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Invasive Deer Demonstrate Species-Specific Niche Habitat Selection in the Australian Alps

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ABSTRACT

Australia's invasive deer populations continue to expand in abundance and distribution, yet there is limited information on their movement patterns and habitat preferences. This inhibits the prioritisation of areas for control and conservation protection. We tracked 20 fallow deer (*Dama dama*), 5 red deer (*Cervus elaphus*), and 14 sambar deer (*Rusa unicolor*) to characterise their seasonal movement and habitat preferences in alpine and sub-alpine southeastern Australia. Autocorrelated kernel density estimated annual home ranges ($km^2 \pm SE$) averaged 226.9 ± 54.3 for male, and 55.1 ± 46.5 for female fallow deer, 70.2 ± 35.5 for female red deer, and 25.3 ± 4.0 for male, and 80.7 (one individual) for female sambar deer. Red and sambar deer were mainly restricted to eucalyptus forest/woodland (97% of fixes for sambar, 92% for red) and native grassland (2% of fixes for sambar; 8% for red). Fallow deer, however, were more generalist, and used comparatively less eucalypt forest/woodland (73%), spending more time in cleared areas (14%), and native grasslands (13%). Seasonal resource selection functions (RSFs) showed that, relative to eucalypt forest/woodland, fallow deer preferred cleared land for all seasons except summer, heathland for all seasons except winter, and inland aquatic areas in summer. All species tended to inhabit higher elevations in summer (average: 1517 m ASL for fallow; 1709 m ASL for red; 1463 m ASL for sambar), and lower elevations in winter (average: 1344 m ASL for fallow; 1483 m ASL for red; 1102 m ASL for sambar). Additionally, seasonal RSFs showed that red deer exhibited a preference for higher elevations within their available range in every season except winter, when they preferred lower elevations. Of concern, we found that sambar deer showed a preference for previously burnt areas in autumn (53% of fixes) and spring (89% of fixes), preferring areas with low to moderate and high-severity fire damage. Prioritising areas for control and conservation should be informed by deer movement and habitat preferences, and differences in such preferences between the three species studied herein suggest the need for tailored approaches for control to be effective in reducing their numbers and impacts on ecosystems.

1 | Introduction

Australia is a megadiverse country (Wilson et al. 1997), but it has been severely degraded since European colonisation (Legge et al. 2023), and has among the highest native species extinction rates globally (IPBES 2023; Woinarski et al. 2019). Colonisation led to extensive land clearing for agriculture and livestock (Bradshaw 2012) and facilitated the human-mediated movement of invasive species into Australia, including through acclimatisation societies. These societies aimed to distribute 'useful' species and make Australia more similar to landscapes in Great Britain (Bentley 1957; Rolls 1984). Today, introduced species are a key contributing threat to the decline of Australia's native flora and fauna (Legge et al. 2023; Woinarski et al. 2019). Indeed, six deer species have now established across a range of ecosystems in all Australian states and territories (Davis

Summary

- Invasive fallow deer, red deer, and sambar deer in the study system exhibit different movement and habitat preferences.
- All three species move between natural areas and cleared areas, but fallow deer spend a greater proportion of time in cleared areas and thus present a greater risk to agriculture through resource competition and disease transmission to livestock.
- Control should be prioritised in accordance with seasonal movements and should occur at higher elevations in summer and lower elevations in the colder months.
- Sambar deer were shown to use and select for burnt areas 2–3.5 years after fire, potentially preventing revegetation and post-fire recovery. Burnt areas should be targeted for control years after the fire.

et al. 2016). Deer browsing alters plant community composition (Wardle et al. 2001), and the exclusion of deer has been shown to lead to the recovery of forest understorey vegetation (Wills et al. 2023). Feral deer can act as reservoirs for pathogens that are transmissible to domestic livestock and other wildlife (Huaman et al. 2021). Additionally, wallowing by some deer species, including sambar deer (*Rusa unicolor*), threatens high elevation peatlands in southeastern Australia (Comte et al. 2022).

Three species of deer, fallow deer (*Dama dama*), red deer (*Cervus elaphus*) and sambar deer, are present within Kosciuszko National Park (hereafter KNP), a mountainous alpine and subalpine region in southeastern New South Wales, Australia (Atlas of Living Australia 2023). Fallow deer are originally native to the Mediterranean, where they inhabit temperate forests and grasslands, Mediterranean shrubby vegetation, as well as pastures and plantations (Masseti and Mertzanidou 2007). Red deer are native to Europe as well as western and central Asia, where they inhabit woodlands, upland moors, and open mountainous areas, but have also been reported along riverbanks in desert areas within their Asian range (Lovari et al. 2018). Sambar deer are the largest deer species present in Australia and are native to southern Asia, where they utilise a wide range of habitats including arid forests, rainforests, and alpine regions (Timmins et al. 2015). Sambar deer, unlike fallow deer and red deer, which have synchronised breeding in autumn (Bocci et al. 2012; Davini et al. 2004), can breed year-round in their native range (Dahlan and Dawend 2013). The Australian Alps cover just 0.15% of the Australian continent and are inhabited by many unique and range-limited flora and fauna (Kirkpatrick 1994; Williams et al. 2014). Uncontrolled livestock grazing occurred in KNP until the mid-1900s when the National Park was created, and since then, extensive rehabilitation and revegetation works have sought to restore the region, with natural vegetation recovery slow (Good and Johnston 2019; Scherrer and Pickering 2005). Recent aerial thermal surveys in the region where this study took place indicate that the three wild deer species co-occur at combined densities of up to 26.2 (95% CI = 15.5–44.3) deer km^{-2} (Cox 2024) and may cause similar damage to domestic livestock (Claridge 2016; Davis et al. 2016). KNP is bordered by agricultural land, and feral deer use of agricultural land can lead to resource competition and disease transmission to livestock (Cripps et al. 2019; Huaman et al. 2023; Smith et al. 2012). Feral deer are subject to ground and aerial control across KNP and surrounding agricultural areas, but the implementation of effective strategies could be improved with information on movement and habitat use by these species in this environment.

The need for deer control in KNP was intensified when more than 30% of the park was burnt in the 2019–2020 bushfires (Department of Planning and Environment 2023) as invasive species such as deer are known to exacerbate damage and prevent vegetation recovery in post-fire landscapes (Legge et al. 2022). Indeed, post-fire herbivory compounds the effects of fire through browsing and grazing of recovering vegetation (Smit and Coetsee 2019), which can alter vegetation species composition, reducing richness and diversity, promoting dominant and unpalatable species (Chard et al. 2022), and delaying the restoration of carbon and nitrogen soil accumulation and recovery (Stritar et al. 2010). Ungulate responses to fire are varied, with selection for burnt areas dependent on season (Ganz et al. 2022), species (Skatter et al. 2017), and time since fire (Lashley et al. 2015). In Australia, reductions in sambar deer activity have been reported immediately following fire, with activity increasing to pre-fire levels in the years following (Forsyth et al. 2012). Australia's alpine vegetation is slow growing, and high levels of bare ground and lower vegetation cover following fire leave burnt areas vulnerable to soil erosion and trampling for years after fire (Bridle et al. 2001; Wahren et al. 2001). Therefore, more research is needed to understand the post-fire responses of Australia's invasive deer species in order to adequately protect these systems.

