



Animal welfare outcomes of professional vehicle-based shooting of peri-urban rusa deer in Australia

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ABSTRACT

Context. Vehicle-based shooting has been widely used to kill deer, but the animal-welfare outcomes of this technique have not been evaluated in Australasia. **Aim.** To assess the animal-welfare outcomes of peri-urban deer culling by quantifying the fates of deer seen and shot at, the duration of procedures, and the number and location of bullet wounds in deer. **Methods.** We assessed vehicle-based night shooting of peri-urban rusa deer (*Cervus timorensis*) by professional contractors in eastern Australia. Shooters targeted the heads of deer using .223 Remington® rifles and 55 grain bullets. Independent veterinarians conducted ante-mortem (i.e. from the shooting vehicle) and post-mortem (i.e. inspecting the carcass) observations. The ante-mortem data were used to estimate the proportion of deer seen that were shot at, killed, wounded, and escaped. The influence of variables predicted to affect shooting outcomes was assessed. The numbers and locations of bullet wounds were recorded post-mortem. **Key results.** Of the 269 deer seen in 21 nights, 48% were shot at and 85% of those shot at were killed by either one (87%), two (10%) or three (3%) shots. The frequency of non-fatal wounding (i.e. escaping wounded) was 3.5% for those shot at and hit, and the median time to insensibility for the deer that were shot multiple times was 289 s. There was variation among shooters in their ability to hit a deer, and also to do so with a killing shot. The number of bullet wounds per deer ranged from 1 to 3 (mean = 1.1), with 83% of shots striking the brain and 17% striking the anterior skull, neck and jaw. **Conclusions.** The animal welfare outcomes we observed were comparable to those reported from other professional ground-based shooting programs for ungulates, but were poorer than those reported for professional ground-based shooting of peri-urban kangaroos. **Implications.** Our results suggest that one way to improve the animal welfare outcomes of vehicle-based shooting of peri-urban deer is by improving shooter training. Assessment of shooter performance should be a routine part of ground-based shooting programs.

Keywords: Cervids, culling, invasive species, pest management, population control, ungulates, urban ecology, wildlife management.

Introduction

Wild deer can have a wide range of undesirable economic, social, environmental and human-health impacts (Côté *et al.* 2004; Conover 2011; Valente *et al.* 2020). In Australia and New Zealand, where deer are non-native and many populations are increasing in range and abundance (Moriarty 2004a; King and Forsyth 2021), the undesirable impacts of deer include altered native vegetation communities (Wardle *et al.* 2001; Burns *et al.* 2021), reduced profitability of agricultural enterprises (Lindeman and Forsyth 2008; Page *et al.* 2017; Cripps *et al.* 2019; Latham *et al.* 2020), vehicle collisions (Burgin *et al.* 2015; Davies *et al.* 2020), and pollution of drinking-water catchments (Bennett *et al.* 2015).

One approach to reducing the undesirable impacts of deer is to remove deer by lethal control. Ground-based shooting has been used to kill deer and other ungulate species in Australia and New Zealand for many decades (Caughley 1983; Moriarty 2004a; Bennett *et al.* 2015). Ground-based shooting is undertaken by either professionals (i.e. remunerated) or volunteers (unpaid 'recreational hunters' or 'sporting shooters'). Shooting deer is

sometimes contentious because of concerns about animal welfare outcomes (Rutberg 1997; Aebischer *et al.* 2014; DeNicola *et al.* 2019), concerns that tend to be exacerbated when shooting occurs in and around human settlements (Curtis *et al.* 1995; Moriarty 2004b; Burgin *et al.* 2015). However, the welfare outcomes of ground-based shooting of deer have not been evaluated in Australasia (Forsyth *et al.* 2017).

The most robust assessments of the animal welfare outcomes of lethal control methods such as shooting have five features (reviewed in Smith and Ryeng 2022). First, independent observers, rather than the shooters themselves, collect the data (so as to minimise potential biases; Schulz *et al.* 2013). Second, a sufficient number of shooting events are observed so that the frequency of adverse animal welfare events can be robustly estimated (Hampton *et al.* 2019a). Third, ante-mortem (before death) and post-mortem (after death) data are combined to quantify the following two parameters (Ryeng and Larsen 2021): (i) the duration of suffering from shooting prior to insensibility or death, and (ii) the frequency of immediate insensibility. Fourth, the frequency of non-fatal wounding, considered the worst animal welfare outcome for any shooting program because it causes protracted (but unmeasured) suffering, is quantified (Aebischer *et al.* 2014). Fifth, the numbers and anatomical locations of bullet wounds, related to the accuracy of shooting, are reported.

The approach described above, in which ante-mortem and post-mortem data are combined to assess shooting methods, was first developed for whaling practices in Scandinavia in the 1980s (Øen 2021). It has since been applied to vehicle-based shooting of impala (*Aepyceros melampus*) in southern Africa (Lewis *et al.* 1997) and to boat-based shooting of seals in Canada (Daoust and Caraguel 2012; Hampton *et al.* 2021a) and Norway (Ryeng and Larsen 2021). In Australia, the approach has been used to assess the welfare outcomes of aerial (helicopter-based) shooting of large ungulates (Hampton *et al.* 2014, 2017), and vehicle-based shooting of European rabbits (*Oryctolagus cuniculus*; Hampton *et al.* 2015, 2016a, 2020) and eastern grey kangaroos (*Macropus giganteus*; Hampton and Forsyth 2016).

Most quantitative assessments of animal welfare outcomes for ground-based shooting of deer have been conducted on red deer (*Cervus elaphus*) in the United Kingdom. Using independent observations of recreational shooters, Bradshaw and Bateson (2000) concluded that ground-based shooting killed 93% of deer within 2 min of being shot at and hit and that 2% escaped wounded. Cockram *et al.* (2011) used biochemical stress markers (e.g. plasma cortisol concentrations) and carcase characteristics to assess four red deer shooting methods. Two other studies used post-mortem data to describe the numbers and locations of bullet wounds (i.e. inference about ante-mortem outcomes could not be made; Urquhart and McKendrick 2003, 2006). Another indirect method applied to four deer species in the United Kingdom was to collect data from interviews with

shooters (Aebischer *et al.* 2014). Other studies have provided information about particular outcomes of relevance to animal welfare, including 'flight distance' for deer and other large mammals, defined as the distance animals run between shooting and incapacitation for animals shot in the thorax (chest-shooting; Kanstrup *et al.* 2016; Stokke *et al.* 2018). None of these studies combined ante-mortem and post-mortem data collected by an independent observer to quantify key animal welfare outcomes.

