

Animal welfare outcomes of helicopter-based shooting of deer in Australia

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Abstract

Context. Helicopter-based shooting has been widely used to kill deer in Australasia, but the animal welfare outcomes of this technique have not been evaluated.

Aim. To assess the animal welfare outcomes of helicopter-based shooting of deer in Australia 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. Three deer control operations were assessed. These operations targeted: (1) chital deer (*Axis axis*) in Queensland, (2) fallow deer (*Dama dama*) in Australian Capital Territory and (3) fallow deer in New South Wales. For each operation, an independent veterinarian conducted ante-mortem (i.e. from the helicopter as shooting occurred) and post-mortem (i.e. from the ground after shooting had ceased) observations. The ante-mortem data were used to estimate the proportion of deer seen that were shot, chase time (CT), time to insensibility (TTI) and total time (TT; CT + TTI). The numbers and locations of bullet wounds were recorded post-mortem.

Key results. Ante-mortem and post-mortem observations were performed for 114–318 and 60–105 deer, respectively, in the three operations. Shots were fired at 69–76% of deer that were observed. Median CT ranged from 73 to 145 s. Median TTI ranged from 17 to 37 s and median TT ranged from 109 to 162 s. The mean number of bullet wounds per deer ranged from 1.43 to 2.57. Animal welfare outcomes were better in the two fallow deer operations than in the chital deer operation. In both fallow deer operations, most deer were shot multiple times and at least once in the head or thorax. In contrast, chital deer were shot fewer times and less often in the head or thorax, and non-fatal wounding was observed.

Conclusions. The best animal welfare outcomes were achieved when helicopter-based shooting operations followed a fly-back procedure and mandated that multiple shots were fired into each animal.

Implications. Animal welfare outcomes for helicopter-based deer shooting in Australia could be improved with a national-level standard operating procedure requiring helicopters to fly back over shot animals and repeatedly shoot animals in the head or thorax.

Keywords: invasive species, pest management, population control, wildlife management.

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Introduction

In Australia and New Zealand, populations of introduced deer can have undesirable economic, social, environmental and human health impacts (Forsyth *et al.* 2010; Burgin *et al.* 2015; Davis *et al.* 2016; Forsyth *et al.* 2017; Latham *et al.* 2020b). One approach to reducing those impacts is through lethal control,

usually by shooting, but this is sometimes contentious because of concerns about animal welfare outcomes (Rutberg 1997; Pecorella *et al.* 2016; DeNicola *et al.* 2019).

Helicopter-based shooting (hereinafter ‘aerial shooting’) has been used to control at least 33 mammalian species worldwide, including at least six species of deer

(Hampton *et al.* 2017). Aerial shooting is considered the most effective method for reducing deer abundances over large geographical areas in New Zealand (Forsyth *et al.* 2013; Latham *et al.* 2018). There is a perception that aerial shooting may cause poor animal welfare outcomes (Chapple 2005), but no study has quantified the animal welfare outcomes of the technique for deer. The animal welfare outcomes of aerial shooting of deer in Australia are a recognised key knowledge gap (Forsyth *et al.* 2017).

The only quantitative assessments of animal welfare outcomes for aerial shooting of ungulates are for feral camels (*Camelus dromedaries*; Hampton *et al.* 2014) and feral horses (*Equus caballus*; Hampton *et al.* 2017). Those two Australian studies used similar field methods to quantify several metrics related to animal welfare outcomes. First, they measured the duration of procedures including: (1) helicopter pursuit (Linklater and Cameron 2002); and (2) the mode of death via shooting (Stokke *et al.* 2018). Second, they estimated the frequency of immediate insensibility, which has sometimes been termed ‘instant death’ (Hampton *et al.* 2014) or ‘instant incapacitation’ (McTee *et al.* 2017), with all terms having identical meaning, but this method is most accurately described as insensibility (Hampton and Forsyth 2016). Third, they documented the frequency of non-fatal wounding, considered the worst animal welfare outcome for any shooting operation because it causes protracted (but unmeasured) suffering (Aebischer *et al.* 2014). Finally, to assess the accuracy of shooting and the frequency of repeat shooting practices (i.e. shooting each animal more than once), the number and anatomical location of bullet wounds were recorded (Hampton *et al.* 2016a).