Animal movement is fundamental to shaping ecological and evolutionary processes at local and ecosystem scales (Hansson et al. 2014), and invasive species have been shown to exhibit unexpected movement characteristics in their new ranges, such as increased rates of dispersal and larger home range sizes (e.g., Amos et al. 2014; Shine et al. 2021). Knowledge of feral deer movement and habitat preferences in Australia is limited, with few tracking studies examining fallow deer (e.g., Bengsen et al. 2024) and red deer (e.g., Amos 2015; Amos et al. 2014) movement characteristics, and none within an alpine environment. Sambar deer have not previously been tracked in Australia, and so our understanding of sambar deer biology has come from camera trapping studies (e.g., Comte et al. 2022), and international tracking studies of the species within its native range (e.g., Yen et al. 2019). A better understanding of invasive species movement and habitat preferences can aid in predicting their impacts, range expansions, and in implementing effective control measures (O'Reilly-Nugent et al. 2016).

In this study, we captured fallow deer, red deer, and sambar deer within KNP and used GPS collars to examine each species' seasonal and annual home range size ranges. We then evaluated each species' seasonal habitat preferences using resource selection functions (RSFs), evaluating preferences for elevation, slope, aspect, landcover type, and distance to perennial water sources. For sambar deer, we also evaluated preferences for burnt areas, as their movements overlapped with recent fire-affected habitat. For habitat preferences, we predicted (1) that

all species would predominately inhabit eucalypt forest/woodland, the most common vegetation type in the region, but would also inhabit native grasslands and cleared areas; (2) they would all inhabit higher elevations during the summer, and lower elevations during winter, where they will be more likely to inhabit cleared grassland areas, and present a greater risk to agriculture; and (3) that sambar deer will show a preference for burnt areas compared with unburnt areas. We use the results to identify areas where deer control should be prioritised, including areas where deer are more likely to be present and areas with high ecological vulnerability.

2 | Methods

2.1 | Study Area

This study took place in the Australian Alps, in an area within and surrounding KNP, on the Country of the Ngarigo People, between April 2021 and May 2023. Elevation in this area, defined as a 20 km radius around the minimum convex polygon (MCP) of all deer location fixes generated (see below), averages 1007 m and ranges from 123 to 2227 m above sea level (ASL). Slope averages 10° and ranges from 0° to 90°, aspect averages 136° and ranges from −1° to 360°, and distance to a perennial water source averages 697 m and ranges from 0 to 3548 m. Vegetation is dominated by eucalyptus forests and woodlands with tussock grass, fern and shrubby understories, and wet open tussock grasslands, interspersed with some shrubland and heathland. Some of the area has been cleared for agricultural and residential settlements (Figure 1). Continuous snow cover for at least 1 month of the year occurs within the sub-alpine zone of the study area (1350–1750 m ASL), while the alpine zone (above 1750 m) is mostly above the tree line and typically experiences continuous snow cover for at least 4 months of the year (MacPhee and Wilks 2013; Sanecki et al. 2006). The mean monthly maximum temperature at Thredbo Top Station (Latitude: −36.49, Longitude: 148.29, 1957 m ASL), centrally located within the study area, ranged from −0.1°C in July 2022 to 17.3°C in January 2022 (Bureau of Meteorology 2023a), and monthly total precipitation during the monitoring period ranged from 22.6 mm in April 2021 to 386 mm in October 2022, with the lowest precipitation typically occurring over winter and summer and the highest over spring (Bureau of Meteorology 2023b).

2.2 | Deer Capture and Collaring

Deer of all three species were captured and collared using aerial net gunning from a helicopter, with sedation administered via hand injection, and a GPS tracking collar with an inbuilt mortality sensor fitted (G52D Iridium, Advanced Telemetry Systems, Isanti, MN, USA) (see McCarthy et al. 2023). The smaller fallow deer were additionally captured in collapsible clover traps set up along game trails. Once set, clover traps were checked daily for trapped deer. If a deer was captured, the animal remained conscious, physically restrained by at least two personnel while a GPS collar was fitted.

In total, 20 fallow (11 males, 9 females), 5 red (2 males, 3 females), and 14 sambar (9 males, 5 females) were collared between April 2021 and December 2022. All collars were programmed to record animal locations hourly. Lowered activity for approximately 10 days following collaring has been reported for fallow deer (Bengsen et al. 2021) red deer, and sambar deer, while some sambar deer have been shown to undertake long-distance movements immediately following collaring (McCarthy et al. 2023). Therefore, the first 10 days of data following collaring were

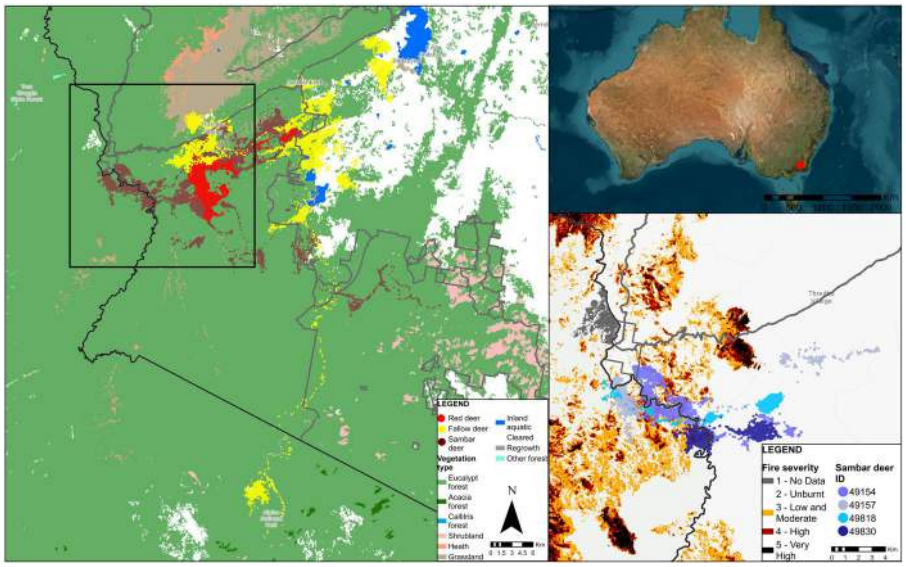

FIGURE 1 | Left: Map of study area, depicting sambar deer (*Rusa unicolor*; brown points; $N = 14$), red deer (*Cervus elaphus*; red points; $N = 5$) and fallow deer (*Dama dama*; yellow points; $N = 14$) GPS locations between April 2021 and May 2023, in and around southern Kosciuszko National Park, Australia. The black line indicates the NSW-Victoria border, the grey lines indicate the borders of Kosciuszko National Park. The black extent indicator shows the area displayed in the bottom right image. Top right: The location of the study area relative to Australia is indicated by the red dot. Bottom right: Location fixes of the four sambar deer (*Rusa unicolor*) between April 2021 and May 2023 that used areas burnt in the 2019–2020 fires, which affected parts of the alpine region in New South Wales and eastern Victoria. Image sources: Esri, Maxar, Earthstar Geographics, Department of Climate Change, Energy, the Environment and Water (2023).

excluded from analyses to allow the deer to resume normal behaviours. Deer in the following analyses were monitored for between three and 25 months, from April 2021 to May 2023. This study was approved by The University of Sydney Animal Ethics Committee (Project number: 2020/1844).

