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ORIGINAL PAPER

Intensive professional vehicle-based shooting provides local control of invasive rusa deer in a peri-urban landscape

Sebastien Comte · Andrew J. Bengsen · Calum X. Cunningham · Michelle Dawson · Anthony R. Pople · David M. Forsyth

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Abstract Non-native deer are becoming increasingly common in peri-urban landscapes, where they pose a risk to the health and wellbeing of people. Professional vehicle-based shooting is commonly used to control deer populations in these complex landscapes, but the effectiveness and cost of this method have seldom been evaluated. We analyzed the effectiveness and cost of using professional vehicle-based shooting to reduce the abundance and impacts of non-native rusa deer (*Cervus timorensis*) in a peri-urban landscape in Wollongong, eastern Australia, during 2011–2021. We incorporated the results from an independent monitoring program into a Bayesian joint-likelihood framework to model spatio-temporal changes in rusa deer abundance. Finally, we used our findings to assess the effect of the management program on the number of complaints from the residents. After eleven years and the removal of 4701 rusa deer from Wollongong LGA (712 km^2), deer abundance did not change in 74.7% of the area, decreased in 19.4% of the area (mostly in and around the sites where the professional shooting occurred), and increased in 5.9% of the area. Shooting was most cost-effective during winter when the longer hours of darkness meant that shooters could visit more sites. In contrast to deer abundance, the probability of residents complaining about deer increased in space and time. Our study shows that professional vehicle-based shooting can locally reduce the abundance of invasive deer in a peri-urban landscape, providing that sufficient control effort is expended. We suggest that shooting effort is currently too thinly spread across this peri-urban landscape, and that concentrating shooting effort on the areas of greatest deer

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S. Comte (✉) · D. M. Forsyth
NSW Department of Primary Industries, Orange, NSW, Australia
e-mail: sebastien.comte@dpi.nsw.gov.au

S. Comte · D. M. Forsyth
The University of New South Wales, Sydney, NSW, Australia

A. J. Bengsen
NSW Department of Primary Industries, Calala, NSW, Australia

C. X. Cunningham
School of Natural Sciences, University of Tasmania, Hobart, TAS, Australia

M. Dawson
South East Local Land Services, Wollongong East, NSW, Australia

M. Dawson
NSW Department of Climate Change, Energy, Environment and Water, Parramatta, NSW, Australia

A. R. Pople
Queensland Department of Agriculture and Fisheries, Dutton Park, QLD, Australia

abundance and resident complaints might be a more cost-effective strategy for managing invasive deer in peri-urban landscapes.

Keywords Cost-effectiveness · Culling · Peri-urban rusa deer · Professional shooting · Resident complaints · Wildlife management

Introduction

Biological invasion of urban areas is a primary source of human-wildlife conflicts. With urbanization increasing worldwide (Grimm et al. 2008) and more people living in cities than in rural landscapes (United Nations 2019), cost-effective management programs are needed to reduce the detrimental impacts of invasive species in urban areas (Gaertner et al. 2017). The fringe of urban habitat (hereafter referred to as peri-urban), characterised by lower density settlements surrounded by vegetation (gardens, parks, green corridors), provides abundant food and shelter for invasive species in which they can reach higher densities than in the more rural surroundings (Polfus and Krausman 2012; Perry et al. 2020). Yet, despite being known hotspots for invasive species, peri-urban landscapes are still neglected in the field of invasion biology, especially for large mammals (Salomon Cavin and Kull 2017).

Although large mammals usually avoid urban areas, deer (family Cervidae) are able to live in close proximity with people (Kilpatrick and Spohr 2000; Ciach and Fröhlich 2019) and reach high densities in peri-urban landscapes due to the availability of high-quality food (e.g., in lawns and gardens) and decreased hunting pressure from humans (Harden et al. 2005). The presence of deer in peri-urban landscapes poses safety and economic risks for the residents due to collisions with vehicles (Gunson et al. 2011; Zuberogoitia et al. 2014). Deer can also have undesirable impacts on urban reserves, recreational parks and private gardens through herbivory and physical damage (e.g., pugging, antler thrashing) (Duarte et al. 2015; Jenkins and Howard 2021). Yet, urban deer management is a complex process involving many stakeholders with different perceptions of deer, resulting in conflicting opinions on best management practices (Raik et al. 2005; Crowley et al. 2017).

The challenge for managing peri-urban deer populations is to find management tools that are cost-effective and socially acceptable (Kilpatrick et al. 2007; Forsyth et al. 2023). Helicopter-based shooting of deer, a cost-effective method in agricultural and protected areas (Bengsen et al. 2023), cannot be used in peri-urban landscapes. Non-lethal methods (e.g., capture and translocation or immunocontraception) are less cost-effective at reducing deer abundance than lethal control (Warren 2011; Boulanger et al. 2012). The preferred technique used in peri-urban landscapes is therefore ground-based shooting by professional shooters (Urbanek et al. 2011). Compared to recreational hunters or volunteer shooters, professional shooters must meet proficiency standards to maintain their licence and generally possess additional licenses to use specialized equipment (e.g., rifle sound suppressors, thermal vision equipment) or operate in restricted ways such as night shooting or vehicle-based shooting (Mysterud et al. 2019; Curtis 2020; Comte et al. 2023b). Professional shooters are also more likely to achieve a given objective of population reduction (Bengsen et al. 2020).

Six non-native species of deer have self-sustaining wild populations in Australia, with populations of some species invading peri-urban landscapes (Moriarty 2004c; Burgin et al. 2015). A species of particular concern in Australian peri-urban landscapes is the rusa deer (*Cervus timorensis*), which is medium-sized (average weight of 140 kg for males and 70 kg for females) and native to Indonesia (Moriarty 2004a). Although rusa deer can breed year-round, in temperate climates such as south-eastern Australia most mating occurs during the winter months (May to September), with calving peaking in March–April (Moriarty 2004b; Chalmers 2018). Since their introduction to Royal National Park (south of Sydney) in 1906, rusa deer have spread south and west into the Illawarra region (Li-Williams et al. 2023), a densely-inhabited coastal area, causing vehicle collisions, impacting native plant species and ornamental gardens (Moriarty 2004b). Since 2011, the Illawarra Wild Deer Management Program (IWDMP) has used professional vehicle-based shooters to mitigate the impacts of deer on private and public land (Dawson 2017; Hampton et al. 2023).

In this study, we analyse data collected during shooting of rusa deer between 2011 and 2022 to assess the cost-effectiveness of professional vehicle-based shooting in a peri-urban landscape. We incorporate the results from an independent monitoring program into a Bayesian joint-likelihood framework to model spatio-temporal changes in rusa deer abundance during the management operations. We use our findings to assess the effect of the management program on the number of complaints from residents. Based on our results, we make recommendations for more cost-effective management of invasive deer in peri-urban landscapes.