A diversity of procedural documents (i.e. standard operation procedures, codes of practice and manuals; Hampton *et al.* 2016b) are used to guide the aerial shooting of deer in Australia, and they are largely jurisdiction-specific, varying between states and territories, with different protocols adopted by shoot managers in each case. There is currently no national model standard operating procedure for the aerial shooting of deer, as exists for other established invasive ungulate species, e.g. feral goats (*Capra hircus*; Sharp 2012). Procedural documents currently used range from those with many stipulations, such as used in New South Wales (NSW; Feral Animal Aerial Shooting Team 2020), to those with few stipulations, such as those used in Queensland (Standing Committee on Agriculture Animal Health Committee 2002). These stipulations govern several variables of potential relevance to animal welfare outcomes, including firearm type (i.e. rifle or shotgun), calibre and bullet mass and pilot and shooter training. Procedural documents also vary in their specifications for how shooting should be conducted. Several aerial shooting procedural documents require that helicopters return to fly over shot animals after initial shooting (‘fly back’) to conduct repeat shooting to minimise the time to insensibility and the likelihood of non-fatal wounding (Hampton *et al.* 2016a).

Here we assess the animal welfare outcomes of aerial shooting of deer in Australia. Our objective was to quantify: (1) the fates of deer seen and shot at; (2) the duration of procedures; and (3) the number and location of bullet wounds in dead deer.

Materials and methods

Study areas and species

Three aerial shooting operations were assessed. All operations occurred on days when weather conditions were suitable for shooting, with no rain and relatively little wind. The first operation targeted chital deer (*Axis axis*) and was conducted on extensive cattle grazing properties in the Einasleigh Uplands bioregion of the North Queensland Dry Tropics (Operation A). The area is primarily open tropical savannah woodland characterised by *Eucalyptus* spp. and *Corymbia* spp. interspersed with patches of tussock grassland and *Acacia* and *Melaleuca* thickets (Forsyth *et al.* 2019). The climate is semiarid tropical with summer-dominant, but highly variable, rainfall (Forsyth *et al.* 2019). The shooting was conducted over 4 days during November 2017.

The second operation targeted fallow deer (*Dama dama*) in the Australian Capital Territory (ACT), over 4 days in June 2019 (Operation B). The operational area is characterised by native grasslands, *Pinus radiata* plantations and areas of native woodland (primarily red stringybark (*Eucalyptus macrorhyncha*) and scribbly gum (*Eucalyptus haemastoma*), as well as red-anthered wallaby grass (*Rytidosperma pallidum*), tall grass-shrub dry sclerophyll open forest on loamy ridges and grassy woodland (Armstrong *et al.* 2013; ACT Government GeoHub 2018). The climate is temperate, and there was sheep and cattle grazing on some properties.

The third operation targeted fallow deer in the Central Tablelands region of NSW over 4 days in August 2020 (Operation C). The climate is similar to the ACT, and cattle and sheep grazing are the dominant land uses. There are areas of improved pasture and cropping (lucerne and oats) in the lower, fertile valley floors. Slopes and ridges are dominated by grassy woodlands and dry sclerophyll forests (Office of Environment and Heritage 2017).

Chital deer and fallow deer are strongly sexually size-dimorphic. Adult female and male chital deer have mean weights of 49 kg and 77 kg respectively (M. Brennan and A. Pople, unpubl. data), and the equivalent masses for fallow deer are 38 kg and 59 kg respectively (Bentley 1995). The fallow deer birth season in Australia is November–December (Bentley 1995). In their native and introduced ranges, chital deer can produce fawns throughout the year but have a seasonal peak of births (Graf and Nichols 1966; Ahrestani *et al.* 2012). In north Queensland, there is typically a broad peak of births during the December–March ‘wet season’ (A. Pople, unpubl. data). Many procedural documents stipulate that shooting should only occur when no dependent young are present; for both species, offspring are considered independent at 3–4 months old (English 1992; Tuckwell 2003; New Zealand Government 2018). All three shooting operations were timed to avoid periods when dependent young were likely to be present.

Shooting procedures

The procedural document used for Operation A was 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). This document specifies that animals must be



Fig. 1. Field methods used to collect post-mortem data from the aerial shooting of deer. Inspection of (a) a chital deer (*Axis axis*) shot from a piston-powered helicopter in Queensland, north-eastern Australia in 2017, and (b) a fallow deer (*Dama dama*) shot from a turbine-powered helicopter in New South Wales, south-eastern Australia in 2020.

shot in accordance with the Queensland *Animal Care and Protection Act 2001*, which states that ‘it is an offence to kill an animal inhumanely’. This document provides guidelines for minimum acceptable outcomes for animal welfare for ‘feral livestock’ (e.g. a rifle should be a minimum calibre of 0.243 and use bullets with a minimum mass of 100 grains).