2.3 | Home Ranges

The study area (Figure 1) is characterised by strong seasonal variations in temperature and precipitation between four annual seasons—summer (December–February); autumn (March–May); winter (June–August) and spring (September–November). Therefore, for all seasonal home range and habitat preference analyses, movement data were broken up into these four seasons. Deer were included in the seasonal home range analyses only if they were monitored for the entire three-month period of a given season. For the home range calculations for each individual, all datapoints with horizontal dilution of precision (HDOP) greater than 2.5 or where HDOP could not be calculated were filtered from the dataset. If a single individual had more than 25% location fixes with a HDOP greater than 2.5 or missing, corresponding to ~22 days of unreliable data for a single season, and ~91 days for a yearly home range estimate, then the home range for this individual for this period(s) was not calculated (see Table S1).

Seasonal home ranges for each deer were calculated by modelling the GPS movement data as a continuous-time stochastic process, which models movement data assuming the animal is moving continuously and accounts for randomness in animal movement (Calabrese et al. 2016). We calculated seasonal 95% home range contours for all range resident individuals using the R package *ctmm* v1.2.0 (Calabrese et al. 2016). Individuals that occupied the same area continuously throughout the monitoring period were termed 'range resident' (Mueller and Fagan 2008). To do so, variograms, which visualise the average square distance travelled by each individual within their monitoring period, were used to assess the range residency of each individual. From visual assessment of variograms, if the semi-variance values reached an asymptote or flattened, before or at 3 months of monitoring, the individual was determined to be a range resident, and home range estimates were only generated for these individuals as range residency is an assumption of home range estimation (following Calabrese et al. 2016; Silva et al. 2021). For each range resident individual, perturbative hybrid residual maximum likelihood estimation, a model parameter estimation method, was used to determine which stationary movement model was most appropriate for each individual based on whether the data was autocorrelated or independently distributed. The models used were the independent and identically distributed (IID) null model, which is used when the animal has no autocorrelation, the Ornstein-Uhlenbeck (OU) model, which is suitable for data with autocorrelation in animal position, and the Ornstein-Uhlenbeck-F model (OUF), which is suitable when there is autocorrelation in animal position and velocity. Additionally, models were anisotropic if autocorrelation varied with direction (see Silva et al. 2021). The most appropriate movement model for each individual was selected based on AIC_C using the ctmm.select function (Calabrese et al. 2016) (Table S1). Then the 95% home range contour and 95% confidence intervals were quantified, via weighted autocorrelated kernel density estimation (wAKDE), for each deer, using the model selected in the previous step.

The seasonal 100% MCP 'movement extent' was then calculated for all individuals, including those that were not range resident, as a measure of each animal's total movement range, using the *adehabitatHR* package v0.4.21. These statistics allow comparison of home range sizes generated here with earlier studies, as the MCP method is widely used, and the range residence assumption is often not tested (Calenge 2007; Laver and Kelly 2008; Silva et al. 2021).

Then, to determine whether seasonal home range or movement extent (response variables) were affected by monitoring year (predictor variable), linear mixed models with Gaussian distributions and individual ID as a random effect were constructed for each species using the *nlme* package v3.1.153 (Pinheiro et al. 2016). To assess the normality and heteroscedasticity of the models, graphs of residuals against fitted values and explanatory variables were generated, and residuals fanned out as fitted values and explanatory variables increased, indicating that the residuals were heteroscedastic for all models. In response to this, the response variables were natural log transformed, and following the transformation, the residuals were homoscedastic for all models. The final models were fitted with the log of movement extent as the response variable and included sex and season in addition to year as fixed effects. Statistical significance was inferred at $\alpha = 0.05$. We report the beta coefficients, standard errors, and p-values for the fixed effects in each model.

Annual home ranges and movement extents were calculated using the wAKDE and MCP methods described above, and included location fixes from April 2021 to November 2023; deer were included in the analyses only if they were monitored for an entire year. If individuals were monitored for 2 years, an annual home range was calculated for each year and the results were averaged by species and sex. The effect of year on annual home ranges could not be tested because individuals were monitored over different year-long periods, depending on when each individual was first collared.

2.4 | Movement Activity

To discern patterns in the movement activity of each species and sex throughout the year, we calculated the mean daily Euclidean distance between hourly location fixes for all individuals. Where individuals were monitored for more than 1 year, distances travelled were averaged between years to generate one resulting value for each calendar day. The mean values for each individual were then averaged to generate a mean for each calendar day for each species and sex.

2.5 | Seasonal Variation in Elevational Use

We calculated the mean elevation used by fallow deer, sambar deer, and red deer for each season and fitted linear mixed models to determine how elevational usages changed between seasons, as described below. For these models and the RSFs described below, deer were excluded from the analyses if they were

monitored for less than 2 months in a given season. For all analyses, all datapoints with HDOP greater than 2.5 or where HDOP could not be calculated were filtered from the dataset, resulting in the removal of 2.8% or 8755 datapoints from the total dataset (similar to Stewart et al. 2022).

To determine whether the mean elevation used for each season by each individual (response variable) was affected by season (predictor variable), linear mixed models with Gaussian distributions and individual ID as a random effect were constructed for each species using the *nlme* package v3.1.153 (Pinheiro et al. 2016). For these models, we applied a weight equal to the number of observations contributing to each seasonal mean elevation, so that averaged observations with higher numbers of observations contributing to their means for each season were weighted higher. Model assumptions were assessed by examining residual plots against fitted values and explanatory variables to check for normality and heteroscedasticity. Statistical significance was inferred at $\alpha = 0.05$. We report the beta coefficients, standard errors, and p-values for the fixed effects in each model.

2.6 | Seasonal Habitat Selection

We used RSFs to examine habitat selection within each deer's seasonal movement extent in relation to a set of environmental covariates relevant to deer ecology (third-order habitat selection; Johnson 1980). The environmental variables included in the RSF model were elevation, slope, aspect, landcover type, distance to perennial water source, and burnt area. Burnt area was only included in RSFs for the four sambar deer which had available habitat in and used fire-affected habitat as fallow deer, and red deer, and all other sambar deer did not have any fire-affected habitat in their available habitat in any season (Figure 1). The aspect of the slope of each location clockwise from north was categorised into eight levels: north (0°–22° and 338°–360°), northeast (23°–67°), east (68°–112°), southeast (113°–157°), south (158°–202°), southwest (203°–247°), west (248°–292°) and northwest (293°–337°). Vegetation was classified into six types: cleared (including cleared areas, non-native vegetation and buildings, this landcover type is predominantly pasture in our study area), eucalyptus forest/woodland (consisting of forests and woodlands dominated by Eucalyptus species with a projective foliage cover of 10%–70%), native grassland (consisting of tussock grasslands and other grasslands, herblands, sedgelands and rushlands), inland aquatic (permanent water bodies, as well as areas which are subject to inundation or have ephemeral streams), shrubland (consisting of acacia and other shrubland) and heath (Table S2). Rasters were resampled to 100 m resolution using nearest neighbour resampling in ArcGIS Pro 3.1 (Environmental Systems Research Institute 2020). Reference categories for categorical variables were 'eucalypt forest/woodland' for landcover type, 'east' for aspect, and 'no fire' for burnt area. For all species, sexes were analysed together, as small sample sizes did not facilitate analysis of the effect of sex on habitat selection.