Materials and methods

Study area

Our study area is the Wollongong Local Government Area (LGA), which is in the Illawarra region, New South Wales, Australia (Fig. 1). The LGA covers a coastal stretch of land bordered by the Tasman Sea (Pacific Ocean) to the east, the Illawarra escarpment to the west, Royal National Park to the north and Lake Illawarra to the south (Fig. 1). The total area is 712 km^2, of which 78 km^2 are protected (i.e., National Parks, Nature Reserves and local protected land areas). In 2020, the human population in the LGA was 220 000 (The Australian Bureau of Statistics 2020). Mean minimum–maximum monthly temperature ranges are 10.2–17.2 °C in July and 19.1–25.0 °C in January. The area receives a mean annual rainfall of 1128 mm with no dry season (mean monthly rainfall is 54.1–155.7 mm), most of which falls along the slopes of the Illawarra escarpment (The Australian Bureau of Meteorology 2022).

The study area consists of three main landscapes: (1) the area west of the Illawarra escarpment, (2) the slopes of the Illawarra escarpment, and (3) the coastal plain. The area west of the Illawarra escarpment is a large plateau covered by continuous native bushland dominated by tall eucalypt forests surrounding large reservoirs that supply water to Sydney and the Illawarra region (NPWS 2002). Public access to most of the escarpment is prohibited. The Illawarra escarpment is an abrupt fracture in the landscape resulting in relatively steep slopes with elevations ranging from 300 m in the north to 700 m in the south (Young 1980). The slopes are covered by a mosaic of moist eucalypt forests and rainforests with dense understorey, including the *Illawarra Subtropical Rainforest in the Sydney Basin Bioregion*, which is an endangered ecological community (NSW Biodiversity Conservation Act 2016). In its narrowest part, the coastal plain now consists of a densely urbanised area encroaching on the foothills of the escarpment (NPWS 2002). Between Lake Illawarra and the escarpment, the plain widens into a more open landscape of grassy paddocks used by livestock.

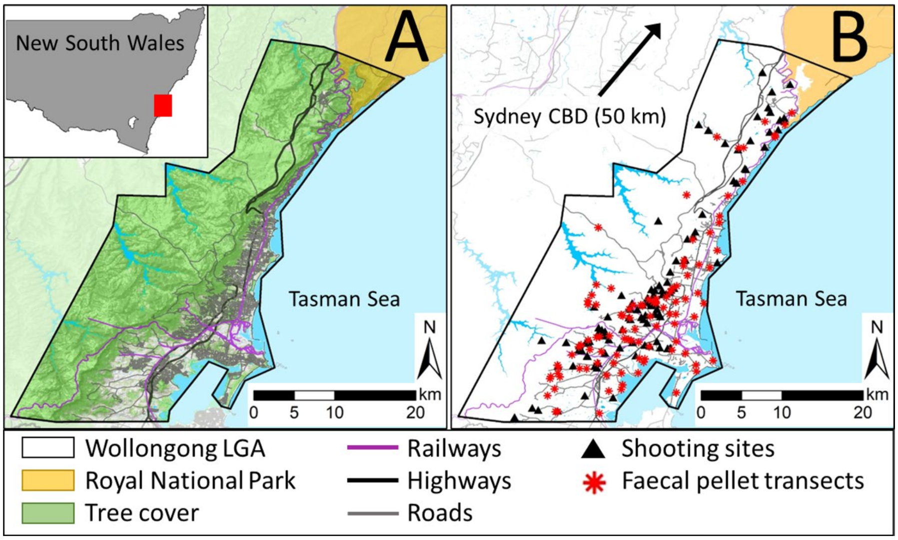

Fig. 1 Location of the Wollongong Local Government Area in New South Wales, eastern Australia. **A** Topography, tree cover, roads, highways and railways. **B** Shooting sites ($n = 108$) and faecal pellet transects ($n = 104$). The inset shows the study area (red) in eastern New South Wales (dark grey)

Vehicle-based shooting

Under the IWDMP protocol, all deer control operations (2011–2021) consisted of professional vehicle-based shooting conducted at night (Dawson 2017). Six teams of shooters were used throughout the management program (Appendix I Table S1). Each team consisted of three people: one driver of a four-wheel-drive utility vehicle, one shooter, and one spotter standing on the tray controlling the white-light spotlight (Hampton et al. 2023). Thermal vision equipment was also used to detect deer, but all shooting was done with white light. All shooters used .223 Remington® rifles equipped with sound suppressors and fired 55 grain soft-point bullets targeting the head of the deer. All shooting teams were accredited by the Firearms Safety and Training Council (https://firearmtraining.com.au) and possessed the relevant authorisations, licenses, and insurances. Given the complexity of peri-urban landscapes, teams of shooters followed strict health and safety protocols. Prior to first shooting at a site, and every three years thereafter, a safety plan identifying risks, hazards, and safe shooting zones (i.e., a bullet would hit a safe background if it missed its target) was developed. For each night of operation, the shooting teams visited one or more sites, and recorded the date, and the numbers of deer seen and shot dead. The annual planning of the shooting operations (date and site visited each night) was left to the discretion of the shooting teams. To minimise the risk to people, shooting did not occur on weekends or on school and public holidays. All deer carcasses were removed from the shooting sites.

The effectiveness of shooting programs is commonly assessed by the change in catch-per-unit-effort (CPUE) (Batcheler and Logan 1963), whereby lower CPUE is indicative of lower abundance. We first considered the CPUE as the number of deer killed (catch) per site-visit (effort). The professional shooters did not consistently record the time spent on each site, but we assumed that, by following a strict safety plan, visits to a given site would be of similar duration. As we expected a nonlinear response of CPUE with increasing effort, we fitted a negative binomial generalised additive mixed model (GAMM) to the number of deer killed per site-visit with the cumulative number of visits (per site) as an explanatory variable (modelled as a cubic spline) and the sites as a random effect (means and smooth terms).