For Operation B, the national feral goat aerial shooting standard operating procedure (Sharp 2012) was the guiding procedural document, presumably because feral goats and fallow deer have similar body masses. This document specifies that a rifle or shotgun can be used, that shots be fired at either the heart or lung (hereinafter ‘thorax’) or head, and that animals should be shot at least twice in total in these anatomical zones. There is a requirement to fly back over each shot animal to apply follow-up shots to the thorax or head. The operational plan added the stipulation that all animals were to receive a minimum of two shots to the thorax before the shooter targeted another deer.

For Operation C, the guiding procedural document was the Feral Animal Aerial Shooting Team (FAAST) Manual (Feral Animal Aerial Shooting Team 2020). This document contains stipulations similar to the national feral goat aerial shooting standard operating procedure (Sharp 2012), including mandatory repeat shooting with at least one shot to the thorax or, if not possible due to the position of the animal, the head. A fly-back procedure is also prescribed to confirm that an animal that has been shot is dead. If there is any doubt, a further shot must be directed into the thorax or head. The document also stipulates that the timing of shooting operations (i.e. what month they occur in) should be chosen to avoid the presence of dependent young (Feral Animal Aerial Shooting Team 2020).

Similarities across all three operations included targeting of all observed deer and adherence to Civil Aviation Safety Authority regulations. For all operations, shooters were accredited by the Civil Aviation Safety Authority to shoot from helicopters, and had a minimum of 2 years’ experience in helicopter shooting of ungulates, including deer. All pilots and aircraft were chartered or contracted, rather than government agency aircraft or staff. All pilots also had a minimum of 2 years’ experience in aerial shooting of ungulates. One shooter and a pilot operated from one shooting helicopter in each operation. In all operations,

pre-loaded rifle magazines were at the shooter’s feet, so that rifles could be reloaded quickly. Deer were shot from distances of 4–40 m. Dissimilarities among the operations included the identity of pilots and shooters (including that the shooter in Operation C was a government agency employee, but shooters were contractors in Operations A and B), type of helicopter, presence of a navigator alongside the pilot (Operations B and C only), firearms, ammunition and repeat shooting practices.

For Operation A, a Robinson 44 (R44) helicopter (Torrance, CA, USA; Fig. 1a) was used. The firearm was a Springfield M1A semi-automatic Winchester 0.308 (7.62 × 51 mm NATO) calibre rifle (Springfield Armory, Inc., Geneseo, IL, USA). Three types of ammunition were used: (1) 150 grain soft point; (2) 130 grain hollow point; and (3) 125 grain soft point. The shooter combined ammunition types in each shooting session so observations of animal welfare outcomes specific to each bullet mass were not recorded. The rifle was fitted with an electronic red-dot sight. For Operation B, the shooter was a private contractor and flew in an Airbus AS350 B2 Squirrel helicopter (Airbus, Marignane, France; Fig. 1b) with two firearms: (1) a Springfield M1A semi-automatic rifle chambered in 0.308 Winchester; and (2) a 12-gauge pump action shotgun. The rifle ammunition was 130 grain hollow-point bullets. The shotgun cartridges were 36 grain AAA lead shot. Both firearms were fitted with electronic red-dot sights. For Operation C, the shooter was a government agency employee, and flew in an Airbus AS350 B2 Squirrel helicopter (Airbus) with one firearm: an FN SCAR-H semi-automatic rifle chambered in 0.308 Winchester (Fabrique National Herstal, Herstal, Belgium), and fitted with a non-magnified red-dot scope. Ammunition was 135 grain hollow-point bullets. In all three operations, the ammunition was lead based.

The position of the independent observer and the shooter varied according to helicopter. In Operation A the shooter sat in the front left (next to the pilot) and the observer in the left rear, and in Operations B and C the shooter sat in the right rear (behind the pilot) and the observer in the left rear.

Helicopter-based observations

We used the methods developed by Hampton *et al.* (2014) for aerial shooting of feral camels.

We recorded similar helicopter-based (ante-mortem) and ground-based (post-mortem) data in all operations. Helicopter-based observations were made by an independent veterinarian ('observer') seated in the shooting helicopter. All chase and shooting events that could be clearly seen by the observer were recorded. The number of deer seen and shot, and the times that elapsed between these events, were spoken into a hand-held voice recorder. Group size was defined as the number of animals initially seen together before shooting began (Pople *et al.* 1998). Assigning group size was occasionally ambiguous, particularly when large (>10 animals) groups of deer split. In these cases, one subgroup was always pursued and the other typically disappeared from the observer's view. In some cases, a similar-sized group to that lost from sight was found soon after. In these cases, each group sighted was assumed to be a new group rather than a subgroup from a previously sighted larger group.