To define availability, we generated 10 random 'available' locations for each GPS location within the seasonal 100% MCP for each individual, then the values of each environmental covariate were extracted for all used and random points using R package *amt* v0.2.1.0 (Signer et al. 2019). For deer that were monitored over multiple years, a separate MCP was generated for each successive season that the animal was monitored, and available points were generated for each MCP. Then, data from each animal was combined into one resulting seasonal dataset for each deer species.

Prior to model fitting, all numerical variables were checked for collinearity using the Pearson correlation coefficient prior to analyses, with 0.7 considered the threshold for correlation, and no variables were correlated. All continuous covariates were scaled and centred, and available points were weighted by 1000 (Muff et al. 2020).

The method outlined by Muff et al. (2020) was used to fit RSFs as generalised linear mixed effects models (GLMMs) with a binomial distribution and a large, fixed variance using the glmmTMB function in the *glmmTMB* package v1.1.7 interfaced through a high-performance computer (Brooks et al. 2017). These RSFs examined the effect of each environmental variable on the binary response variable that was either a true location used by a deer ("case" = 1), or a random location within the individual's seasonal movement extent ("case" = 0). Each combination of deer species and season was modelled separately ($N = 12$). We included individuals as a random effect and random slopes for each covariate to account for variation in responses among individual deer (Muff et al. 2020). The global model that was run for each species and season is given below:

$$\begin{aligned}\text{Case} \sim\ & \text{elevation} + \text{slope} + \text{distance to water} \\ & + \text{vegetation type} + \text{aspect} + (1|\,\text{ID}) + (0 + \text{elevation}|\,\text{ID}) \\ & + (0 + \text{slope}|\,\text{ID}) + (0 + \text{distance to water}|\,\text{ID}) \\ & + (0 + \text{vegetation type}|\,\text{ID}) + (0 + \text{aspect}|\,\text{ID}).\end{aligned}$$

First, we fitted the global models and checked for model convergence issues. If a global model did not converge, we examined the full set of sub-models to identify which variables or their random slopes might be causing non-convergence. For all models, random slopes for the categorical variables vegetation type and aspect had a variance close to zero, which led to model convergence issues, so these random slopes were removed from all global models and all sub-models (as in Hooven et al. 2023). To evaluate model fit, we compared AICc values of the global model and full sub-model sets and selected the model with the lowest AICc value for each season and species, using *AICcmodavg* (Mazerolle 2023). To determine the effect of each environmental variable on deer resource selection, we examined the β coefficients and confidence intervals of each environmental variable in the best-fitting model. Here, model inference was drawn from the magnitude of effect size and its corresponding confidence intervals.

2.7 | Burn Severity Selection by Sambar Deer

An area in the north-west of the study area was burnt with low to very high intensity during extensive bushfires between December 2019 and January 2020 (Figure 1; Department of Planning and Environment 2023). Step-selection functions (SSFs) were

evaluated to examine sambar deer movement decision-making in their use of fire-affected areas and their burn-severity preferences. Only four collared sambar deer (3 males, 1 female) had available habitat in the burnt area; therefore, all other animals were excluded from this analysis. To examine fine-scale sambar deer preferences when they were close to burnt areas, the location data was subset to include only locations within 500 m of burnt areas. Some collars recorded location information less frequently than hourly towards the end of their life, so location data were resampled to 8 h for consistency between individuals. Then, 100 random steps were generated for each used step by drawing from a gamma distribution of step lengths (rate = 430.256, shape = 0.984) and a von Mises distribution of turn angles (mean = 0.003, kappa = 0.093). The parameters of each distribution were calculated using packages *MASS* v7.3–64 (Ripley et al. 2025) and *circular* v0.5–1 (Lund et al. 2024). Fire-severity scores: 'no data' (unknown fire status, likely due to cloud contamination in imagery within a fire extent [W. Dorrington, personal communication, September 5, 2023]), 'unburnt', 'low–moderate' (burnt understory, unburnt canopy), 'moderate' (partial canopy scorch), 'high' (complete canopy scorch, partial canopy consumption), or 'very high' (full canopy consumption) were extracted for all steps at the end point of each step using a Fire Extent and Severity map (Table S2), and 'unburnt' was selected as the reference category. Individuals were modelled separately using conditional logistic regression models in the *survival* package v.3.8.3 (Therneau et al. 2023). To infer group-level responses, we calculated inverse-variance weighted averages of the coefficients across individuals; we calculated confidence intervals from the average weighted estimates. One female sambar deer (ID: 049818) was excluded from model-averaged estimates due to model convergence issues, likely due to low sampling of the very high-severity burn class by this individual. The statistical significance of results was inferred if the confidence intervals of the model did not include zero. All statistical analyses were conducted in R (R Core Team 2021) interfaced via RStudio Desktop (v. 4.3.2).

3 | Results

3.1 | Animals Monitored

In total, location data from 13 sambar (8 males, 5 females), 5 red (2 males, 3 females), and 14 fallow deer (7 males, 7 females) were included in this study. Of the 14 sambar deer collared, one deer was excluded due to unconfirmed mortality/collar malfunction less than 2 months following collaring. Of the 20 fallow deer collared, six were excluded from the analysis, two because of confirmed mortality by a human hunter, and four because of unconfirmed mortality/collar malfunction less than 2 months after capture.

3.2 | Home Ranges and Movement Activity

Year of monitoring did not have an effect on the resulting seasonal movement extent and home ranges of fallow deer, red deer, or sambar deer (Table S3). Therefore, mean seasonal home ranges are presented with data from 2021 to 2023, with seasonal home ranges combined across years to generate means and standard errors (Table S4). We found that fallow deer home ranges and movement extents were highest in spring and autumn for males, while for females, movement extents were smallest in winter but stable across the other seasons, while home ranges were smallest in spring but stable across the other seasons (Figure 2). For red deer, movement extents and home ranges were highest in summer (and autumn for movement extent) for males, while for females, movement extent and home range were lowest in winter and relatively stable across the other seasons (Figure 2). For fallow deer and red deer, acute increases in movement activity were recorded in April, in alignment with the breeding season (rut; Figures S1–S3). For sambar deer, male movement extent was highest in autumn and winter, and home range was highest in spring and autumn; for females, movement extent was relatively stable throughout the year, while home range was highest in autumn and relatively stable across the other seasons (Figure 2; Table S4).

Fallow deer males had an annual home range of $226.9 \pm 54.3\,km^2$ ($N = 4$), and a movement extent of $78.2 \pm 5.9\,km^2$ ($N = 5$), while females had a home range of $55.1 \pm 46.5\,km^2$ ($N = 3$), and a movement extent of $50.2 \pm 14.1\,km^2$ ($N = 7$; Table S4). No red deer males were monitored for a full year, so only the female red deer annual home range is reported and was $70.2 \pm 35.5\,km^2$ ($N = 4$); the female red deer annual movement extent was $35.3 \pm 5.2\,km^2$ ($N = 4$; Table S4). Sambar deer males had an annual home range of $25.3 \pm 4.0\,km^2$ ($N = 2$) and a movement extent of $111.9 \pm 56.7\,km^2$ ($N = 5$); sambar deer females had a home range of $80.7\,km^2$ ($N = 1$), and a movement extent of $64.9 \pm 3.3\,km^2$ ($N = 3$; Table S4).