At the operational and financial level, the shooting was organised nightly with varying number of sites visited each night. We therefore calculated a nightly CPUE as the number of deer killed (catch) per night of shooting (effort). For each night of shooting, we also calculated the cost-per-deer-killed (Cook et al. 2017) based on a fixed nightly fee (2022 AUD) of $1,486 and an additional $147 per deer killed. We used GAMMs to investigate the non-linear inter- and intra-annual changes in nightly CPUE and cost-per-deer-killed. We fitted the models using a negative binomial distribution for the nightly CPUE (i.e., count of deer killed per night) and a Gaussian distribution for the cost-per-deer-killed. We fitted each model in response to (i) a cyclic cubic spline for month (January to December), which forced the ends of the spline to meet up for this circular variable (Wood 2017), and (ii) a cubic spline for year (2011–2021). We included the shooting teams as a random effect (means and smooth terms). We fitted all GAMMs with the package mgcv v1.8–42 (Wood 2011) in the R software v4.2.3 (R Core Team 2023). We checked the goodness of fit of the models by the absence of pattern in the model residuals and a k-index close to 1 with an effective degree of freedom below the maximum degree of freedom (Wood 2017).

Spatial variables

Peri-urban landscapes consist of a mosaic of natural and anthropogenic features which can affect deer abundance. We focused on three major features characterising our study area. First, the Illawarra escarpment running north–south across the LGA creates a strong topographical gradient that can influence deer movements (Pérez-Espona et al. 2008). We modelled the average slope (°) over the study area on a 1-ha grid, based on the eight neighbouring cells (Horn 1981) of a digital elevation model (NSW Department of Planning and Environment 2022). Rusa deer rest in dense vegetation during the day, moving out at night to feed in more open grassy areas (Moriarty 2004b). We used the NSW Native Vegetation Extent 5-m Raster v1.2 (Fisher et al. 2016) to create a presence-absence tree cover raster (5-m grid). For each cell, we then calculated the proportion of tree cover (0–100) within a moving square window of 1-km^2. Human activity can influence the distribution and abundance of deer (Hewison et al. 2001; Bonnot et al. 2013) and road density is negatively associated with deer damage on forests in the United Kingdom (Spake et al. 2020). We calculated the road density on a 1-ha grid as the total distance of road per square kilometre (km/km^2) using a 500 m buffer around each cell (Department of Customer Service NSW 2023). For consistency with the spatial extent of the shooting and monitoring sites (see details below), we resampled, through pixel averaging, the three spatial variables on a 250-m grid. Spatial calculations were performed in ArcGis v10.8.2 (ESRI 2021) and in the R software using the package raster v3.6–23 (Hijmans 2020).

Rusa deer abundance indices

We used faecal pellet counts as an index of rusa deer abundance (Forsyth et al. 2007). Monitoring occurred in April (i.e., the end of the austral summer) to avoid potential seasonal variations on pellet counts. The frequency and extent of the monitoring increased from 35 transects in 2012, 2015, 2018 and 2019, to 42 transects in 2020 and 104 transects in 2021 and 2022. We used 150-m transects defined by a starting point and a bearing so they could be repeated in subsequent years. Transects were located in mostly open habitats such as paddocks, private gardens, and public parks and reserves. Along each transect, we counted intact faecal pellets within plots (1-m radius) located every 5 m (i.e., there were 30 plots per transect).

Up until 2021, the spatial extent of the faecal pellet monitoring was much smaller than the area covered by the vehicle-based shooting. We therefore complemented the faecal pellet counts with a second index of abundance based on the number of deer seen during the shooting operations (Fig. 1). In order to provide a relevant index of abundance, the number of deer seen needs to be adjusted for search effort (Mysterud et al. 2007; Simard et al. 2013). In our study, the most pertinent index was the number of deer seen per site-visit.

As both indices of abundance varied in their annual spatial coverage (i.e., number of transects and number of shooting sites), we used a Bayesian joint likelihood model to combine the faecal pellet counts and the deer sightings. The model was implemented with integrated nested Laplace approximation (INLA) using the inlabru R-package v2.9.0 (Bachl et al. 2019). Joint likelihood models integrate sub-models for each dataset, with some (but not necessarily all) explanatory variables shared between the sub-models (Miller et al. 2019; Isaac et al. 2020). We first modelled both abundance indices with negative binomial distributions and shared likelihood for all three spatial covariates (slope, tree cover and road density) using quadratic terms. We used a one-dimensional stochastic partial differential equation (SPDE) with Matèrn correlation (Lindgren et al. 2011) to model the cyclic non-linear effect of the month on deer sightings only (faecal pellets counts occurred only in April). We modelled the spatio-temporal dependence of deer abundance (shared likelihood) using a two-dimensional (UTM coordinates) SPDE with an autoregressive structure of order one for the year effect (2011 to 2021 as a discrete index 1–11) (Fioravanti et al. 2021). As preliminary analyses showed no support for a quadratic response to road density (i.e., the 95% credible intervals included zero), we retained only the linear effect. Unlike road density and slope, tree cover had contrasting effects on each index of abundance and was therefore modelled separately. Our final model took the form:

$$\log(\mathit{deer\,sightings}) \sim \alpha_1 + \beta_1 \mathit{road} + \beta_2 \mathit{slope} + \beta_3(\mathit{slope})^2 + \beta_4 \mathit{tree} + \beta_5(\mathit{tree})^2 + f_1(\mathit{month}) + \mathit{SPDE}_{\mathit{coord,year}}$$

$$\log(\mathit{pellet\,counts}) \sim \alpha_2 + \beta_1 \mathit{road} + \beta_2 \mathit{slope} + \beta_3(\mathit{slope})^2 + \beta_6 \mathit{tree} + \beta_7(\mathit{tree})^2 + \mathit{SPDE}_{\mathit{coord,year}},$$

where α_1 and α_2 are intercepts for each sub-model, β_{1-3} are shared fixed effects, β_{4-7} are sub-model specific fixed effects, and f_1 is a cyclic non-linear effect and $\mathit{SPDE}_{\mathit{coord,year}}$ is a shared spatio-temporal random field. Our final model was more parsimonious (Watanabe–Akaike information criterion and conditional predictive ordinates) than the model with full joint likelihood (Pettit 1990; Watanabe and Opper 2010).

As the number and the location of the shooting sites varied annually, we considered that estimating a general deer abundance trend for the whole LGA would not be sensible. We therefore spatially predicted the annual (2011–2021) deer abundance (expected faecal pellet count) on a 250-m grid across the study area by repeatedly drawing samples from the posterior distributions of the model parameters. For each cell, we then fitted a linear regression to estimate the local annual change in deer abundance during the management program (i.e., the slope of the regression). We only considered changes with significant regression slopes ($P<0.05$), with all other grid cells set to zero.

To estimate the effect of the cumulative shooting on deer abundance, we predicted the expected change in deer sighting (same method as for the faecal pellet counts) for each shooting site ($n=108$) used during the management program. We used univariate GAMMs to model the effect of total site-visits and deer killed (during 2011–2021) on the expected annual change in deer sighting.