Three time-to-event parameters were quantified from the voice recordings. Chase time (CT; seconds) was the interval between the onset of group escape behaviour (a group beginning to run in response to helicopter disturbance) and the first shot being fired at each individual animal (Hampton *et al.* 2017). Time to insensibility (TTI; seconds) was the duration between the first shooting event and insensibility (i.e. the moment the animal became recumbent and ceased moving; Hampton *et al.* 2014; Hampton *et al.* 2017). This parameter has been termed 'time to death' (TTD) in previous aerial shooting studies, but helicopter-based observations do not necessarily detect deer that are hit and rendered insensible but return to consciousness (i.e. that are rendered insensible but do not die; Hampton *et al.* 2017). Finally, total time (TT) was the total duration of stress imposed by helicopter shooting, beginning at the onset of escape behaviour and ending with insensibility, i.e. $TT = CT + TTI$ (Hampton *et al.* 2017).

Ground-based observations

Ground-based data were collected during each operation by the same independent veterinarians that conducted the helicopter-based observations. Culled deer were selected opportunistically for *in situ* ground-based inspection (Fig. 1) to determine if they were dead and, if so, to conduct post-mortem assessments of the numbers and locations of bullet wounds. Deer that were found to be non-fatally wounded were euthanased with a firearm by ground-based observers. To reduce the likelihood of altered shooting behaviour due to the presence of the observer, we did not make shooters aware of which animals would be inspected. The duration between shooting and ground-based inspection was recorded. In Operation A, shot deer were inspected immediately after shooting to allow transport via slinging (Fig. 1a) and permit *ex situ* dissection for other research. We recorded the sex and age-class (juvenile or adult) of inspected animals and assigned bullet wound locations on the basis of the anatomical zones (head, neck, thorax, abdomen and limbs) displaying the most damage (Hampton *et al.* 2014).

Non-fatal wounding

Non-fatal wounding is defined as deer that are shot but not killed (Aebischer *et al.* 2014). This occurrence could have been

detected from either helicopter-based observations (wounded and mobile animals) or ground-based observations (wounded and immobile animals). Helicopter-based observations do not necessarily detect deer that are hit and rendered insensible but return to consciousness (Hampton *et al.* 2017). Likewise, ground-based observations (Fig. 1b) do not necessarily detect deer that are hit and regain mobility. As a consequence, our estimates of the frequency of non-fatal wounding should be considered minimum estimates (Hampton *et al.* 2017).

Procedural document compliance

We estimated the frequency of three metrics related to compliance with jurisdictional procedural documents. These were: (1) flybacks (helicopter-based assessment: when the helicopter returned to hover over an immobile deer); (2) repeat shooting (ground-based assessment: when more than one bullet wound was found in a deer); and (3) shots to the head or thorax (ground-based assessment: when wounds were found in at least one of these zones).

Sample sizes

Desired sample sizes for ante-mortem and post-mortem observations were guided by published statistical guidelines for animal welfare studies (Hampton *et al.* 2019a). Where logistically possible, we sought minimum ante-mortem and post-mortem sample sizes of >113, assuming an expected frequency of animal welfare outcomes of interest of ~5% (Hampton *et al.* 2017).

Statistical analysis

Probability of encounter and shooting outcomes

We classified the immediate outcomes of each encounter with a deer into one of two events: (1) ≥ 1 shot was fired at the deer; or (2) no shots were fired at the deer. We estimated the probability of shots being fired at a deer after it was encountered for each operation using logistic regression. We specified group size as a covariate because we expected that the probability of shots being fired at any individual might be lower in larger groups where there were more targets to choose from. Group size was centred by subtracting the mean group size across all sites.

We next assigned the outcome for each deer at which shots were fired into one of three categories: (1) the deer escaped uninjured; (2) the deer escaped wounded; or (3) the deer was rendered insensible. For those deer that were rendered insensible, we also estimated the probability of insensibility occurring immediately from the first shot (equivalent to 'instantaneous death rate' in Hampton *et al.* (2014)). These probabilities were estimated using logistic regression.

Time-to-event data

An exponential survival model was fitted to chase time (CT) and time-to-insensibility (TTI) data, with operation ($K = 3$) specified as a covariate in the likelihood functions for each event. Many TTI observations could not be assigned an exact time to insensibility because the position of the observer in the helicopter prevented them from observing and definitively inferring an animal's insensibility or, in one operation, because

the helicopter sometimes moved away before insensibility could be confirmed. In these cases, the minimum TTI was recorded (i.e. these data were right censored). The expected TTI for each censored datum was imputed by sampling an interval distribution such that expected TTI was greater than the minimum TTI observed for that point and less than the maximum TTI across all data (Plummer 2017). TT was derived within the model as the sum of CT and the observed or imputed TTI for each observation. These values were used to fit survival functions for TT in a second exponential model, again using operation as a covariate.