3.3 | Seasonal Habitat Preferences

For fallow deer, the mean elevation used in summer was 1517 m ASL (Q1: 1235 m, Q3: 1762 m) and the mean slope used was 11° (Q1: 6°, Q3: 14°). In autumn, this reduced to 1449 m (Q1: 1187 m, Q3: 1740 m), and the mean slope used was 11° (Q1: 6°, Q3: 15°). By winter, they used a mean elevation of 1334 m (Q1: 1151 m, Q3: 1520 m) and the mean slope used increased to 16° (Q1: 9°, Q3: 22°). Fallow deer remained at a similar elevational range in spring (mean: 1334 m, Q1: 1157 m, Q3: 1560 m), and used a mean slope of 11° (Q1: 6°, Q3: 16°). The linear mixed model evaluating between-season elevational usage by fallow deer showed that the mean elevation used by the species was significantly lower in winter ($\beta = -205.013$, SE = 95.322) compared with summer (Table S5).

For RSFs for all seasons and species, the global model was the best performing model, with $\Delta AIC_C \geq 3$ when compared to the next best competing sub-model (Table S6). For fallow deer, seasonal RSFs indicated that they had no elevational preference within their seasonally available ranges (Figure 3A–D), but they showed a preference for gentler slopes in summer and autumn (Figure 3A,B; Table S6). Fallow deer showed no clear preference for proximity to water in any season (Figure 3A–D). The majority of vegetation used by fallow deer was eucalypt forest/woodland; however, in summer, fallow deer preferred heath and inland aquatic areas, and avoided native grasslands (Figures 3A and 4). In autumn, fallow deer preferred cleared areas and heath, and avoided inland aquatic areas and native grasslands (Figure 3B). In winter, fallow deer were never located in heath, inland aquatic areas, or shrubland. They preferred cleared areas compared to eucalypt forest/woodland and avoided native grassland (Figure 3C). By spring, fallow deer showed a preference for cleared areas and heath, and avoidance of native grassland and inland aquatic areas (Figure 3D). In summer and autumn, fallow deer preferred east

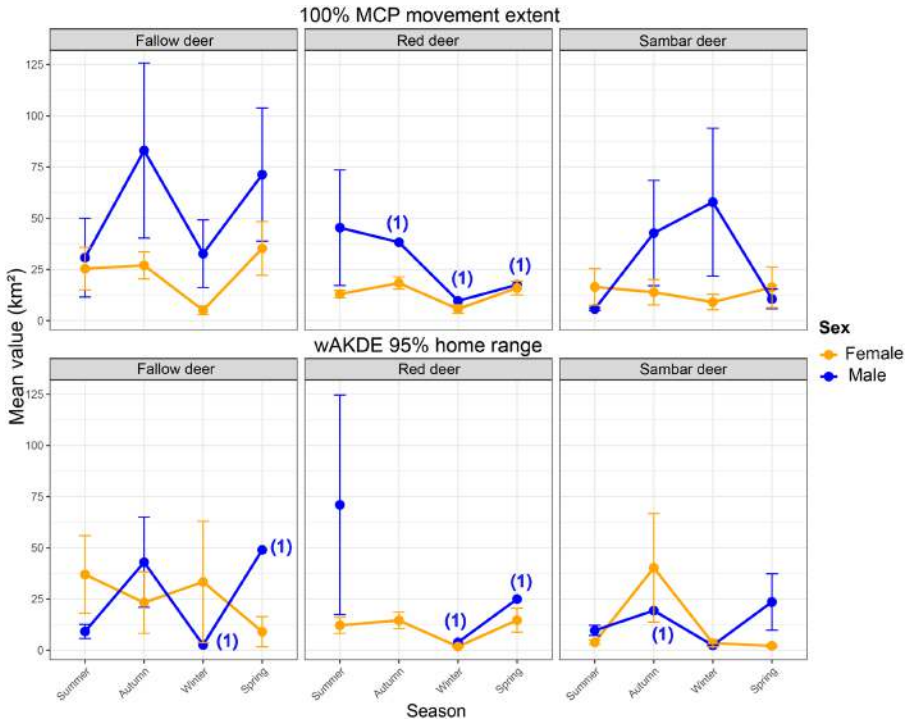

FIGURE 2 | Seasonal mean movement extents (100% minimum convex polygons; top row) and home ranges (95% weighted autocorrelated kernel density estimates; bottom row) of fallow deer, red deer and sambar deer males (blue) and females (orange) in a sub-alpine area of Kosciuszko National Park, Australia. Points with a (1) beside them indicate that only one animal contributed to the estimate for that season.

and north-facing slopes (Figure 3A,B); in winter, they preferred east and west-facing slopes (Figure 3C); and in spring, they preferred east facing slopes (Figure 3D; Table S6).

For red deer, the mean elevation used in summer was 1709 m ASL (Q1: 1672 m, Q3: 1759 m) and the mean slope used was 13° (Q1: 8°, Q3: 17°). In autumn, the mean elevation used reduced to 1672 m (Q1: 1616 m, Q3: 1778 m) and the mean slope used was 14° (Q1: 8°, Q3: 19°). In winter, the mean elevation used reduced again to 1483 m (Q1: 1348 m, Q3: 1636 m), and the mean slope used increased to 21° (Q1: 17°, Q3: 25°). In spring, the mean elevation used increased to 1633 m (Q1: 1607 m, Q3: 1749 m), and the mean slope used decreased to 14° (Q1: 8°, Q3: 19°). The linear mixed model evaluating between-season elevational usage by red deer showed that the mean elevation used by the species was significantly lower in winter ($\beta = -218.230$, SE = 44.853), compared with summer (Table S5).

Seasonal RSFs indicated that red deer showed a strong preference for higher elevations within their seasonally available habitats for all seasons except winter, where they showed a preference for lower elevations (Figure 3E–H). Red deer preferred steeper slopes in winter and spring (Figure 3G,H; Table S6); in spring and autumn, they showed a preference for habitats away from continuous waterbodies (Figure 3F,H). The majority of vegetation used by red deer was eucalypt forest/woodland, which red deer preferred in all seasons, compared to other used habitat types, cleared areas, and native grasslands (Figures 3E–H and 4). In winter, red deer used and selected for shrubland (Figure 3G). In spring, red deer used inland aquatic areas, for which they did not show a preference compared to other used habitat types (Figure 3H). In summer and autumn, red deer avoided east and west-facing slopes, preferring south and north-facing slopes (Figure 3E,F). In winter, they showed the strongest preference for southeast and west facing slopes; (Figure 3G). By spring, they showed a strong preference for southeast and west-facing slopes (Figure 3H; Table S6).

For sambar deer, in summer, the mean elevation used was 1463 m ASL (Q1: 1461 m, Q3: 1695 m) and the mean slope used was 15° (Q1: 9, Q3: 20°). In autumn, the mean elevation used was 1353 m (Q1: 854 m, Q3: 1693 m), and the mean slope used was 16° (Q1: 10, Q3: 20°). In winter, the mean elevation used reduced to 1102 m (Q1: 683 m, Q3: 1457 m), and the mean slope used was 18° (Q1: 11, Q3: 24°). In spring, the mean elevation used was 1162 m (Q1: 743 m, Q3: 1433 m), and the mean slope used was 17° (Q1: 11°, Q3: 23°). The linear mixed model evaluating between-season elevational usage by sambar deer showed that the mean elevation used by the species was significantly lower in winter ($\beta = -496.106$, SE = 84.029) and spring ($\beta = -434.214$, SE = 103.587), compared with summer (Table S5).