Resident complaints

Deer impacts in peri-urban landscapes are varied and often difficult to quantify and monitor. Complaints by residents are an index of deer impacts in space and time. These complaints can be actively collected through stratified or randomised surveys, but these are costly to conduct regularly. Rather, the Wollongong City Council recorded the date and location of any complaint from residents about deer impact during the first eight years of the program (May 2011 to April 2019). For privacy reasons, each complaint was anonymised, and provided as spatial coordinates (UTM) with the month and year.

Resident complaints were recorded as presence-only locations (González et al. 2016). We consequently generated 100 pseudo-absence locations for each month of the dataset (May 2011 to April 2019, 96 months) randomly distributed across the study area. Given that true complaints were initially recorded by residential addresses, we restricted the pseudo-absence locations to the area between the coast and the top of the Illawarra escarpment (beyond which there are few residences). We modelled complaints using the binomial distribution (1 = complaint, 0 = pseudo-absence) in response to quadratic effects of road density, tree cover and slope. We used a cyclic one-dimensional SPDE to model the effect of month (January–December). To model the spatial dependence of complaints, we used a two-dimensional SPDE (UTM coordinates) with a first-order autoregressive structure for the year effect (indexed 1–8). The final model took the form:

$$\begin{aligned}&\text{logit}(complaint) \sim \alpha + \beta_1 road + \beta_2 (road)^2 + \beta_3 slope \\ &+ \beta_4 (slope)^2 + \beta_5 tree + \beta_6 (tree)^2 + f_1(month) + SPDE_{coord,year},\end{aligned}$$

Owith α the intercept, β_{1-6} linear fixed effects, and f_1 a cyclic non-linear effect and $SPDE_{coord,year}$ a spatio-temporal random field.

Results

Between May 2011 and April 2022, the six teams of shooters conducted 845 nights of vehicle-based shooting with a mean of 5.3 sites visited per night (SE = 0.1, range = 1–21) for a total of 4503 site-visits. The number of sites visited each night increased from 3.8 (SE = 0.3) in 2011 to 13.4 (SE = 0.5) in 2021 and was highest in August (7.9; SE = 0.3) and lowest in December (5.7, SE = 0.2; Appendix I, Figure S1). The number of sites visited each year increased from 18 in 2011 (~0.4% of the LGA) to 72 in 2021 (~1.6% of the LGA). Not all sites were visited every year; of the 108 sites included in the program, only three were visited in all 11 years, 35 sites were visited in six or more years and 45 sites were visited only in one or two years.

Cost-effectiveness of vehicle-based shooting

The professional shooters killed on average 427.4 deer per year (SE = 58.5, range = 125–728) for a total of 4701 deer killed during 2011–2021. The shooting effort increased weakly over time but varied widely from year to year (mean number of nights per year = 76.8, SE = 9.8, range = 29–132, Table 1). Shooting nights were spread across each year (monthly average = 8.2, SE = 0.5, range 1–28) but, due to school holidays, there were fewer operations in April and July and almost none in January (only one night in 2019 and 2022).

During the study, the mean number of deer killed per site-visit fluctuated annually, decreasing from 0.85 (SE = 0.11) when the shooting began in 2011, to 0.43 (SE = 0.06) in 2021. There was a strong monthly pattern in the number of deer killed per site visit, being highest in August (0.73; SE = 0.08) and lowest in March (0.53; SE = 0.05). Our model showed that the number of deer killed per site-visit decreased with increasing effort at a site, with the largest decline in CPUE occurring during the first 50 site-visits (Fig. 2).

In comparison, the shooters' nightly CPUE (i.e., the number of deer killed per night) changed little during the study with a mean of 5.39 (SE = 0.60) deer-killed-per-night (Fig. 3). The nightly CPUE was highest in August (6.71, SE = 0.72) and lowest in February (4.45, SE = 0.46; Fig. 3). The six shooter teams performed similarly (Appendix I, Table S1). The cost-per-deer-killed did not change

Table 1 Summary of professional vehicle-based shooting of rusa deer during the Illawarra Wild Deer Management Program in the Wollongong LGA, eastern Australia, 2011–2021. Years start in May and end in April

Year	Nights	Sites	Site-visits	Deer killed	Deer per night	Deer per site	Deer per site-visit
2011	39	18	132	193	4.9	10.7	1.5
2012	73	37	349	403	5.5	10.9	1.2
2013	78	38	393	378	4.8	9.9	1.0
2014	29	35	146	125	4.3	3.6	0.9
2015	93	40	476	449	4.8	11.2	0.9
2016	36	36	193	260	7.2	7.2	1.3
2017	118	40	373	674	5.7	16.9	1.8
2018	72	41	362	362	5.0	8.8	1.0
2019	132	50	710	728	5.5	14.6	1.0
2020	89	71	709	616	6.9	8.7	0.9
2021	86	72	660	513	6.0	7.1	0.8

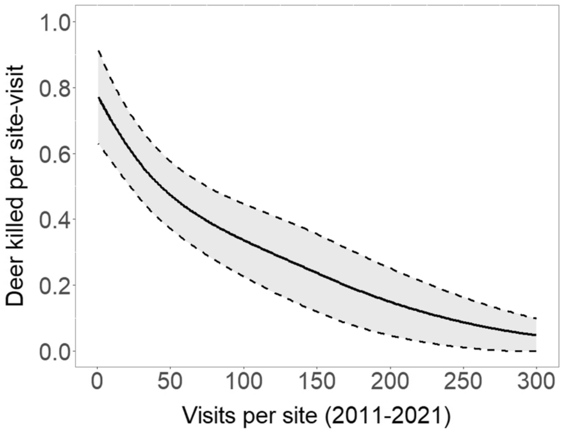

Fig. 2 Expected CPUE (deer killed per site-visit) with increasing effort (visits per site) of professional vehicle-based shooting of rusa deer during the Illawarra Wild Deer Management Program in the Wollongong LGA, eastern Australia, 2011–2021. Model outputs are mean (solid line) and 95% confidence interval (dashed lines)

annually ($536.7 per deer, SE = 11.9) but did vary monthly: the maximum and minimum cost per deer were in February ($672.0, SE = 75.2) and August ($448.5, SE = 36.4), respectively (Fig. 3).

Rusa deer abundance indices

The joint-likelihood model integrated independent data streams – deer sightings and faecal pellet counts – to simultaneously model the latent distribution of deer. The intercepts for the two sub models were 57.7 (95% CrI: 9.3–386.8) for the deer sightings and 0.002 (95% CrI: 0.0001–0.02) for the faecal pellet counts (Fig. 4A). There was no effect of the month on the number of deer seen per site-visit (Fig. 4B). Tree cover had the strongest influence on faecal pellet counts, with highest pellet counts occurring at ~75% tree cover (Fig. 4C). In contrast, deer sightings were highest in low tree cover (<25%) and lowest in dense tree cover (>75%, Fig. 4D). For both faecal pellet counts and deer sightings (joint-likelihood in the model), rusa deer abundance was negatively influenced by road density and was highest on slopes between 15° and 20° (Fig. 4E, F). Deer abundance indices strongly declined on steeper slopes, and, due to small sample sizes, the relationship was estimated less precisely.