Wound numbers and locations

The mean number of wounds per deer was estimated for each operation from the post-mortem data using Poisson regression. The probabilities of bullet wounds in deer in each of five major anatomical zones (head, neck, thorax, abdomen and limbs) and the probability of a deer having only one detectable wound were compared among operations using logistic regression.

All models were implemented in JAGS version 4.3.0 (Plummer 2017) called via the runjags package version 2.04–2 (Denwood 2016) in R version 4.0.3 (R Core Team 2020). We used 10 000 MCMC draws from each of four chains after discarding 5000 burn-in draws. Convergence and burn-in adequacy were assessed by examining trace plots, overlap of posterior distributions from each chain and the Gelman-Rubin statistic \hat{R} (Brooks and Gelman 1998). Parameter estimates are reported as posterior means and 95% credible intervals (CrIs).

Results

Sample sizes

Ante-mortem and post-mortem sample sizes for each of the three operations are shown in Table 1. All deer were shot with rifles, except for six juvenile fallow deer in Operation B that were shot with a shotgun; these six deer were included in the ante-mortem observations but, by chance, none were assessed in the post-mortem observations.

Probability of being shot at and shooting outcomes

The probability of shots being fired at any given deer in an average-sized group comprising seven individuals was similar for all three operations (Operation A = 0.69, 0.62–0.76; Operation B = 0.73, 0.61–0.83; Operation C = 0.76, 0.70–0.81). The log odds of shots being fired at an individual deer declined with

increasing group size for operations A (regression coefficient: $-0.16, -0.25$ to -0.08) and C ($-0.13, -0.19$ to -0.07), but there was no strong relationship between these variables in Operation B ($0.11, -0.05$ to 0.28 ; Fig. 2).

The probability of a deer being rendered insensible after shots were fired at it was 1.0 for Operation C and 0.93 for both Operations A and B (Table 1). In Operation B, all deer that were not rendered insensible after being shot at escaped uninjured, whereas in Operation A, three of 135 deer (2%, 0–5%) that were shot at and struck were wounded but mobile and escaped. For those deer that were rendered insensible, the probability of insensibility being immediate was nine times greater in Operation B (0.18, 0.1–0.28) than in Operation C (0.02, 0.0–0.04) and 4.5 times greater in Operation B than in Operation A (0.04, 0.02–0.09).