Several variables could potentially affect the welfare outcomes of ground-based shooting programs. The precision of a firearm/optics/ammunition configuration is central to the ability of a shooter to strike a desired anatomical zone (Hampton *et al.* 2021a). Rifle calibre and ammunition characteristics (bullet mass and powder load) determine the amount of kinetic energy transferred to the target, which declines with an increasing shooting distance (Aebischer *et al.* 2014; Hampton *et al.* 2016a). Shooting distance has been shown to be an important determinant of welfare outcomes for ground-based shooting of deer (Aebischer *et al.* 2014) and other mammals, such as, for example, European rabbits (Hampton *et al.* 2015). The mass of the target animal is also likely to be important because, all other things being equal, heavier individuals are less likely to be killed as quickly as are smaller individuals (Stokke *et al.* 2018). Because many deer species are strongly sexually dimorphic, with adult males being larger than adult females (Weckerly 1998), welfare outcomes might differ between those age–sex classes. Welfare outcomes are also likely to vary among shooters because of consistent individual differences in target acquisition and shooting accuracy, even after accounting for shooting distance (Aebischer *et al.* 2014; Hampton *et al.* 2014, 2017). For example, Aebischer *et al.* (2014) reported that the probability of a shot hitting its target for red deer stalking in the United Kingdom was higher for shooters who practiced at least once a week and for those shooters with an advanced certificate or qualification in deer stalking.

One aspect of the welfare outcomes of ground-based shooting that has not, to our knowledge, been previously assessed is the number of animals shot from the group. A procedural document for ground-based shooting of deer (Sharp 2013) proposed that, when possible, all deer in a group should be killed before another group is targeted, and that the smallest groups should be targeted first by shooters. It is not known how feasible this advice is for deer. Following the discharge of a rifle, other deer in the group are likely to flee (Reimoser 2012). Hence, as deer group size increases, it is expected that the proportion of deer that escape will increase. Such a relationship is described by the functional response (Hone 1990, 1994), the form of which depends on (i) a threshold group size at which the total number of shots fired at deer in the group is saturated, and (ii) the effect of declining deer group size on the total number of shots fired at deer in the group. Evaluating this relationship for ground-based shooting of deer requires the number of deer in the group being shot

at to be recorded, along with the shots fired at deer in the group (i.e. these are ante-mortem observations).

Here, we assess the animal welfare outcomes of vehicle-based shooting of peri-urban deer in eastern Australia. Our objective was to quantify (1) the fates of deer seen and shot at, (2) the duration of key procedures, and (3) the numbers and locations of bullet wounds in shot deer. We compare and contrast these results with similar studies conducted on ungulates and macropods. Finally, we make recommendations as to how the animal welfare outcomes of ground-based deer shooting programs could be improved.

Materials and methods

Study area and species

Our study was conducted in the Illawarra region (~80 km south of Sydney), New South Wales, Australia. The rusa deer (*Cervus timorensis*) population in this region is descended from animals released in Royal National Park in 1906 (Moriarty 2004c; Keith and Pellow 2005; Moriarty 2009). Rusa deer are the third-largest deer species present in Australia, with adult females and males weighing approximately 70 and 140 kg respectively (Moriarty 2004c). Native to tropical Southeast Asia, rusa deer can breed year-round; in our study area, most births occur in March–April (Bentley 1995). Young become independent at 3–4 months (Tuckwell 2003; New Zealand Government 2018). Rusa deer typically rest in thick cover during the day, emerging at or after dusk to feed on grasses in open areas (Moriarty 2004c). The only strong social bond in deer is that between the mother and her dependent offspring (Albon *et al.* 1992; Rosenberry *et al.* 2009), but temporary groups of up to 15 rusa deer can form in preferred habitats (see below).

A management program was established in the Illawarra region in 2011 to minimise the impacts of rusa deer on road and rail accidents, the damage to residential gardens and fences, competition with livestock through competition for forage, impacts on native plant species, and illegal hunting (Dawson 2017). In the Wollongong and Lake Illawarra region, there were 107 motor vehicle accidents involving deer during 2005–2017, of which 90 were rated as serious and resulted in 28 injuries and one death (Invasive Species Council 2018). Professional shooters were contracted to shoot deer in urban, peri-urban and rural areas. Land types include suburban streets, golf courses, ‘hobby’ farms and water catchments. Some areas are heavily infested with the introduced plant *Lantana camara* (Gooden *et al.* 2009), which rusa deer use as refuges.

Shooting procedure

Several procedural documents (i.e. standard operating procedures, codes of practice and manuals; Hampton *et al.* 2016b) guide the ground-based shooting of deer in Australia. There is

a national model standard operating procedure for ground-based shooting of deer (Sharp 2013), but a unique methodology is often developed for a particular management program (Brown 2017). Stipulations within standard operating procedures govern several variables of potential relevance to animal welfare outcomes, including permitted shooting seasons, rifle calibre and bullet weight, and shooter training and proficiency.

For the program studied here, shooting was conducted during the hours of darkness (typically beginning 1 h after sunset and ending ~6 h later) during 2018 and 2019. Dry and calm (minimal wind) nights were selected for shooting, and shooting did not occur on weekends, public holidays or school holidays (Dawson 2017). The shooting teams consisted of three people (excluding the independent veterinarian observer) in dual-cab four-wheel drive utility vehicles. One team member drove the vehicle (up to 10 km hour⁻¹) and two team members stood in the tray (truck bed); one was the shooter, and the other controlled the white-light spotlight (100 W, 240 mm diameter). Four shooters employed by professional pest control companies conducted the shooting. All shooters used bolt-action .223 Remington[®] rifles, fitted with telescopic scopes, and fired 55 grain lead-based soft-point bullets, identical to that typically used in professional kangaroo culling (Hampton and Forsyth 2016). Suppressors were used to reduce shooting noise (Williams *et al.* 2018). The shooters conducted their own precision testing (Hampton *et al.* 2021a) off-site prior to arriving at the study area (i.e. it was not observed by the independent veterinarian). As for kangaroo shooting (Commonwealth of Australia 2008), the only anatomical target was the cranium (‘head shooting’; Urquhart and McKendrick 2006). Dead deer were removed from the site by the shooting team.

Observations

We adapted the methods developed for observation of vehicle-based shooting of European rabbits (Hampton *et al.* 2015, 2016a, 2020) to enable ante-mortem and post-mortem data to be collected by independent veterinarians. Briefly, veterinarians experienced in collecting animal welfare data from wildlife shooting programs accompanied deer culling teams and sat in the front passenger seat of the shooting vehicles. Observers were independent in that they were not employees of the managing agency or the contracted culling companies. Three independent veterinarian observers collected data, but only one in each vehicle. The number of deer seen and shot at were recorded. Group size was defined as the number of animals initially seen together before a shot was fired at any group member, as used by Hampton and Forsyth (2016) for peri-urban kangaroo shooting. The number of shots fired at each deer was recorded.