Rusa deer were present across most of the Wollongong LGA. The joint-likelihood model estimated that 9.5% (67.4 km^2) of the LGA in 2011, increasing to 10.8% (76.8 km^2) in 2021, had an expected faecal pellet count < 1. These likely deer-free areas mostly consisted of densely human-populated coastal areas and open grasslands in the south of the LGA (Fig. 5). The large continuous forested landscape west of the Illawarra escarpment generally held a relatively intermediate abundance of deer. The highest estimated relative abundance (> 100 pellets per transect) occurred along the eastern slopes of the escarpment, with a small area of very high relative abundance (> 500 pellets per transects) adjacent to the suburb of Figtree (Fig. 5). By the end of the study, this area of very high pellet counts declined from 8.3 km^2 (1.2% of the LGA) to 4.7 km^2 (0.7% of the LGA).

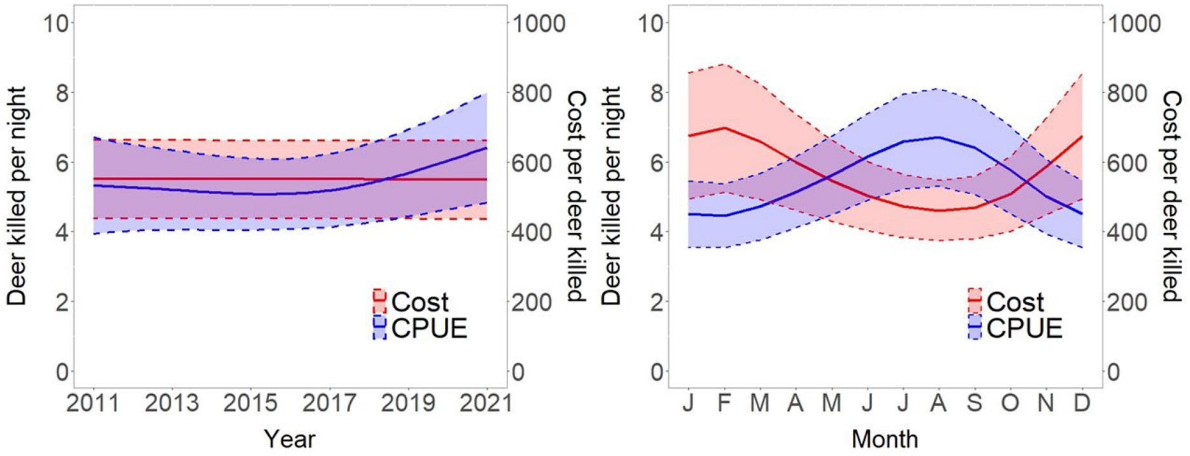

Fig. 3 Annual and monthly expected nightly CPUE (deer killed per night, blue) and cost (cost per deer killed, red) of professional vehicle-based shooting of rusa deer during the Illawarra Wild Deer Management Program in the Wollongong LGA, eastern Australia, 2011–2021. Model outputs are means (solid line) and 95% confidence intervals (dashed lines). Years start in May and end in April. Cost given in AUD, 2022

Across the eleven years of the management program, trends in rusa deer abundance were spatially heterogenous (Fig. 5B). Rusa deer relative abundance was stable across most of the LGA (532.2 km^2, 74.7%), but there was a decrease in expected faecal pellet counts over 138.6 km^2 (19.4% of the LGA) and an increase in expected faecal pellet counts over 42.1 km^2 (5.9% of the LGA). Most shooting sites were in areas in which deer abundance declined (57%) or did not change (30%), but deer abundance increased in 13% of the sites and in adjacent areas with no vehicle-based shooting (Fig. 6A,B).

Our models indicated that the expected reduction in deer seen per site-visit was greater for sites that received higher cumulative shooting effort during 2011–2021 (Fig. 7A). The number of deer seen decreased almost linearly by ~ 1.4 deer for every 50 site-visits (Fig. 7A). The relationship between number of deer killed at a site and the change in deer seen per site-visit (Fig. 7B) was characterised by large uncertainty because there were few sites with > 100 deer killed. However, the most precisely estimated part of that relationship shows that a decrease of two deer seen per site-visit can be expected for every ~ 100 deer killed (Fig. 7B).

Resident complaints

Wollongong City Council recorded a total of 365 complaints from residents between May 2011 and April 2019, with an annual mean of 45.6 complaints (SE = 3.8, range = 35–64). The probability of receiving a complaint peaked annually between May and September (i.e., winter; Fig. 8A) and was lowest in December and January (summer). The probability of a resident complaint being lodged was highest in areas with medium road density (~ 10 km/km^2; Fig. 8B), low slopes (< 15°; Fig. 8C) and high tree cover (> 75%; Fig. 8D).

Our model showed that during those eight years, the expected probability of receiving a complaint was initially concentrated on the slopes of the escarpment adjacent to the City of Wollongong but then intensified and slowly expanded east and north. The area with > 10% probability of lodging a complaint doubled from 30.4 km^2 (8.0%) in 2011 to 62.2 km^2 (16.4%) in 2018 (Fig. 9). During the same period, the area with a high probability of complaint (> 75%) increased from 0.8 km^2 to 2.2 km^2.