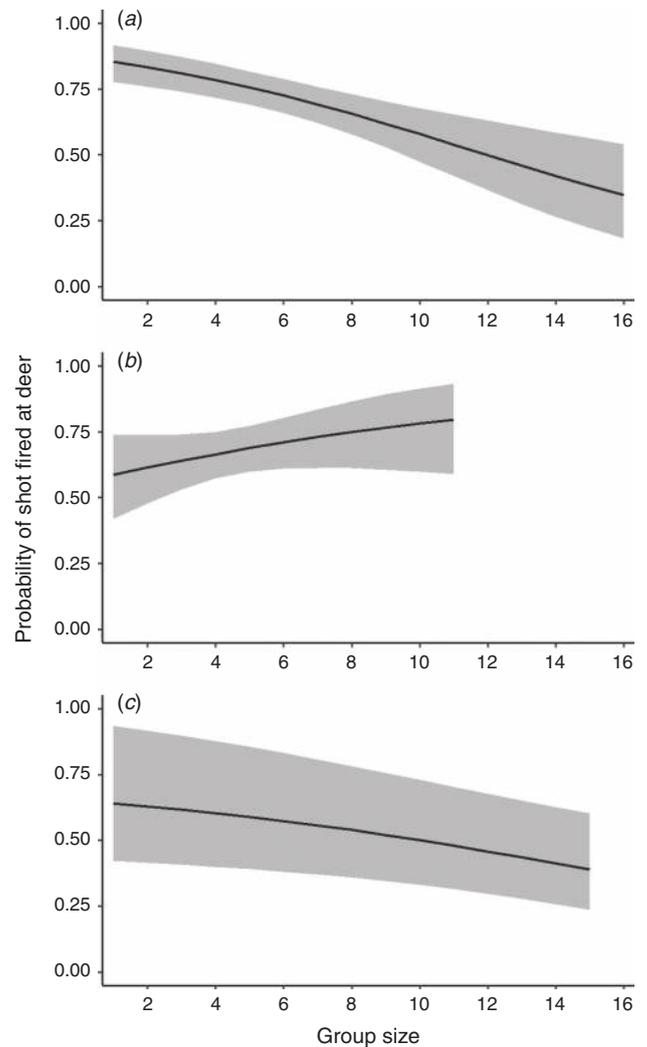


Fig. 2. Probability of an individual deer being shot at, as a function of the number of deer in the group, for each of three aerial shooting operations in eastern Australia, 2017–20. Shaded areas are 95% credible intervals: (a) Operation A; (b) Operation B; and (c) Operation C. For operational details, see Table 1.

Table 1. Details and sample sizes (*n*) for ante-mortem and post-mortem observations for the three helicopter-based deer shooting operations in eastern Australia, 2017–20

| Operation | Year | Jurisdiction | Species | <i>n</i> (ante-mortem) | <i>n</i> (post-mortem) |
|-----------|------|--------------|-------------|------------------------|------------------------|
| A | 2017 | Queensland | Chital deer | 200 | 60 |
| B | 2019 | ACT | Fallow deer | 114 | 60 |
| C | 2020 | NSW | Fallow deer | 318 | 105 |
| Total | | | | 632 | 225 |

Time-to-event

CT ranged from 7 s to 11 min 13 s. Median CTs for Operation B (2 min 25 s, 95% CrI = 1 min 55 s–3 min 3 s) and Operation C (1 min 55 s, 95% CrI = 1 min 41 s–2 min 11 s) were 2 and 1.6 times greater than for Operation A (1 min 13 s, 95% CrI = 1 min 1 s–1 min 26 s), respectively (Fig. 3a).

Observed TTI for deer not rendered immediately insensible ranged from 1 s to 7 min 6 s. Across all three operations, 95% of deer were rendered insensible within 57 s of the first shot being fired at them. The proportion of censored TTI values ranged from 0.26 (Operation B) to 0.34 (Operation C). The TTI hazard, or instantaneous risk of being rendered insensible, was 2.0 and 1.5 times greater for deer in Operations B and C, respectively, than for deer in Operation A. Median TTI for Operation A (37 s, 95% CrI = 29–46 s) was approximately double that of Operation

B (17 s, 95% CrI = 13–23 s) and Operation C (18 s, 95% CrI = 15–22 s; Fig. 3b).

Observed TT from the beginning of pursuit until insensibility ranged from 11 s in Operation A to 11 min 22 s in Operation C. Median TT for Operation B (2 min 42 s, 2 min 8 s–3 min 25 s) was 1.5 times greater than for Operation A (1 min 49 s, 1 min 32 s–2 min 9 s), whereas median TT for Operation C (2 min 14 s, 1 min 57 s–2 min 32 s) was 1.2 times greater than for Operation A (Fig. 3c).

Wound numbers and locations

For logistical and safety reasons, the interval between shooting and inspection was variable. For some deer, this interval was >12 h. The average duration from shooting to ground-based inspection was 9.1 min for Operation A, 11.8 h for Operation B and 4.0 h for Operation C. For Operation A, ground-based observations showed that four of 60 (7%, 2–14%) deer were found to be alive, sensible and wounded (but recumbent and immobile). All deer assessed via ground-based observations in Operations B and C were dead. Scavenging by feral pigs (Gregory 2017) prevented accurate assessment of the number or location of bullet wounds for 10% of carcasses in Operation B. Post-mortem examinations showed that deer in Operation A had fewer wound tracts (mean = 1.43, 95% CrI = 1.15–1.75) than deer in Operation B (mean = 2.65, 95% CrI = 2.24–3.09) or Operation C (mean = 2.57, 95% CrI = 2.26–2.89). The probability of a deer having only a single bullet wound tract was 0.60 in Operation A (95% CrI = 0.48–0.72), but only 0.04 in Operation B (95% CrI = 0.00–0.10) and 0.02 in Operation C (95% CrI = 0.00–0.05; Table 2).