One time-to-event parameter was quantified for each deer shot, namely, time to insensibility (‘unconsciousness’; TTI, seconds), which was the duration between initial shooting

and insensibility (Hampton *et al.* 2021b). Insensibility was defined as the moment at which the animal ceased voluntary movements, including the absence of respiratory movements, with sudden relaxation of the body, as used previously in wildlife shooting studies (Lewis *et al.* 1997; Smith and Ryeng 2022). There is debate about the definition of insensibility in wildlife studies (Hampton and Forsyth 2016). In particular, recognising insensibility relies on distinguishing conscious or voluntary movements (e.g. mobile animals, lifting of the head in recumbent animals) from unconscious or involuntary movements (e.g. muscular twitches or kicking; Smith and Ryeng 2022). Autonomic movements that do not reflect sensibility typically occur in animals rendered insensible via cranial trauma, as has been observed in livestock studies (Claudia Terlouw *et al.* 2015). Observational studies of livestock slaughter and lethal wildlife control methods such as kill-traps typically use palpation to assess physiological responses (e.g. palpebral (blinking) reflexes; Littin *et al.* 2002). In contrast, studies of ballistic methods used to kill wildlife (Hampton *et al.* 2021a) rely on remote observation, and hence slightly different criteria for assessing insensibility have been applied (Knudsen 2005). There is more subjectivity in the application of remote methods of identifying insensibility and, hence, some studies have used terms such as ‘apparent time to death’ (Hampton *et al.* 2015) for this metric.

We then quantified the proportion of deer for which time to insensibility was zero. This parameter has been quantified in the same way in several similar studies but has sometimes been termed ‘instantaneously killed’ (Lewis *et al.* 1997), ‘instant immobilisation’ (Parker *et al.* 2006), ‘instant death’ (Hampton *et al.* 2014), ‘instant incapacitation’ (McTee *et al.* 2017) or ‘immediate collapse’ (Ryeng and Larsen 2021), with all terms having identical meaning. We reported the probability of being rendered immediately insensible, which is equivalent to ‘instantaneous death rate’ (Ryeng and Larsen 2021).

Shooting distance was estimated in one of two ways, namely, either through the use of a laser range finder (Pulsar Digisight N960[®], Yukon Advanced Optics Worldwide, Vilnius, Lithuania) or by measuring the linear distance between a GPS waypoint saved where the shooting vehicle stopped, and a GPS waypoint saved where the targeted deer had been standing (Stokke *et al.* 2018).

Sample size

The desired sample size for our observations was guided by published statistical guidelines for animal welfare studies (Hampton *et al.* 2019a); we sought minimum ante-mortem and post-mortem sample sizes of 113, assuming a frequency of animal welfare outcomes of interest of ~5% (see Hampton and Forsyth 2016).

Statistical analyses

All statistical analyses were conducted using the software R version 3.6.6 software (R Core Team 2020, R: a language

and environment for statistical computing; R Foundation for Statistical Computing, Vienna, Austria)).

Relationship between shots fired and deer group size

The relationship between number of shots fired and deer group size was evaluated using five models, three of which assumed non-linear ‘saturating’ relationships and two of which assumed linear relationships (Table 1). These types of model have been used to evaluate the ‘functional response’ between ungulates killed per unit effort and ungulate density for helicopter-based shooting of feral pigs (*Sus scrofa*; Hone 1990; Choquenot *et al.* 1999) and deer (Bengsen *et al.* 2022), but our objective was to assess how shots fired changed with deer group size because this relationship is of interest from an animal welfare perspective (Sharp 2013). All five models were fitted using the `nls` and `lm` functions in R (R Core Team 2020, R: a language and environment for statistical computing; R Foundation for Statistical Computing, Vienna, Austria), for non-linear and linear models respectively. Models were ranked by Akaike’s information criterion (AIC; Burnham and Anderson 2002).

Shooting outcomes

Shooting data were analysed using the same methods as used by Hampton *et al.* (2015), with the outcomes conceived as the results of a series of binary processes. The following three main outcomes can arise from any event in which a deer is shot at: the deer can be killed, escape wounded or escape non-wounded (Fig. 1). Each process has an associated probability: the probability of a shooter hitting a deer (p_H), the probability the shot kills a deer that was hit (p_K), and the probability of a deer escaping without being hit (p_E). The probability of any observed outcome was expressed as the product of the respective probabilities for the relevant sequence. For example, if a shooter killed a deer with their first shot (K), then the probability for that outcome was expressed as:

$$\Pr(K) = p_H p_K$$

Table 1. Functional response models fitted to the relationship between number of shots fired and rusa deer (*Cervus timorensis*) group size during vehicle-based professional shooting in a peri-urban environment in Australia, 2018–2019.

Model	Definition	Form
Michaelis–Menten	$\hat{y} = \frac{aG}{b+G}$	Non-linear
Power	$\hat{y} = aG^b$	Non-linear
Ivlev	$\hat{y} = a(1 - \exp(-bG))$	Non-linear
Linear	$\hat{y} = a + bG$	Linear
Mean	$\hat{y} = a$	Linear

\hat{y} is the expected number of shots fired, G is deer group size and a and b are parameters to be estimated.