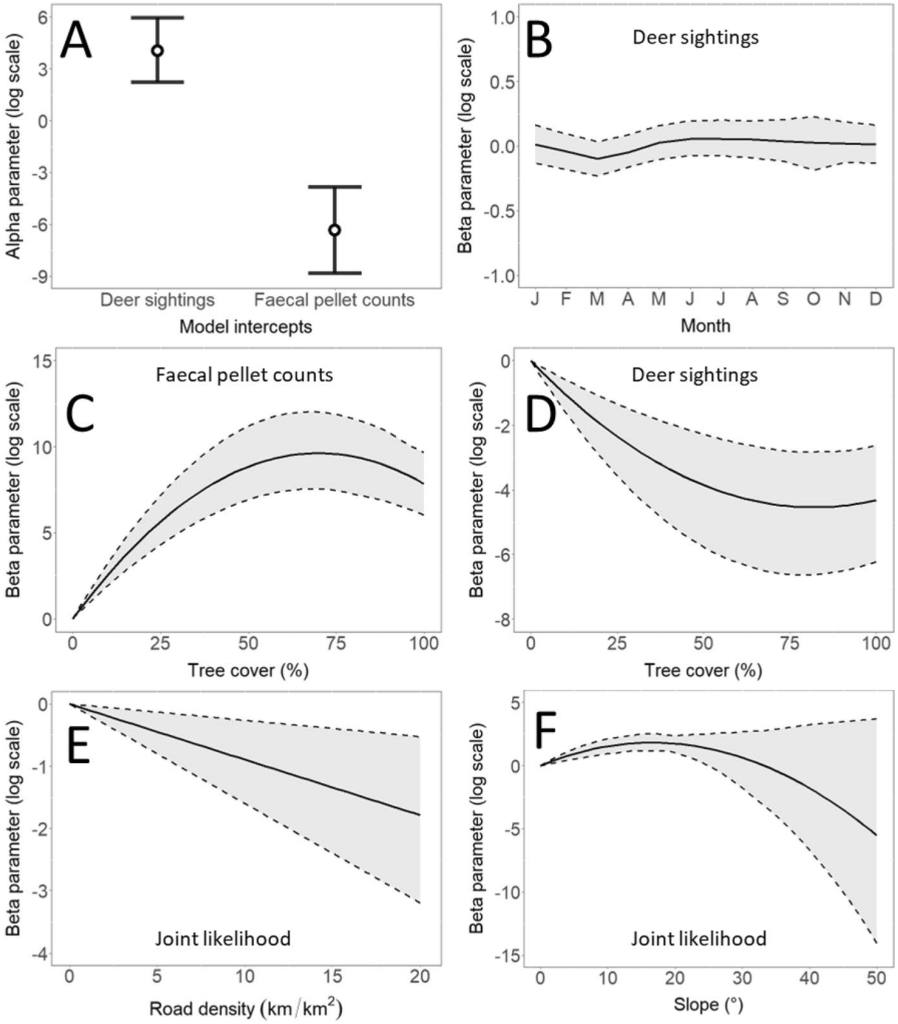

Fig. 4 Mean effects (solid lines) and 95% credible intervals (dashed lines) of spatio-temporal variables on faecal pellet counts and deer sightings during the Illawarra Wild Deer Management Program in the Wollongong LGA, eastern Australia, 2011–2021. All effects (alpha and beta parameters) are shown on the link-scale (i.e., log scale for negative binomial regressions), see Materials and methods for the full joint likelihood model formula. **A** Intercepts (alpha parameters) for the two sub-models of our joint likelihood model; **B** effect (beta parameter) of month on deer sightings; **C** effect of tree cover on faecal pellet counts; **D** effect of tree cover on deer sightings; **E** effect of road density on both faecal pellet counts and deer sightings (i.e., joint likelihood); **F** effect of slope on both faecal pellet counts and deer sightings

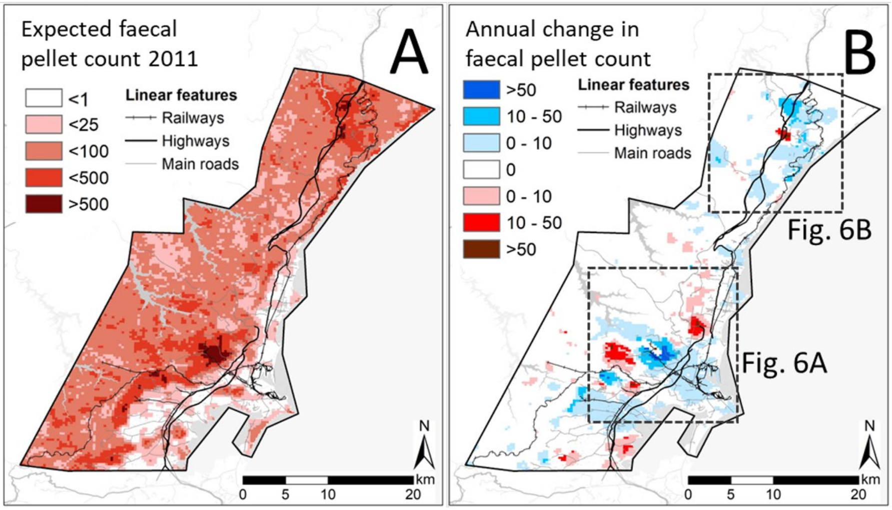

Fig. 5 **A** Expected faecal pellet counts (shades of red) at the start (2011) of the monitoring period during the Illawarra Wild Deer Management Program in the Wollongong LGA, eastern Australia, 2011–2021. **B** Expected annual change in faecal pellet counts (2011–2021), blue = decrease (negative linear regression slopes with 95% confidence intervals excluding zero) and red = increase (positive linear regression slope). See Appendix II Fig. S1 for all annual predicted maps (2011–2021)

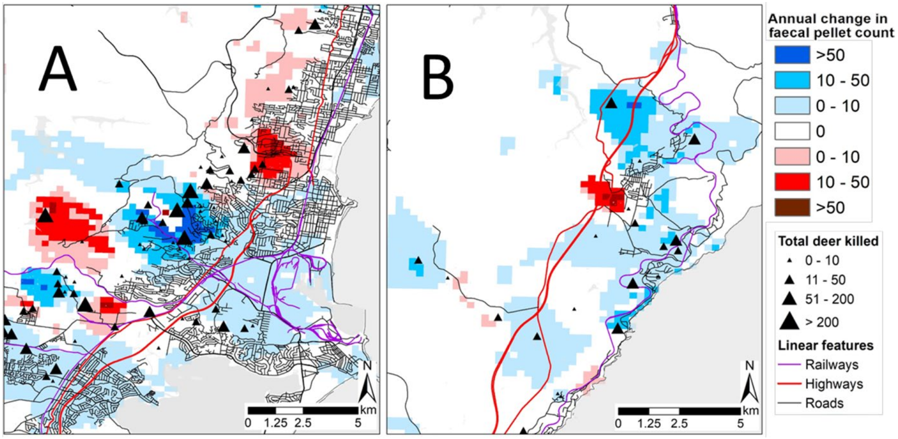

Fig. 6 Expected annual change in faecal pellet counts and cumulative vehicle-based professional shooting of rusa deer during the Illawarra Wild Deer Management Program in the Wollongong LGA, eastern Australia, 2011–2021. Blue = decrease (negative linear regression slopes with 95% confidence intervals excluding zero) and red = increase (positive linear regression slopes). The black triangles are the shooting sites, scaled to the total number of deer killed during 2011–2021. The location of areas A and B are delineated in Fig. 5B