In all three operations, most deer had at least one bullet wound in the thorax, but the probability of a deer having a wound in the thorax was 25% lower for Operation A than for Operations B and C (Fig. 4). No deer examined in Operation A had a head wound, whereas the probability of at least one head wound was 0.13 (95% CrI = 0.06–0.23) in Operation B and 0.15 (0.09–0.23) in Operation C. Consequently, the probability of deer in Operation A having no visible wounds in either the thorax or head (0.28, 0.18–0.40) was seven times

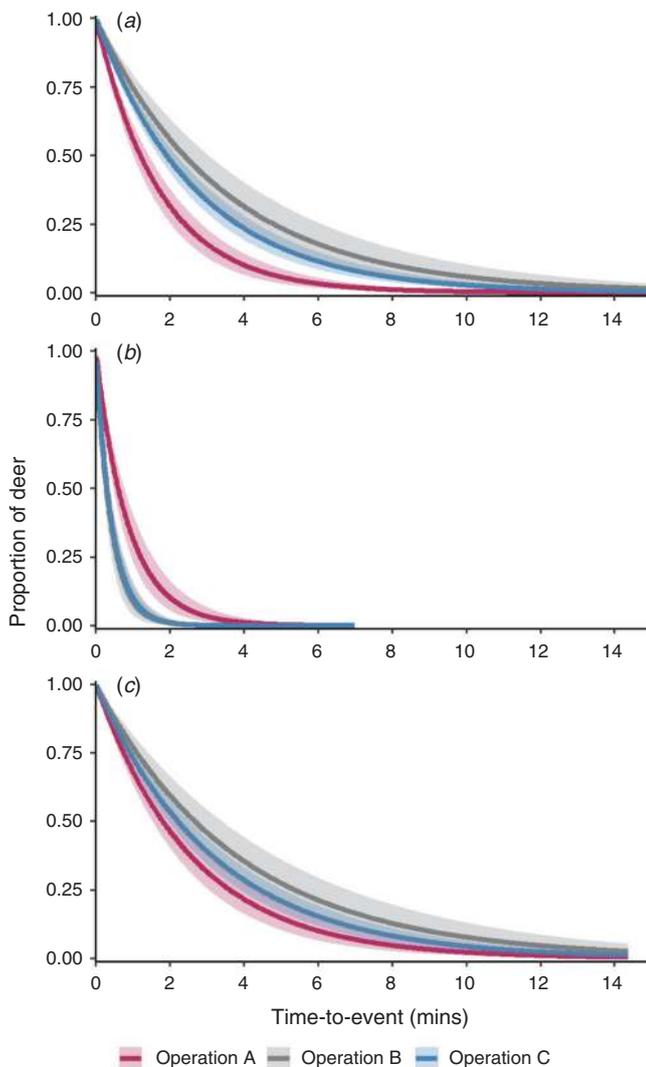


Fig. 3. Estimated duration of three to time-to-event parameters: (a) chase time; (b) time-to-insensibility; and (c) total time for 432 deer killed during three aerial shooting operations in eastern Australia, 2017–20. Shaded areas show 95% credible intervals. For operational details, see Table 1.

Table 2. Probabilities of deer being rendered insensible, wounded or escaping uninjured after being shot at in three aerial shooting operations in eastern Australia, 2017–20

Helicopter-based observations cannot detect the death of shot animals, therefore the outcomes are reported as ‘insensible’ rather than ‘killed’. For operational details, see Table 1. CrL, credible limit

| Outcome | Operation | n | P(outcome) | Lower 95% CrL | Upper 95% CrL |
|------------|-----------|-----|------------|---------------|---------------|
| Insensible | A | 132 | 0.93 | 0.87 | 0.96 |
| Insensible | B | 71 | 0.93 | 0.85 | 0.97 |
| Insensible | C | 229 | 1.00 | 1.00 | 1.00 |
| Wounded | A | 3 | 0.02 | 0.00 | 0.05 |
| Wounded | B | 0 | 0.00 | 0.00 | 0.00 |
| Wounded | C | 0 | 0.00 | 0.00 | 0.00 |
| Escaped | A | 8 | 0.05 | 0.02 | 0.10 |
| Escaped | B | 6 | 0.07 | 0.03 | 0.15 |
| Escaped | C | 0 | 0.00 | 0.00 | 0.00 |

greater than for deer in Operation B (0.04, 0.00–0.10) or Operation C (0.04, 0.01–0.08). In Operation B, 50% of deer had ≥ 1 neck wound – much greater than for Operations A and C ($\leq 30\%$).

Compliance with jurisdictional procedural documents

Fly backs were performed for all deer observed to be shot and hit in Operations B and C, but the probability of a fly back was 0.55 (0.46–0.63) in Operation A (Table 3). Likewise, the probability of repeat shooting was 0.96 (0.90–1.00) for operation B and 0.98 (0.95–1.00) for operation C, but

0.40 (0.28–0.53) for Operation A. Finally, the probability of deer having a bullet wound in either the head or thorax was 0.96 (0.90–1.00) for operation B and 0.96 (0.92–0.99) for operation C, but 0.72 (0.60–0.82) for Operation A.