Seasonal RSFs indicated that sambar deer showed no substantial elevation or slope preferences within their seasonally available ranges (Figure 3I–L; Table S6). In winter, sambar deer preferred locations closer to perennial water sources compared with what was available within their available ranges (Figure 3K). The majority of vegetation used by sambar deer was eucalypt forest/woodland, which sambar preferred in all seasons, compared to other used habitat types, cleared areas and native grasslands (Figures 3I–L and 4). In summer, sambar deer preferred east and southeast-facing slopes (Figure 3I). In autumn, they selected for north and northeast facing and southeast facing slopes (Figure 3J). In winter and spring, they selected for northeast,

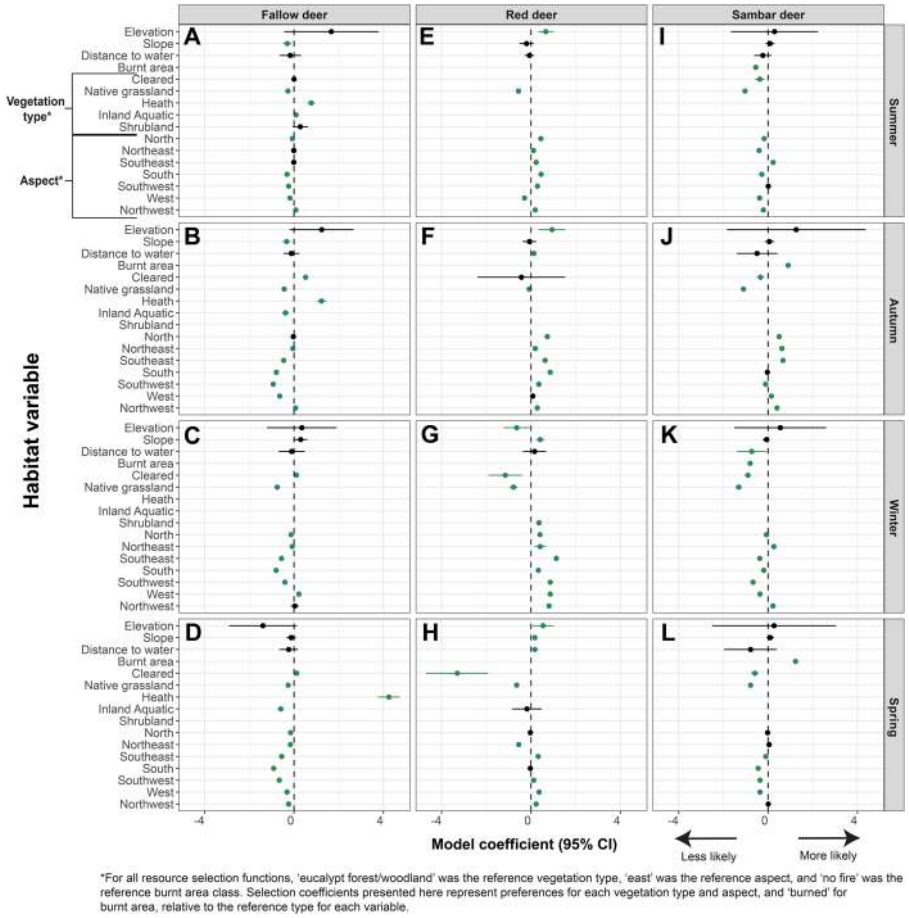

FIGURE 3 | Selection coefficients (β parameter estimates) and 95% confidence intervals of generalised linear mixed effects resource selection functions, modelling the habitat preferences of fallow deer, red deer, and sambar deer in the Snowy Mountains region, in and around Kosciuszko National Park, in southeastern Australia. Coefficients coloured green have confidence intervals that do not include zero. For continuous variables, the direction of the coefficient indicates whether a species was more (coefficient above zero) or less (coefficient below zero) likely to be present at higher values of each variable. For categorical variables, the direction of the coefficient indicates whether the species was more (coefficient above zero) or less likely (coefficient below zero) to be present in that category relative to the reference class. Where a selection coefficient is not present, this habitat type was not experienced by any collared animal of that species for that season.

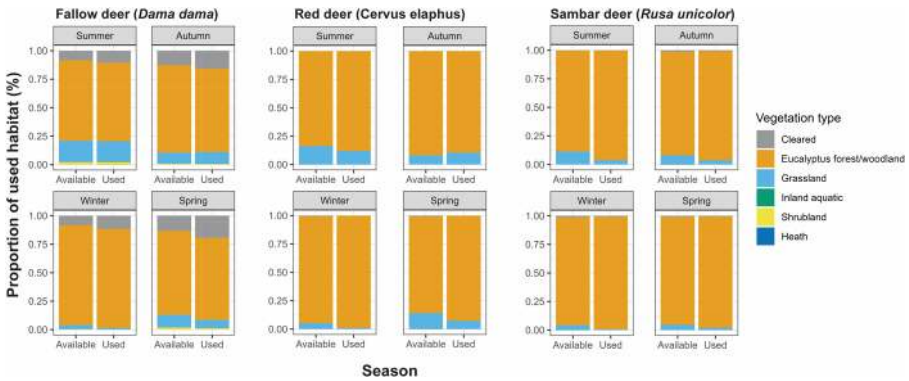

FIGURE 4 | The proportion of used versus available habitat types for three species of feral deer, fallow deer, red deer, and sambar deer, which are present in the Snowy Mountains region, in and around Kosciuszko National Park, in southeastern Australia, between April 2021 and May 2023.

east and northwest facing slopes (Figure 3K,L). In summer and winter, the four sambar deer that used fire-affected habitat avoided burnt areas but selected for burnt areas in autumn and spring (Figure 3I–L; Table S6).

3.4 | Burnt Severity Selection by Sambar Deer

For the three sambar deer that were included in this analysis, individual preferences were variable, with one individual

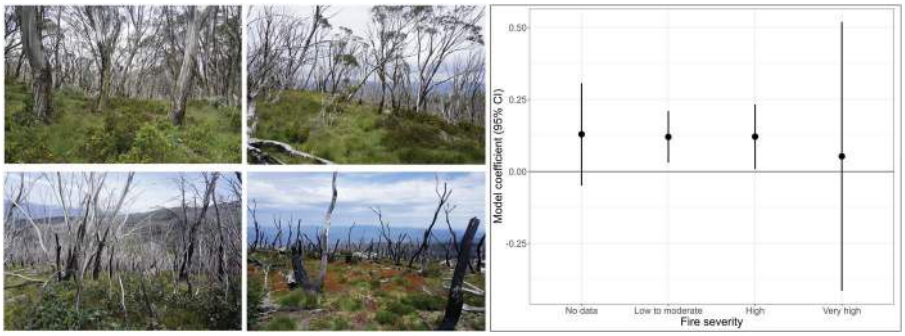

FIGURE 5 | Left: Images of landscape affected by the 2019–2020 fires in the region, showing unburnt (top left), low to moderate severity (top right), high-severity (bottom left) and very high-severity burnt forest (bottom right); all images were taken in December 2023. Burn-severity data source: Department of Planning and Environment (2023). Right: Averaged step-selection function coefficients and 95% confidence intervals of burn-severity class preference relative to unburnt areas (the reference class) of GPS-collared sambar deer between 2021 and 2023 in the Snowy Mountains region of southeastern Australia, when within 500 m of a burnt area. The three individuals were modelled separately using conditional logistic regressions, and coefficients were inverse-variance averaged for group-level inferences.

selecting for low to moderate and high-severity burnt areas, and one individual selecting for low to moderate burnt areas; the third individual did not show a preference (Table S7). The inverse distance weighted average selection coefficients of the SSFs run for each individual showed that when these individuals were within 500 m of burnt habitat, they preferentially inhabited areas that were burnt in the 2019–2020 fires with low to moderate and high-severity intensity (Figure 5).