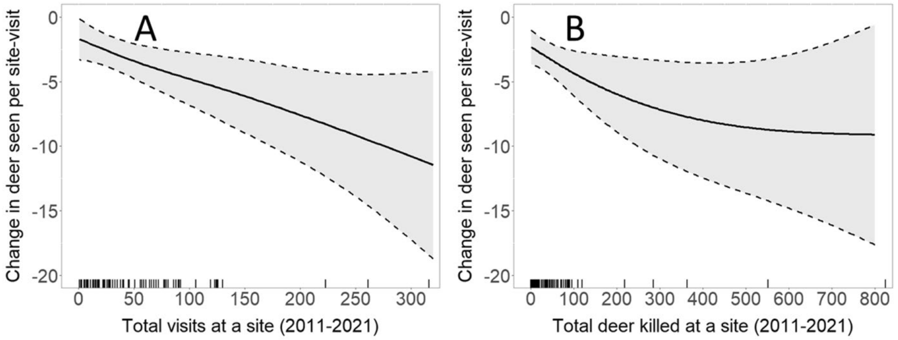

Fig. 7 Expected change in deer sighting with increasing site-visits (**A**) and total deer killed per site (**B**) from vehicle-based professional shooting of rusa deer during the Illawarra Wild Deer Management Program in the Wollongong LGA, eastern Australia, 2011–2021. Model outputs are means (solid lines) and 95% confidence intervals (dashed lines). Bottom ticks show empirical observations

Discussion

During the eleven-year study, professional vehicle-based shooters removed 4701 rusa deer from the peri-urban landscape in the Wollongong LGA. In this period, the deer population remained stable over most of the LGA (74.7%), but decreased in 19.4% and increased in 5.9% of the LGA. Our results showed that increasing the shooting effort (number of visits to a site) and removing more deer at a site resulted in a local decrease in deer abundance and shooters' CPUE. During the first eight years of the study, resident complaints spread from the base of the Illawarra escarpment into the adjacent more urbanised landscape. Residents were more likely to lodge a complaint in winter than in summer. Our study showed that a management program using professional vehicle-based shooting can reduce the local abundance of non-native deer in a peri-urban landscape, providing that sufficient effort is expended.

The effectiveness of a shooting operation mostly depends on the shooter's ability to detect and shoot deer (Comte et al. 2023b). Given the use of a standardised shooting protocol, the observed seasonality

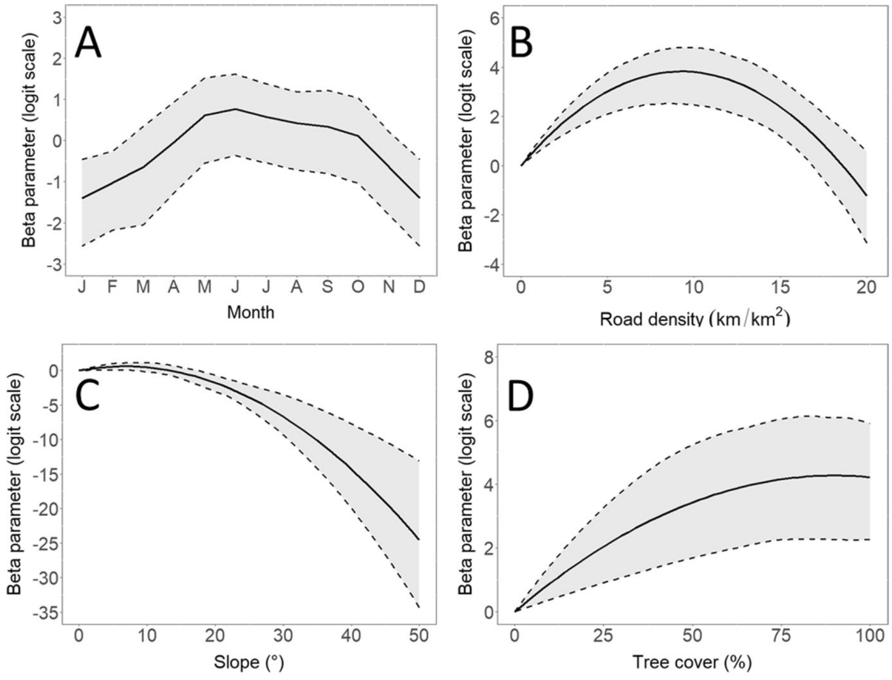

Fig. 8 Effects of spatio-temporal variables on the probability of resident complaints about rusa deer impacts during the Illawarra Wild Deer Management Program in the Wollongong LGA, eastern Australia, 2011–2018. Model outputs are means (solid lines) and 95% credible intervals (dashed lines) for beta parameters

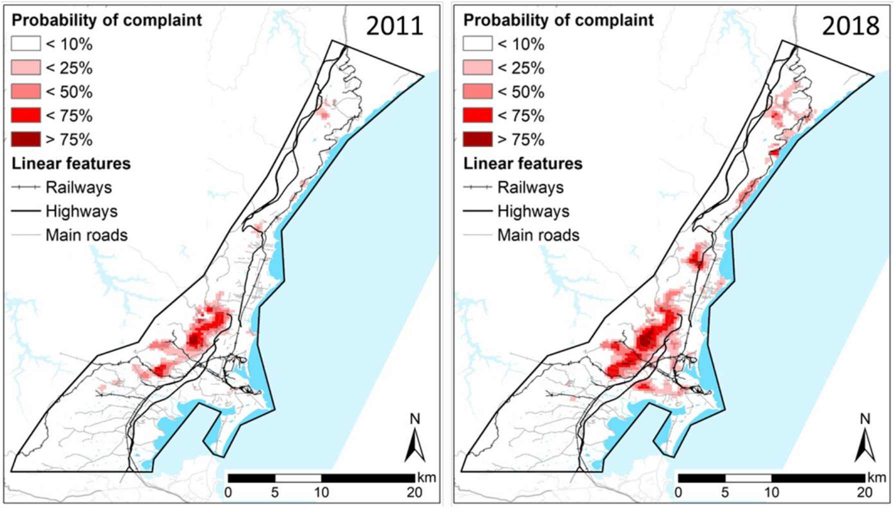

Fig. 9 Expected annual probability of a resident complaint for rusa deer impacts during the Illawarra Wild Deer Management Program in the Wollongong LGA, eastern Australia, 2011–2018. Years start in May and end in April. See Appendix III for all annual predicted maps

in cost-effectiveness in our study was more likely a result of deer being more available to the shooters in winter (i.e., more opportunities to shoot). Although the number of deer seen per site visit was only marginally higher in winter, shooters were indeed more successful (i.e., more deer killed per site-visit). Furthermore, the longer hours of darkness meant that the shooting teams could visit more sites per night, leading to more deer killed per night. In our study area, winter also coincided with the peak of the mating season (Moriarty 2023) when rusa deer, and particularly males, are more active and potentially easier to detect (Moriarty 2004b). Intensifying the shooting operations with more nights and more site-visits per night during the winter months could therefore be expected to increase the cost-effectiveness of the deer management program.