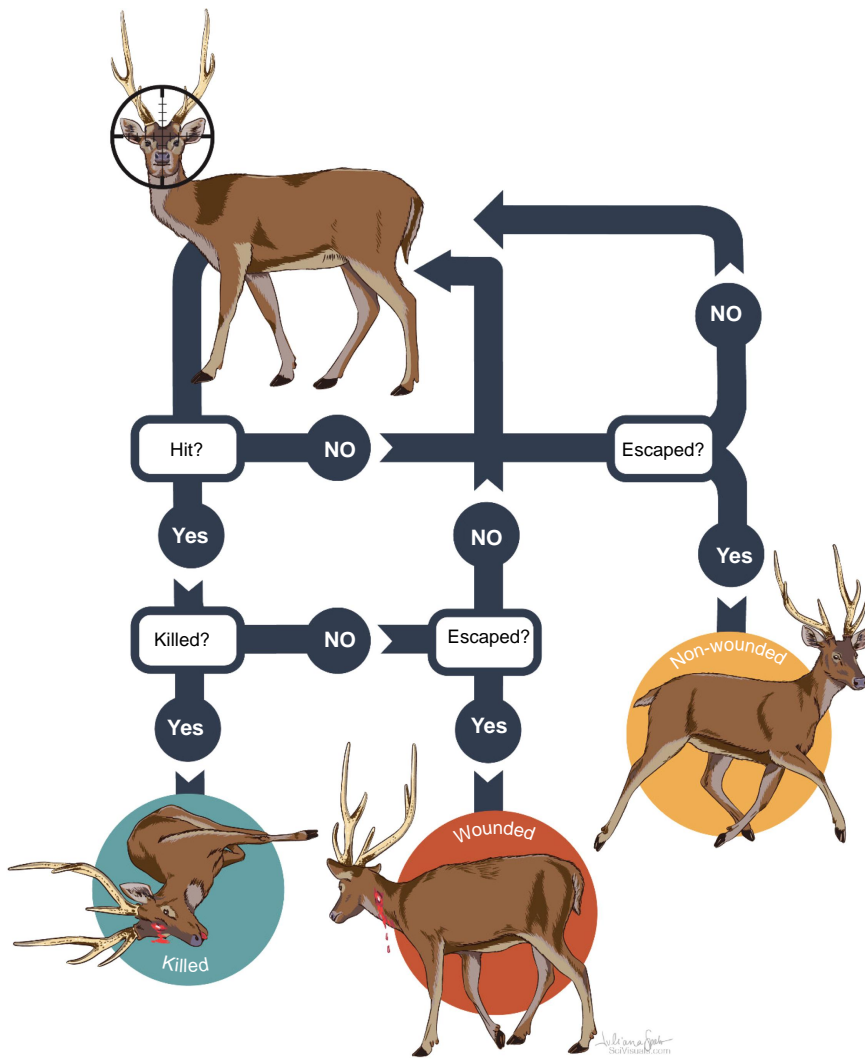


Fig. 1. Flowchart of the shooting process for vehicle-based professional shooting of peri-urban rusa deer (*Cervus timorensis*) in Australia, 2018–2019. The three observed outcomes (deer being killed, escaping wounded or escaping non-wounded) are the results of a series of binary processes. Illustration credit: J. Spahr (SciVisuals).

If a shooter’s first shot wounded a deer, their second shot missed, and the deer escaped before a third shot (i.e. the sequence WME), then the probability was expressed as:

$$\text{Pr}(WME) = p_H(1 - p_K)(1 - p_E)(1 - p_H)p_E$$

That is, the first shot hit but did not kill the deer (with probability $p_H(1 - p_K)$), the deer did not escape but the second shot missed ($(1 - p_E)(1 - p_H)$), and then the animal escaped wounded (p_E). It was assumed that the outcomes for each deer were independent.

Influence of predictor variables

Each of the component probabilities (p_H , p_K and p_E) was modelled as a function of predictor variables (hereinafter ‘predictors’), allowing the relative importance of different predictors of interest, and the effect of these predictors, to be estimated. A technique similar to logistic regression was used, in which probabilities were transformed on to the logit

(or log-odds) scale for regression analysis. Incorporation of predictors into the modelling allows a probability to vary according to the value of associated predictors and estimated effect sizes. For example,

$$\text{logit}(q_i) = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i}$$

where q_i is a probability for Shot i , x_{1i} and x_{2i} are the values of two predictors associated with Shot i (e.g. number of previous shots, or shooting distance) and β_0 , β_1 and β_2 are effect sizes (i.e. model parameters) to be estimated.

We included four predictors in this analysis (Table 2). Each combination of predictors defines a model that represents a different set of hypotheses about what factors affect the respective probability. Therefore, models that were identified as being ‘better’ indicate which set of hypotheses had greater support from the available data. We again used AIC to compare the fit of the models and perform model selection. AIC model weights (w) were calculated as a measure of support for each model and were summed across

Table 2. The four predictor variables considered for modelling probabilities of the outcomes from vehicle-based professional shooting of peri-urban rusa deer (*Cervus timorensis*) in Australia, 2018–2019.

Predictor	Explanation	Model notation	Probability		
			p_H	p_K	p_E
Distance	Shooting distance (range: 20–284 m)	Distance	Y	Y	N
Shooter ID	Unique shooter identified ($n = 4$ shooters)	Shooter	Y	Y	N
Previous number of wounding shots	Number of shots resulting in non-fatal wounding fired at that deer before the current shot (range: 0–2)	PNWS	Y	Y	N
Number of wounding shots	Total number of shots resulting in non-fatal wounding fired at that deer (range: 0–2)	NWS	N	N	Y

models as a measure of overall support for the importance of a predictor variable that was common to that set of models. Summed model weights (s_x ; for predictor variable x) were interpreted in terms of evidence ratios (ER; Burnham and Anderson 2002; Anderson 2007), as follows:

$$ER_x = \frac{s_x}{1 - s_x}$$

A two-stage approach was used to identify which combination of predictors was the most important. First, a separate model selection process was conducted for each component probability to avoid fitting a very large number of models to the data (when fitting all possible combinations of predictors for all combinations of probabilities). Predictors that had evidence ratios of >1 were considered in a second model selection process that involved fitting models with all combinations of the identified predictors for each probability, for all combinations of probabilities. Note that in the first round of model selection, a general structure was assumed for the two non-focal probabilities (e.g. for p_E and p_K if focusing on p_H). The general structure involved all predictors that were being considered for that particular probability to allow variation in the non-focal probabilities should it be required. Model-averaging was again used to combine the results from each model included in the second round of model selection. Inference was made from these model-averaged estimates.

Time to insensibility

For those deer that were killed, we estimated the probability of being rendered immediately insensible. Cox's proportional hazards models (Cox 1972) were used to evaluate whether time to insensibility was different for adult males (having larger mass) from that for other age–sex classes, and also whether there was a relationship with shooting distance. We expected that adult males would have a lower probability of being killed, and, conversely, a higher probability of being wounded, than for all other age–sex classes (Hampton et al. 2014). The following four models were fit to the data and compared using AIC: (1) null; (2) distance; (3) age–sex class, and; (4) age–sex class and distance. The proportional hazard quantifies the multiplicative effect on

the mortality rate; hence, hazard values of <1 indicate lower mortality (higher survival) and values of >1 indicate higher mortality (lower survival).

