent farmland and areas open to recreational hunting, which could influence their activity once they returned to our study areas. In south-eastern Australia, sambar deer are eaten by wild dogs/dingoes, and there was one detection of wild dogs eating a calf by one camera in our study, but the extent to which this is scavenging (Forsyth *et al.* 2014) or predation is unclear (Forsyth *et al.* 2019). Wild dogs/dingoes are unlikely to kill a healthy adult sambar deer, but they can kill calves (Bentley 1998). In Borneo, the presence of a predator, Diardi's clouded leopard (*Neofelis diardi*), was

associated with a shift in sambar deer activity from nocturnal to crepuscular (Ross *et al.* 2013). Although unlikely to have a limiting effect on sambar deer abundance, the presence of wild dogs/dingoes in our study areas have contributed to the crepuscular nature of sambar deer activity.

This is the first study to quantify the wallowing activity of sambar deer, a behaviour impacting the endangered high-elevation peatlands. Our study confirmed that sambar deer was the main species wallowing in high-elevation peatlands of the Bogong High Plains. Although our study areas were selected to be outside the most-heavily occupied parts of the feral horse distribution in Alpine National Park, feral horses were also observed wallowing, adding to the pressure on high-elevation peatlands. Additionally, domestic horses were detected by the camera traps while being ridden in and around existing wallows, adding to the trampling and grazing impacts on high-elevation peatlands. In our study, only male sambar deer wallowed, and usually when they were in hard antler. These findings are consistent with male sambar deer wallowing when rutting (Semiadi *et al.* 1994; Bentley 1998; Harrison 2010; Dahlan and Dawend 2013; Chalmers 2018). Sambar deer wallowing was concentrated just before sunset, matching the general crepuscular activity pattern of this species in the study areas. In addition to a reduced abundance of sambar deer in the treatment area, the ground-based shooting may also have reduced the propensity of surviving sambar deer to use the high-elevation peatlands for wallowing during the afternoon (*sensu* Cromsigt *et al.* 2013; Ikeda *et al.* 2019). A broader survey of peatlands across the whole Victorian Alps between 2004 and 2009 suggested that wallows were more frequent in peatlands close to forested areas (Tolsma 2009). Although limited by the small sample size, our results suggest that not all wallows are visited equally by sambar deer. Understanding what physical characteristics and environmental context are associated with the wallowing activity could improve the cost-effectiveness of ground-based shooting by targeting the most visited wallows.

Management implications

Effective management of an invasive species and its impacts requires understanding the ecology of the target species. The results of our study have important implications for the management of sambar deer and their impacts on the high-elevation peatlands in south-eastern Australia. First, in our study areas sambar deer were the main non-native species active in high-elevation peatlands, and are therefore the species causing the greatest disturbance to these endangered communities, through trampling, antler thrashing, grazing and browsing and also through wallowing by males. Hence, it is reasonable to focus management activities on sambar deer to reduce these impacts. The abundance and impacts of feral horses should be monitored because they can significantly impact high-elevation peatlands (Robertson *et al.* 2019).

Second, the decrease in sambar deer activity in the treatment area supports the potential of ground-based shooting as a tool to manage this species in high-elevation peatlands in south-eastern Australia. Third, sambar deer made seasonal use of high-elevation peatlands, being present and wallowing from October to June (i.e. spring–autumn). The departure of sambar deer from these high-elevation areas coincided with the accumulation of snow. There seems little point in attempting to shoot sambar deer in and around high-elevation peatlands during July–September, when they are absent. Fourth, sambar deer activity (including wallowing) was concentrated around sunset. We therefore predict that ground-based shooters would most likely encounter and shoot sambar deer around sunset rather than at other times (Little *et al.* 2014).

Supplementary material

Supplementary material is available online.

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Author affiliations

[A]Vertebrate Pest Research Unit, NSW Department of Primary Industries, 1447 Forest Road, Orange, NSW 2800, Australia.

[B]Parks Victoria, Mt Beauty, Vic. 3699, Australia.

[C]School of BioSciences, The University of Melbourne, Melbourne, Vic. 3010, Australia.

[D]Parks Victoria, 535 Bourke Street, Melbourne, Vic. 3000, Australia.

[E]Department of Environment, Land, Water and Planning, Arthur Rylah Institute for Environmental Research, 123 Brown Street, Heidelberg, Vic. 3084, Australia.

[F]Parks Victoria, Bright, Vic. 3741, Australia.

[G]Present address: North Coast Local Land Services, 24–26 Mulgi Drive, South Grafton, NSW 2460, Australia.

[H]Present address: Australian Museum Research Institute, 1 William Street, Sydney, NSW 2010, Australia.