4 | Discussion

In this study, we sought to understand fallow deer, sambar deer, and red deer habitat preferences based on home range and movement data, so that control efforts can be more precisely targeted to at-risk environmentally sensitive areas and locations where deer are most likely to be present. Sample sizes for all three species, particularly red deer, were low, so our findings may not be representative of the species; nonetheless, our study provides insight into habitat use by invasive deer within the Australian Alps. As predicted, (1) all species mainly inhabited eucalypt forest/woodland; however, while red deer and sambar deer-inhabited eucalypt forest/woodland more than 90% of the time, fallow deer were more varied in their habitat use and spent time in cleared areas, heathland, and inland aquatic areas. (2) All species tended to inhabit higher elevations in summer and lower elevations in winter, with all species using significantly lower mean elevations in winter compared to summer, and for sambar deer, in spring compared to summer. Additionally, within their seasonally available ranges, red deer selected for higher elevations in summer, autumn, and spring, but lower elevations in winter. (3) Fallow deer and red deer did not inhabit burnt areas, and while only four sambar deer used burnt areas, these sambar deer preferentially inhabited these areas in spring and autumn, selecting for low to moderate and high-severity burnt areas. The three invasive deer species found in alpine Australia display distinct seasonal movement patterns and habitat preferences. Recognising and understanding these differences is crucial when devising control programmes and prioritising conservation efforts.

4.1 | Fallow Deer Home Range and Habitat Use

Annual home range estimates of fallow deer in this study exceeded prior estimates from the USA (Morse et al. 2009), Poland (Borkowski and Pudełko 2007), and Italy (Ciuti et al. 2003; Davini et al. 2004). Seasonal home ranges recorded in this study were also considerably larger than previously reported estimates from Poland (Borkowski and Pudełko 2007) and Italy (Ciuti et al. 2003; Davini et al. 2004) across all seasons. Fallow deer in our study had the largest home ranges in spring for males, and in summer for females (Figure 2; Table S4). Previous research on fallow deer in Italy, within the native range of fallow deer, showed that the home range was largest in autumn for both sexes (Borkowski and Pudełko 2007; Ciuti et al. 2003). Despite home ranges not being the largest in autumn in this study, male movement extents were largest in autumn (Figure 2), suggesting non-range residents were undertaking longer-distance movements. Additionally, we saw a spike in male activity, or mean hourly distances travelled, in April (during autumn), which coincides with the breeding season (rut; Figure S1), when adult males are known to follow and defend groups of females and fight with other males (Alvarez et al. 1990; Jennings et al. 2013).

In our study area, fallow deer appeared to be a more generalist species than red deer and sambar deer, inhabiting a wider variety of habitat types (Figure 3A–D). Fallow deer also showed a preference for inland aquatic areas in summer (Figures 3A and 4). Although we could not uncover what fallow deer were using these aquatic areas for, swimming has been reported in Persian fallow deer (Khademi 2014). While fallow deer were shown to avoid native grasslands, they did use native grasslands more often than their heterospecifics, particularly in summer (Figures 3A and 4). Fallow deer also used a higher proportion of cleared land in all seasons compared with sambar deer and red deer, selecting for cleared areas in autumn, winter, and spring (Figures 3B–D and 4). Fallow deer are known to be opportunistic generalist grazers and browsers (Davis et al. 2023), and are highly adaptable to seasonal food availability (Esattore et al. 2022). They browse on lower-quality food while snow covers ground vegetation

during the European winter (Kamler and Homolka 2011), and graze on crops and pasture in agricultural areas in Australia (Bentley 1998; Davis et al. 2023; Hall and Gill 2005). Their adaptable dietary requirements and use of a variety of vegetation types in alpine Australia suggest that fallow deer present a widespread risk and should be targeted for control in a variety of habitat types in the Australian Alps.

4.2 | Red Deer Home Range and Habitat Use

Like fallow deer, red deer home range estimates from this study were considerably larger than previous estimates of the red deer home range from Australia and abroad (Amos et al. 2014; Catt and Staines 1987; Jerina 2012; Reinecke et al. 2014). In Queensland, in a low elevation subtropical environment, red deer had home ranges that were lowest during the rut (6 km^2 for males and ~1 km^2 for females) for 1 year and second lowest behind summer for another year. The one male in our study that was monitored during the autumn period was not range resident and had a movement range almost twofold the mean summer range for males (Figure 2; Table S4). The mean movement extent of red deer females in this study also peaked in autumn (Figure 2; Table S4), where only three of five individuals were range resident, and like fallow deer, male red deer also had a peak in movement activity between late March and early April (Figure S2). Heightened activity during the rut for red deer males is well documented and increases mating success (Csányi et al. 2022). Previous research has shown that females may also make extraordinary movements when in oestrus during the rut, potentially to pursue novel matings (Stopher et al. 2011); however, we did not see a peak in activity for female red deer during this period (Figure S2). This may be because the red deer population has a restricted range within the study area (suggested in Figure 1) and movements outside of this range would not lead to novel matings. Tracking greater numbers of red deer or conducting indirect sampling (either through camera trapping or faecal pellet surveys) would establish the total movement range of the red deer population within the study area, and if they were locally confined, control could aim for local eradication.

In summer, red deer tended to inhabit higher elevations than the other two species and had no cleared land within their used habitat, indicating that all individuals remained within the national park for the duration of the season, despite the summer home range being the largest seasonal home range for male red deer (Figures 2, 3E and 4). This peak in home range size in summer has previously been reported for male red deer in Europe (Clutton-Brock et al. 1982; Georgii and Schröder 1983), but was not found for red deer in subtropical Australia (Amos et al. 2014). In areas with more extreme seasonal and temperature variation, like our study area in alpine and sub-alpine KNP and surrounds, red deer may behave more similarly to their European conspecifics and may seek out habitats that maximise energy gains in summer in preparation for the rut, as seen in Europe (Bocci et al. 2012). For autumn, winter, and spring, red deer in our study continued to occupy higher mean elevations than the other two species and used a more limited range of vegetation types than fallow, using predominantly eucalypt forest/woodland, but also native grassland, cleared lands (in all seasons except summer) and inland aquatic areas (in spring). Previous research indicates that the likelihood of red deer presence on agricultural land decreases with distance to forest (Månsson et al. 2021); similarly, while red deer in this study did use a small proportion of cleared land close to sub-alpine KNP, they used cleared areas the least of the three species studied. Red deer predominantly inhabited the high elevation forested areas within KNP; these results suggest that control targeting this species in the summer may be most efficient, as red deer are likely to be within the national park and not on private property.