Wound numbers and locations

For each deer that was shot and killed, the carcass was examined and its sex and age class (adult or juvenile, the latter including fawns and yearlings), and the number and location of bullet wound tracts were recorded. For logistical and safety reasons, the interval between shooting and inspection varied from 1 to 33 min. We assigned bullet wound locations on the basis of the peri-cranial anatomical zones (brain, neck, jaw, anterior skull) displaying the most damage, as was assigned for peri-urban kangaroos (Hampton and Forsyth 2016). Anatomical landmarks for the location of the brain were as per convention (Shearer and Ramirez 2012; Sharp 2013). Our definition of the anterior skull consisted of the orbit (eye sockets) and maxilla (upper jaw and snout). See DeNicola et al. (2019) for radiographic examination of ballistic trauma of cranial structures in head and neck shooting of deer. The probabilities of bullet wound tracts affecting these four anatomical structures were estimated. 'Head shots' (Urquhart and McKendrick 2006) were deemed to have occurred when bullets penetrated the brain (calvarium of the skull; Daoust and Caraguel 2012).

Results

Data scope

In total, 269 rusa deer were seen in 110 groups during the 21 nights of our study, with 148 shots being fired at 130 of those deer. The mean (\pm s.d.) shooting distance was 83 ± 49 m (range: 20–284 m).

Relationship between shots fired and deer group size

Deer group sizes ranged from 1 to 15, with one being the modal group size encountered by shooters (Table 3). On the

Table 3. Summary of the model selection procedure for the functional response of the number of shots fired at groups of deer as a function of group size during vehicle-based professional shooting of peri-urban rusa deer (*Cervus timorensis*) in Australia, 2018–2019.

Model name	ΔAIC	w	$-2ll$	NPar	a		b	
					Est	s.e.	Est	s.e.
Ivlev	0.00	0.49	137.29	2	1.42	0.08	1.17	0.20
Michaelis–Menten	0.01	0.48	137.30	2	1.62	0.13	0.62	0.19
Power	2.63	0.03	139.92	2	1.03	0.06	0.20	0.05
Linear	8.97	0.00	146.25	2	1.02	0.07	0.06	0.02
Mean	15.75	0.00	155.03	1	1.18	0.05		

Presented is the relative difference in AIC (ΔAIC), the AIC model weight (w), twice the negative log-likelihood value ($-2ll$) and number of parameters in the model (NPar). The estimated value and standard error of the model parameters (a and b ; see Table 2 for definitions) are also given.

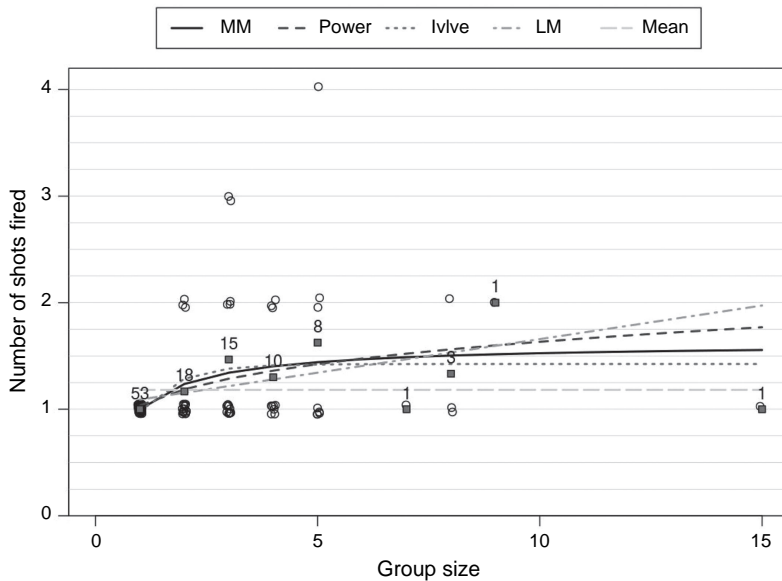


Fig. 2. Relationship between the number of shots fired at each group of rusa deer (*Cervus timorensis*) and number of deer in the group, during vehicle-based professional shooting of peri-urban rusa deer in Australia, 2018–2019. A small random value was added to make individual points distinguishable. The estimated relationships from each of the five models are presented, along with the observed mean number of shots for each group size (grey squares; sample size indicated). Abbreviations are used for the Michaelis–Menten (MM) and linear model (LM).

basis of AIC, the Ivlev and Michaelis–Menten models were clearly better than were the other models (Table 3). These two models had similar support and showed similar non-linear relationships between the number of shots fired and deer group size (Fig. 2). The estimated mean (\pm s.e.) number of shots fired at a group size of one for the top-ranked Ivlev models was 1.00 ± 0.06 , increasing rapidly to an asymptotic value of 1.56 ± 0.11 . That is, even for rusa deer groups much larger than one, shooters fired an average of 1.6 shots at the group.

Shooting outcomes

Of the 269 deer seen, the probability that any one of them would be shot at was 0.48 (95% CI: 0.42–0.54). Of the deer shot at, 114 were hit ($p_H = 0.88$; 0.81–0.93), and 16 escaped without being hit ($p_E = 0.12$; 0.07–0.19). Of the deer that were hit, 110 were killed ($p_K = 0.97$; 0.91–0.99). Of the deer that were killed, 96 (0.87; 0.80–0.93) were rendered immediately insensible. The remaining deer had various outcomes, including 16 deer escaped without apparently being hit, 14

were killed after first being wounded, and four escaped wounded (Table 4). Of the 110 deer that were killed, only one carcass was not located, but this deer was assumed to have been killed because it was observed to be rendered immediately insensible with what appeared to be a head shot and then rolled down a steep hill into thick vegetation where the shooting team could not safely venture.

Influence of predictor variables

The first stage of model selection evaluating the influence of four predictor variables is summarised in Supplementary Tables S1–S6. The second stage of model selection indicated that the probability of hitting a deer (p_H) varied with shooter ID and the number of previous wounding shots (Table 5, Fig. 3). There was variation among shooters in their ability to hit a deer (Fig. 3a), and also to do so with a killing shot (Fig. 3b). The probability of hitting a deer increased as the number of previous wounding shots increased. p_H was close to 1 for all four shooters, except for if the deer had not been previously wounded (which includes when the first shot is

Table 4. Probabilities of deer being killed, wounded or escaping unwounded after being shot at during vehicle-based professional shooting of peri-urban rusa deer (*Cervus timorensis*) in Australia, 2018–2019.