Quantifying the abundance or density of deer is challenging in peri-urban landscapes due to the difficulty of accessing private property, legal restrictions (e.g., for aerial survey), and the high risk of vandalism or theft for survey equipment such as motion-sensitive cameras (Meek et al. 2019; Forsyth et al. 2022). Monitoring strategies are therefore limited or absent from most peri-urban management programs, which often only report the number of animals killed (Krull et al. 2016). Due to its relatively low cost, minimal physical intrusion in the landscape and high social acceptability with landholders, faecal pellet counts were well suited to our peri-urban landscape. As expected for rusa deer, dense tree cover was an important driver of abundance (Spaggiari and de Garine-Wichatitsky 2006). The highest pellet counts were in areas with medium road densities, which are on the fringe of the urban area where the escarpment's slopes rarely exceed 30°. In these areas, the mosaic between dense forests and open habitats (e.g., creek line bushland, paddocks and sporting fields) appear to provide a balance between food availability and shelter (Pattiselanno and Arobaya 2009). This is of particular concern for the future, as new residential developments are expanding these favourable habitats for deer (Duarte et al. 2015). Compared to the faecal pellet counts, deer sightings during the vehicle-based shooting operations decreased with increasing tree cover. As the shooters mostly relied on white light during night-time, an increase in tree density would reduce deer detectability. Additionally, at night, rusa deer are more likely to be feeding in more open grassy areas than resting in forested areas (Moriarty 2004b).

Our results showed that shooting operations conducted on less than 2% of the Wollongong LGA annually were associated with a decrease in deer abundance over 19.4% of the LGA, mostly in areas surrounding the shooting sites. This larger footprint of population reduction can be explained by the ranging behaviour of rusa deer. In Royal National Park and in peri-urban Brisbane, rusa deer showed strong site fidelity over areas of 195–245 ha (Moriarty 2004a; Amos et al. 2023), which is more than ten times the average size of the shooting sites in our study (~15 ha). As described for red deer (*Cervus elaphus*) management in rural Scotland (Putman 2012), local removal of deer could create a source-sink spatial dynamic in which increased immigration from adjacent habitats expands the reduction in abundance further away from the shooting sites. The effect of localised shooting on deer abundance will then decline and eventually cease (Porter et al. 2004), as observed in our study in areas away from shooting sites. In contrast, increased deer abundance near shooting sites is most likely a result of deer seeking refuge away from shooting operations. This is a common behaviour of deer subject to a landscape of fear from predator or hunting pressure (Laundre et al. 2010; Cromsigt et al. 2013).

Given the observed localised effect of vehicle-based shooting on deer abundance and the difficulty of accessing suitable shooting sites, coordinated planning of the shooting operations appears critical to optimise the management outcomes. Throughout the IWDMP, the timing and selection of sites were left to the discretion of the shooting teams. In addition, shooter teams were paid a fixed rate per night with additional money for each deer killed. This meant that shooter teams had financial incentive to visit the sites with the highest CPUE. This likely resulted in uncoordinated spread of the annual shooting effort across the whole management area with limited revisitation of sites as the CPUE decreased. Changing the remuneration system (e.g., fixed nightly or weekly payment) or setting minimum site-visits could allow program managers to influence the location of the shooting operations. Some incentive would still be needed for shooters to maintain a high CPUE (Nugent and Choquenot 2004). Concentrating annual shooting effort into smaller areas with a higher density of shooting sites would allow more site-visits per night therefore increasing the cost-efficiency of the program (McMahon et al. 2010).Vehicle-based shooting is not suitable for the forested water catchments above the escarpment because there are few access roads. There, aerial shooting could be used for large-scale population control of rusa deer (Bengsen et al. 2023). Elsewhere, robust monitoring supplemented by genetic sequencing of deer have defined potential management units on which to concentrate the shooting operations (Li-Williams et al. 2023). Additional research on deer movements (e.g., GPS tracking, landscape genetics) may identify connecting corridors that could be targeted by the shooting operations to prevent the recolonisation of previously controlled areas.

Engaging with the local residents has been identified as a key element for successfully managing deer in peri-urban landscapes (Raik et al. 2006). Most complaints came from the high deer abundance cluster of Figtree, yet the observed reduction of deer population there did not result in fewer complaints from residents; rather, they increased over time. Deer abundance was a major influence on complaints, but our results support a context-dependent perception of overabundance or impacts (Côté et al. 2004; Carpio et al. 2021). More frequent media coverage of the IWDMP and of deer impacts could have increased awareness of residents resulting in more active reporting. Complaints were more frequent in winter, which is potentially the combined effect of the mating season of rusa deer and shorter daylengths, which lead to greater overlap between humans and deer (Cunningham et al. 2022). Residents are more likely to encounter deer during winter because typical human activity extends for longer after nightfall when deer are most active, which leads to spikes in deer-vehicle collisions elsewhere (Cunningham et al. 2022). Recording resident complaints can help local land managers target areas of emerging and established deer impact but should not be solely relied upon to monitor the changes in deer abundance or the efficacy of management operations. Proactive surveys of the resident population could provide more robust information on the nature and intensity of deer impacts and, more broadly, of the perceived nuisance of biological invasions in peri-urban landscapes. As a measure of success, deer impacts should be specifically quantified before and after management operations (Comte et al. 2023a).

Conclusion

Our case study illustrates how the invasion of a large peri-urban landscape by non-native deer can be managed by professional vehicle-based shooting. It was more cost-effective to visit more shooting sites during the longer winter nights. Although faecal pellet counts were well suited to monitoring deer relative abundance in this peri-urban landscape, the frequency and extent of the monitoring was too limited in the first years of the study to provide robust spatio-temporal trends. This was compensated by combining faecal pellet counts with a second index of abundance (i.e., deer sightings during shooting operations) into a Bayesian joint likelihood model. Rusa deer were more abundant along the slopes of the Illawarra escarpment where there was high tree cover and medium road density. Most resident complaints were recorded from those areas of high deer abundance, but although deer abundance decreased there due to the vehicle-based shooting, reporting of complaints about deer by residents increased. Robust monitoring of deer abundance and impacts, although often difficult in peri-urban landscapes, will enable management efforts to focus on priority areas rather than being spread across large administrative areas.

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Data availability Data and code are available at: https://doi.org/10.6084/m9.figshare.25906894.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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