4.3 | Sambar Deer Home Range and Habitat Use

Sambar deer are reported to be mainly sedentary (Leslie Jr. 2011) and we saw that home ranges of range resident males and females tended to be lower than for the other two species for range resident males in all seasons except summer, and range resident females in summer and spring (Figure 2; Table S4). Despite this, annual movement extents of non-range residents were the largest of the three species, and markedly larger than other previously reported annual home range estimates for the species in Taiwan (Yen et al. 2019), India (Sankar 1994), and the USA (Richardson 1972; Shea 1986). Notably, home ranges for all three species were larger than several other earlier reported estimates of their conspecifics in other regions. In tracking efforts with a small effective sample size, conventional home range estimators have been shown to markedly underestimate home range size, so in this study we used an AKDE home range estimator to mitigate this effect (Silva et al. 2021), and this may have also contributed to the larger home ranges we found. Notably, however, invasive species at the invasion front have been reported to exhibit larger daily movement distances than conspecifics in their native ranges (Shine et al. 2021), as well as larger exploratory home ranges compared to those in longer-established areas (Burstal et al. 2020). The larger home ranges we report in this study could also potentially be a function of low resource density and preferable habitat within the study region, as higher forage quality (Tomaszewski et al. 2022) and productivity (Bjørneraas et al. 2012) have been associated with smaller home range sizes.

Sambar deer exhibited seasonal movement patterns, moving to lower elevations in winter, compared with their summer range (Table S5); this behaviour has been reported for sambar deer in Australia (Comte et al. 2022; Greene 2022), as well as within their native range (Yen et al. 2019). Across the monitoring period, however, sambar deer location fixes ranged from elevations between 123 and 2046 m ASL, and they tended to utilise lower mean elevations than the other two species throughout the seasons, despite lower available elevations not being selected for within their seasonally available range in any season (Figure 3I–L). Sambar deer may be occupying lower elevations than the other two species because they are a predominantly tropical species, and have a lighter weight coat and lower capacity for heat production than the other species (Semiadi et al. 1996). Unlike the other two species, sambar deer are known to mate year-round closer to the equator, within their native ranges (Dahlan and Dawend 2013). However, further from the equator, they may have a more distinct breeding

season; for example, in alpine and sub-alpine Victoria, peak rutting occurs in spring (Watter et al. 2020). However, in this study, unlike the other two species, there are no visually distinct peaks in sambar deer distances travelled throughout the year that may be indicative of altered activity due to breeding, suggesting they exhibit a broad breeding pattern in this study (Figure S3). While fallow deer and red deer exhibit heightened activity during the autumn rut, sambar deer maintain relatively consistent activity levels throughout the year, and instead, their movements are more likely dictated by seasonally dependent habitat selection.

Sambar deer showed a preference for areas closer to perennial water sources in winter; for other seasons, estimates suggested a preference but were not reliable due to high variance (Figure 3I–L). In Victoria, sambar deer presence and density have previously been correlated with closeness to water, as these areas likely support higher quality forage (Fedrigo et al. 2024; Forsyth et al. 2009; Sotorra et al. 2020); however, another study in sub-alpine Victoria suggests lower activity of sambar deer close to watercourses (Comte et al. 2022). Sambar deer used the most limited range of vegetation types, using only eucalypt forest/woodland, native grassland, and cleared area throughout the monitoring period, showing a strong preference for eucalypt forest/woodland for all seasons (Figures 3I–L and 4). Sambar deer are known to be forest-dwelling and have previously been reported to only enter open areas at night to feed (Porwal et al. 1996); despite this, open habitats are thought to be important feeding habitats for sambar deer (Forsyth et al. 2009). Our study indicates that sambar deer exhibit a preference for forested regions near water sources. Sambar deer may therefore pose a heightened risk to waterways, with greater potential for damage through trampling and wallowing (as in Comte et al. 2023). Consequently, targeted control measures in proximity to sub-alpine and alpine wetlands and waterways should be considered to safeguard these ecosystems.

In autumn and spring of 2021–2023, sambar with available habitats intersecting fire-affected areas in the 2019–2020 megafires showed a preference for burnt areas 2–3.5 years post-fire (Figure 3J,L). SSFs showed that, compared with unburnt areas, sambar deer preferred low to moderate (burnt understory and unburnt canopy) and high-severity (complete understory scorch, partial canopy consumption) burnt areas (Figure 5; Department of Planning and Environment 2023). Previous studies of sambar deer in Australia show that populations were substantially reduced immediately following fire, but that burnt habitat was reoccupied 1.3–2 years post-fire (Forsyth et al. 2012). Post-fire successional changes in vegetation may provide higher quantities of high-quality forage and denser understorey for shelter, which sambar may be selecting for (Downes 1983; Fuhlendorf et al. 2009); this has previously been shown for elk in North America (Bailey and Whitlam 2002). Post-fire herbivory can prevent the regeneration of native vegetation and alter plant community composition (Tuft et al. 2012). Sambar deer are known to eat invasive plant species, such as Hawkweed (*Pilosella* spp.), in Alpine areas (Quin et al. 2023), and so could potentially aid in the colonisation of invasive plant species in fire-affected areas in Australia via seed dispersal. Future research on plant species preferred by sambar deer post-fire could clarify vulnerability to herbivory and trampling in native species and identify invasive species at risk of dispersal by sambar deer. This information could aid in prioritising control efforts for at-risk ecological communities.

4.4 | Management Implications for Invasive Deer

In Australia, limited knowledge of invasive deer movement potential, interactions with threatened habitats, and their agricultural impact prevents the development of targeted management approaches (Davis et al. 2016). Knowledge of deer movement and habitat preferences should be used to develop scientifically informed control programmes (as described in Comte et al. 2022; Forsyth et al. 2010; Latham et al. 2015). All three deer species studied herein exhibited seasonal altitudinal migration, inhabiting higher elevations in summer and moving to lower elevations in winter. This pattern is reflected in the mean elevations used by all three species, and statistical testing supported this seasonal shift for all three species (Table S5). Therefore, we recommend control be prioritised in accordance with seasonal movements and should occur at higher elevations in summer and lower elevations in the colder months (previously proposed for sambar in alpine Australia in Comte et al. 2022). In the colder months, we saw that the three species had lowered activity and small seasonal home ranges and had the lowest proportion of fixes in native grassland. Therefore, as animals will be less active, they may be less visible and more difficult to target in aerial shooting operations, and control during the colder months may be less effective, although lower temperatures would be more favourable for thermal aerial culling operations (Cox et al. 2023). Our habitat selection analyses imply that we can selectively target species by targeting specific habitats; for example, control on cleared or agricultural areas may more likely result in a population reduction for fallow deer, as they occupy cleared areas more often than the other two species, particularly in autumn and, to a lesser extent, winter and spring, when they exhibit the strongest selection for cleared areas. The effectiveness of targeting preferred vegetation types for deer population control should be formally evaluated for our study area. Moreover, fallow deer movement between agricultural land and adjacent national park creates the opportunity for dispersal of plants, including invasive species, between the two zones, and of particular concern would be the movement of plants from the agricultural areas to the national park (Claridge et al. 2016). Fallow deer are also more likely to be vectors of disease to domestic animals and livestock, particularly in the warmer months when they are more likely to move between agricultural and wilderness areas (Pacioni et al. 2022). Critically, control efforts typically target burnt areas immediately after fire, where the open post-fire canopy improves visibility (Rumpff et al. 2023); however, deer populations have been shown to decrease in burnt areas immediately post-fire and increase in the years following (Forsyth et al. 2012). In addition to post-fire control, burnt areas should therefore be targeted in the years following a fire, when invasive herbivores like sambar deer use burnt areas and likely increase damage and prevent regeneration and post-fire recovery.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy restrictions.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.