Category	Number	Probability	Lower 95% CL	Upper 95% CL
Shot at	130			
Escaped unwounded	16	0.12	0.07	0.19
Hit	114	0.88	0.81	0.93
Escaped wounded	4	0.03	0.01	0.08
Killed	110	0.85	0.77	0.90
Rendered immediately insensible	96	0.74	0.65	0.81
Killed after wounding	14	0.11	0.06	0.17
Killed after missed shots	0	0.00	0.00	0.03

Table 5. Summary of the second stage of the model selection procedure for identifying important predictor variables for the probability of a rusa deer (*Cervus timorensis*) being hit (p_H), probability of a shot killing a rusa deer that was hit (p_K), and probability of a rusa deer escaping (p_E) during peri-urban vehicle-based professional shooting in Australia, 2018–2019.

p_H	p_K	p_E	ΔAIC	w	$-2ll$	$NPar$
Shooter + PNWS	Constant	Constant	0.00	0.26	230.17	7
Shooter + PNWS	Shooter	Constant	0.00	0.26	224.17	10
PNWS	Constant	Constant	0.63	0.19	236.79	4
PNWS	Shooter	Constant	0.63	0.19	230.80	7
Shooter	Constant	Constant	3.45	0.05	235.62	6
Shooter	Shooter	Constant	3.46	0.05	229.63	9

Presented is the relative difference in AIC (ΔAIC), the AIC model weight (w), twice the negative log-likelihood value ($-2ll$) and number of parameters in the model ($NPar$). For predictor explanation, see Table 2.

taken). In that case, Shooter 2 was estimated to have the lowest mean (\pm s.e.) p_H (0.78 ± 0.12), Shooters 1 and 3 had similar probabilities (0.88 ± 0.04), and Shooter 4 had the highest probability (0.95 ± 0.06 ; Fig. 3a). The probability of killing a deer that was hit was estimated to be lowest for Shooter 2 (0.72 ± 0.15), and similar for the other three shooters (approximately 0.85 ± 0.05). All deer that were missed by the first shot escaped; hence, p_E was constrained to be 1 for this group of animals. Shooting distance was not an important predictor of the probability of hitting a deer.

Time to insensibility

For the 14 deer that were killed but not rendered immediately insensible, the median TTI was 289 s (range: 100–840 s; Fig. 4). Our analysis indicated that the most-supported model did not include any predictors ($w_i = 0.51$; Table 6). Distance and adult males as predictors explained little additional variation in the data, but the respective models had non-negligible AIC model weights because they had similar numbers of parameters to the best-supported model. The estimated effect sizes are in the direction we predicted (i.e. TTI increases with an increasing distance, and is higher for adult males than for other age–sex classes), although they are close to zero and have large standard errors.

Wound numbers and locations

The mean (\pm s.d.) duration from shooting to carcass inspection was 8 ± 7 min (range = 1–33 min). Of the 109 carcasses that were inspected, 31 animals were adult males, 45 were adult females, 17 were juvenile males and 16 were juvenile females. Bullet-wound tract counts showed that 95 deer were shot once, 11 deer were shot twice and three deer were shot three times, with the mean (\pm s.d.) number of times an animal was shot being 1.16 ± 0.43 . Of 126 bullet-wound tracts examined, 83% (95% CI: 75–89%) of wound tracts indicated that the brain had been hit, 7% the anterior skull (3–13%), 5% the neck (2–11%), and 5% (1–10%) the jaw. No deer exhibited wounds to other parts of the body (i.e. thorax, abdomen or limbs). The mean (\pm s.d.) number of shots required to kill adult male rusa deer (1.23 ± 0.50) was only slightly higher than for other age–sex classes (i.e. adult female and all juveniles pooled; 1.14 ± 0.42).

Discussion

Many hundreds of thousands of deer have been shot at by ground-based shooters in Australasia (Caughley 1983; Harris 2002; Bengsen et al. 2020), but this is the first study to quantify the welfare outcomes of this technique.

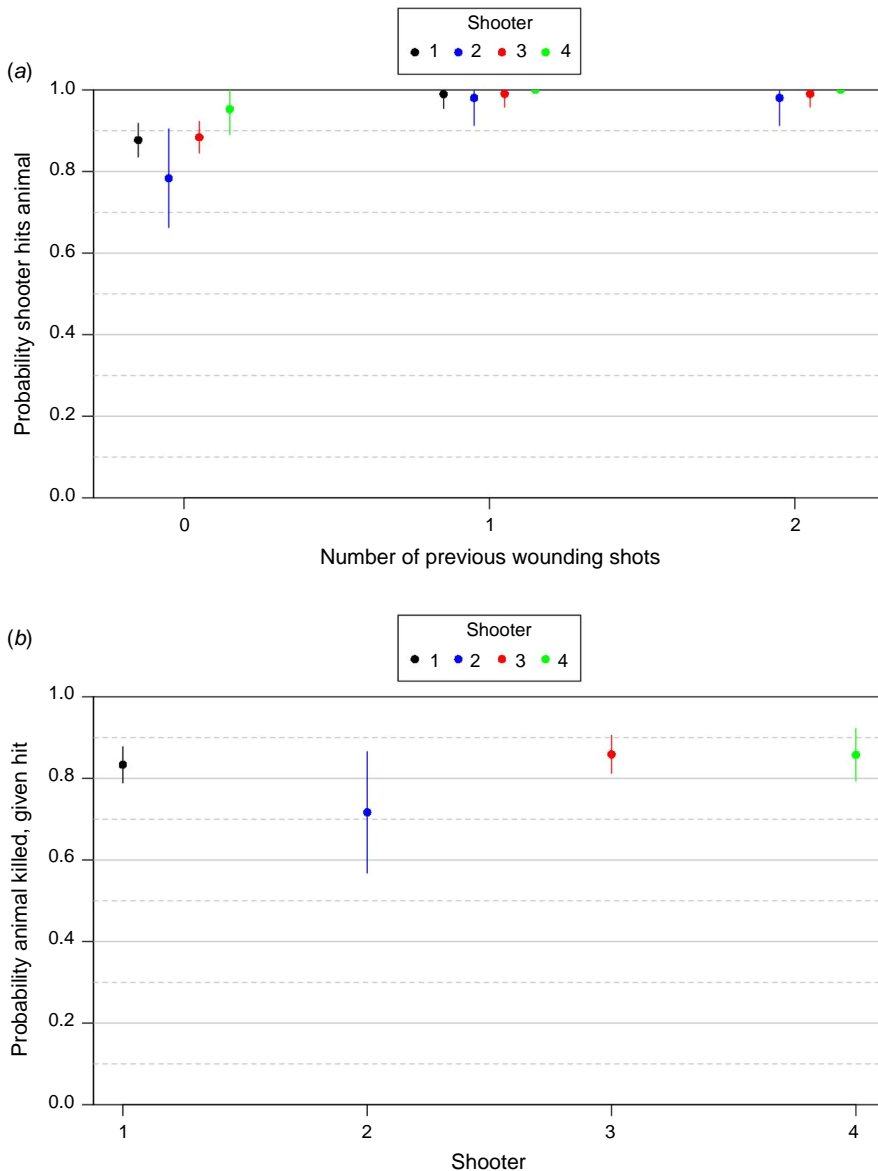


Fig. 3. Model-averaged estimates and standard errors of the probability of shooting outcomes during vehicle-based professional shooting of peri-urban rusa deer (*Cervus timorensis*) in Australia, 2018–2019. (a) The probability that a shot hits a deer (p_H), and (b) the probability that a shot kills a deer that was hit (p_K) are shown for the four different shooters. In (a), Shooter 1 did not fire ≥ 2 shots at a wounded deer.

We found that professional vehicle-based shooters operating in a peri-urban environment shot at approximately half of the rusa deer that they encountered. However, regardless of the observed group size, only one deer was usually shot at. Of the deer that were killed, 13% required one or more subsequent shots. Hence, time to insensibility was usually zero. Of the deer that were shot at and hit, non-fatal wounding occurred in 3.5% of cases. The probability of hitting a deer increased as the number of previous wounding shots increased, presumably owing to increasing incapacitation of the deer. Animal welfare outcomes varied among shooters. Our post-mortem observations indicated that all deer had been shot in the head or neck, as was stipulated in the program plan.

Non-fatal wounding is the least desirable animal welfare outcome (Aebischer *et al.* 2014). Several factors could have

contributed to four deer escaping wounded in this study. First, the practice of head shooting might have increased the risk of wounding because fatal haemorrhage is less likely than with chest-shooting (Stokke *et al.* 2018) if anatomical structures surrounding the brain (neck, jaw, anterior skull) are struck. In our study, 17% of deer that were killed and found were initially struck in these peri-cranial structures, and 74% of these deer required subsequent shots to the brain. For this reason, for deer shot in other contexts (e.g. aerial shooting), shooters are more likely to shoot at the thorax to incapacitate a deer rather than attempting a head shot (Sharp 2012; NSW National Parks and Wildlife Service 2020; Hampton *et al.* 2021b). Second, the flight responses of rusa deer made achieving a second shot for wounded deer difficult. Third, habitat features, particularly the dense *Lantana* thickets (Gooden *et al.* 2009), made wounded but

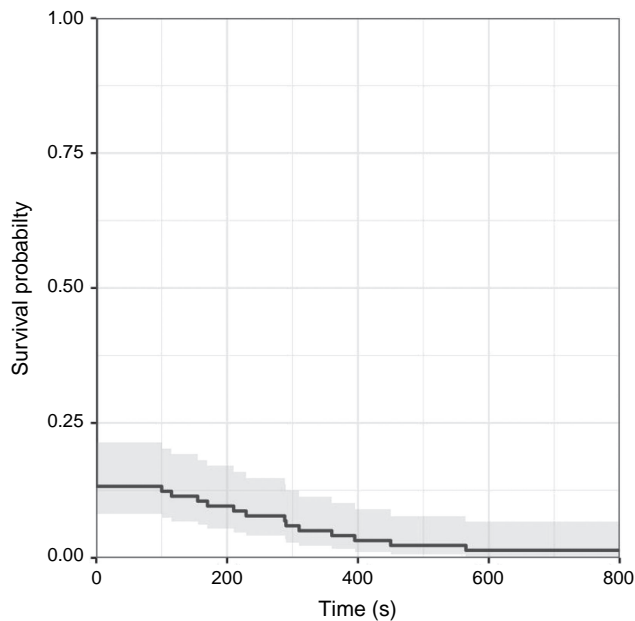


Fig. 4. Estimated time to insensibility for 110 peri-urban rusa deer (*Cervus timorensis*) shot in a peri-urban environment by vehicle-based professional shooters in Australia, 2018–2019. Shaded areas are 95% confidence intervals.

Table 6. Model selection summary for Cox's proportional hazards model used to evaluate the role of predictors influencing time to insensibility for peri-urban rusa deer (*Cervus timorensis*) shot during vehicle-based professional shooting in a peri-urban environment in Australia, 2018–2019.

Model	ΔAIC	w	LogLik	Npar
Null	0.00	0.51	811.24	0
Distance	1.78	0.21	811.02	1
Adult male	1.88	0.20	811.12	1
Adult male + Distance	3.62	0.08	810.87	2

Presented is the relative difference in AIC (ΔAIC), the AIC model weight (w), log-likelihood value ($LogLik$) and number of parameters in the model ($NPar$).

mobile deer difficult for the shooting team to detect. Similar findings have been reported from the aerial shooting of chital deer (*Axis axis*) in Queensland, whereby wounded deer have escaped follow-up shooting by sheltering in thickets of rubber vine (*Cryptostegia grandiflora*; Hampton et al. 2021b).

Our data suggested that adult male rusa deer were slightly more difficult to render immediately insensible than were other age–sex classes. This was expected because of the larger size of male rusa deer. Stokke et al. (2018) demonstrated the importance of animal mass in determining flight distance for mammals shot in the thorax, with larger animals being less quickly incapacitated. Similar effects relating to male animals being more likely to have adverse welfare outcomes have been shown for aerial shooting of

other sexually dimorphic ungulates, e.g. feral camels (*Camelus dromedarius*; Hampton et al. 2014).

The importance of the identity of shooters for animal welfare outcomes was also unsurprising. Shooters must anticipate and react to animal movement, place their shots accurately, and track and locate wounded animals (Hampton et al. 2021a). There is likely to be individual variation in these skills. Several other studies have demonstrated the importance of shooter identity for ground-based shooting of deer (Langenau 1986; Aebischer et al. 2014). This effect has also been shown for aerial shooting of feral camels (Hampton et al. 2014) and feral horses (*Equus caballus*; Hampton et al. 2017) in Australia. That there is an effect of shooter identity suggests that animal welfare outcomes in vehicle-based deer culling programs might be improved by screening or auditing shooters (Hampton et al. 2021a), and by providing training so that minimum welfare outcome standards are achieved (DeNicola et al. 2019).

The animal welfare outcomes reported here can be compared and contrasted with those reported for other ground-based shooting methods. Of most similarity to our study is the vehicle-based shooting of eastern grey kangaroos in a peri-urban environment (Hampton and Forsyth 2016). The frequency of adverse animal welfare events, including animals missed and non-fatally wounded, was higher for rusa deer in our study than for kangaroos. Median time to insensibility for rusa deer not rendered immediately insensible (289 s, $n = 14$) was much longer than for kangaroos (12 s, $n = 3$) and was likely to be related to the thick vegetation and steep terrain typically encountered in this study when compared with open and flat habitats typical of kangaroo shooting in the ACT (Hampton and Forsyth 2016). The frequency of immediate insensibility for deer hit (78%) was lower than that reported for vehicle-based shooting of kangaroos (98%; Hampton et al. 2019b) but was comparable to that for other professional shooting methods such as boat-based shooting of harp seals (*Pagophilus groenlandicus*; 84%; Ryeng and Larsen 2021), and exceeded that of other non-professional shooting methods such as vehicle-based shooting of European rabbits (60%; Hampton et al. 2015). Interspecific differences in the anatomy and bone density of the skulls of deer and kangaroos are also likely to have influenced shooting outcomes.

Ground-based and helicopter-based shooting are fundamentally different techniques, but the results derived here can be compared with those from aerial shooting of deer in eastern Australia (Hampton et al. 2021b). Unlike vehicle-based shooting, aerial shooting involves a pursuit phase, often involves repeat shooting, utilises much shorter shooting distances and typically uses the thorax rather than the head as the anatomical aim point. Accordingly, the frequency of immediate insensibility for deer hit in this study (78%) was substantially higher than for aerial shooting (<20%). Non-fatal wounding also occurred in aerial shooting (Hampton et al. 2021b), but the methods used to estimate this parameter

were different from those applied in this study, precluding direct comparison.

Rusa deer seem to be more difficult to kill than are other mammals commonly subject to ground-based shooting in Australasia (e.g. macropods). The well developed flight response of rusa deer was reflected by the observation that no deer that were first missed were subsequently killed. That is, shooters only got one shot at a deer before it fled such that there was no opportunity for a subsequent shot. Groups of rusa deer also proved hard to kill; even for larger groups of deer, shooters managed to fire only an average of 1.6 shots at a group. This result suggests that it is infeasible to kill all deer in a group before targeting another group, as proposed by Sharp (2013). However, it may make sense to target small groups first when multiple groups are encountered (Sharp 2013). Indeed, the modal rusa deer group size in our study was one. Our findings about the difficulty of killing a deer that was missed, or other members of a group that was shot at, are consistent with rusa deer developing behavioural responses to ground-based shooting (such as increasing vigilance rates and staying close to escape cover) that have been documented in other deer species (e.g. fallow deer *Dama dama*; Pecorella *et al.* 2016). Our results are in stark contrast to those for eastern grey kangaroos, a species for which it is common for vehicle-based professional shooters to kill multiple, or all, animals from a social group (Hampton and Forsyth 2016). Understanding the functional response of ground-based shooters to increasing deer group size is important because functional responses determine relative effort required to kill a deer and, in turn, influence the costs associated with this deer control method (Van Deelen and Etter 2003; Bengsen *et al.* 2022).

The rifle and ammunition could have influenced the animal welfare outcomes we observed. The ammunition (55 grain bullets loaded in .223[®] Remington cartridges) delivered lower muzzle kinetic-energy levels (~1700 J) than those typically associated with deer shooting, for example, a legally stipulated minimum of 2373 J for red deer in Scotland (Urquhart and McKendrick 2006). The calibre of the rifle (.223) was smaller than that recommended by the national deer code of practice, which states 'the minimum calibre is .243 with 100 grain projectile' (Sharp 2013). The same prescription is made by the voluntary Model Code of Practice for the Welfare of Animals: Feral Livestock Animals: Destruction or Capture, Handling and Marketing (Standing Committee on Agriculture, Animal Health Committee 2002), which guides helicopter-based shooting of deer in some Australian jurisdictions (Hampton *et al.* 2021b). However, .223 calibre rifles and even lighter bullets (50 grain) have been used for vehicle-based professional shooting of deer using the head (and neck) as targets for Philippine deer (*Rusa marianna*), which are of a similar mass to that of rusa deer, in Guam (DeNicola *et al.* 2019). The shooting equipment used in the program we evaluated was chosen for community safety reasons (Dawson 2017). Lighter bullets

delivering less kinetic energy carry several advantages for public safety and convenience. First, they are less likely to create pass-through shots whereby a bullet or its fragments may create an exit wound and continue to travel after striking a deer (DeNicola *et al.* 2019). Second, they are less likely to injure a person, domestic animal or damage property in the event of a missed shot. Third, they typically create less noise, a source of public nuisance in peri-urban shooting, which can also be reduced through the use of sound suppressors (Williams *et al.* 2018).

White-light illumination was used in the rusa deer shooting program, but thermal and night-vision rifle scopes are commonly used in ground-based deer shooting programs in Australia, for example, for sambar deer (*Cervus unicolor*) in Victoria (Brown 2017; Watter *et al.* 2020), and for peri-urban kangaroos in the Australian Capital Territory (Hampton and Forsyth 2016). The use of thermal or night vision might improve animal welfare outcomes through: (a) increasing the probability of detecting deer, including wounded deer; (b) reducing shooting distances because shooters can approach closer without being detected than with white-light (although our study did not show a strong effect of shooting distance on animal welfare outcomes); and (c) reducing flight responses from conspecifics (Hanson *et al.* 2019; Logan *et al.* 2019). The relatively weak influence of shooting distance on outcomes was somewhat surprising, given the strength of this variable in other published studies, for example, in Hampton *et al.* (2015).

Specialised techniques are often required for shooting in peri-urban areas to be safe, effective and socially acceptable (DeNicola *et al.* 2000). Managing deer in close proximity to high-density human settlements is a relatively recent challenge in Australia (Burgin *et al.* 2015), whereas methods used to manage peri-urban deer internationally (especially in the USA) have been refined over many decades (Kilpatrick *et al.* 1997; Curtis 2020). Methods used in the USA for shooting peri-urban deer that are not yet widely used in Australia include the use of suppressors (DeNicola and Williams 2008), bait to attract deer to shooting sites that are safer from a community safety perspective but more lethal for deer (Kilpatrick and Stober 2002), alternative anatomical aim points (e.g. neck shooting; DeNicola *et al.* 2019) and alternative bullet construction (e.g. copper bullets; McCann *et al.* 2016). These methods could improve the animal welfare outcomes of ground-based shooting programs in Australia. We encourage a quantitative approach to the evaluation of these methods.

Conclusions

Vehicle-based shooting of peri-urban rusa deer produced animal welfare outcomes comparable to those of professional ground-based shooting programs for ungulates, but the outcomes were poorer than those reported for

professional ground-based shooting of kangaroos. The poorer outcomes for rusa deer than for kangaroos were likely to be related to differences in terrain, shooting distance and species susceptibility, especially their flight behaviours. Our study suggests that one way to improve the animal welfare outcomes of vehicle-based shooting of peri-urban deer is by improving shooter training. Assessment of shooter performance should be a routine part of ground-based shooting programs.

Supplementary material

Supplementary material is available [online](#).

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Data availability. The data that support this study cannot be publicly shared due to privacy reasons and may be shared upon reasonable request to the corresponding author if appropriate.

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