Discussion

Many hundreds of thousands of deer have been shot from helicopters in Australasia (Challies 1985; Nugent and Choquenot 2004; Warburton *et al.* 2018), but ours is the first study to quantify the welfare outcomes of this technique. For the three

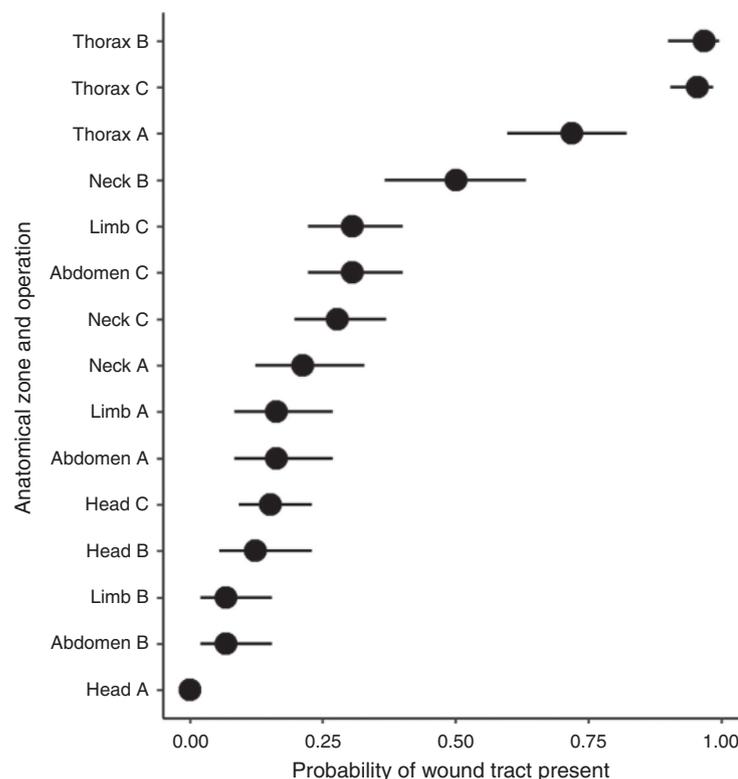


Fig. 4. Caterpillar chart of the mean probability (and 95% credible interval) that each of five anatomical zones were struck by at least one bullet during three aerial deer shooting operations in eastern Australia, 2017–20. Operations are designated by the letters A, B and C; for details, see Table 1.

Table 3. A comparison of compliance with jurisdictional procedural documents for each of three aerial deer shooting operations in eastern Australia, 2017–20

Observed frequencies are given with lower and upper 95% credible intervals in parentheses. For operational details, see Table 1

| Jurisdiction | Operation | Procedural document | Fly back required? | Frequency observed | Repeat shooting required? | Frequency observed | Head/thorax shooting required? | Frequency observed |
|--------------|-----------|--|--------------------|----------------------|---------------------------|----------------------|--------------------------------|----------------------|
| Qld | A | Standing Committee on Agriculture Animal Health Committee 2002 | No | 0.55 (0.46, 0.63) | No | 0.40 (0.28, 0.53) | No | 0.72 (0.60, 0.82) |
| ACT | B | Sharp 2012 | Yes | 1.00 | Yes | 0.96 (0.90, 1.00) | Yes | 0.96 (0.90, 1.00) |
| NSW | C | Feral Animal Aerial Shooting Team 2020 | Yes | 1.00 | Yes | 0.98 (0.95, 1.00) | Yes | 0.96 (0.92, 0.99) |

operations we assessed, approximately three-quarters of deer seen were shot, mean total time for shot deer was 2–3 min, non-fatal wounding was observed in only one operation and the majority of deer were shot multiple times. Based on our findings, we suggest several changes to procedures that should improve the welfare outcomes of future aerial deer shooting operations.

The best animal welfare outcomes were observed in Operations B and C, with almost all deer shot more than once and having at least one wound in the thorax or head; thus, times to insensibility were short and no deer were observed to be wounded and sensible (although times to ground-based inspection were sometimes long). Poorer welfare outcomes occurred in Operation A, with fewer deer shot multiple times and having at least one wound in the thorax or head, resulting in longer times to insensibility and several deer escaping wounded or being found immobile, but wounded and sensible. Non-fatal wounding is the least desirable animal welfare outcome (Aebischer *et al.* 2014), and occurred in two ways in Operation A. First, four deer were hit, became immobile and were rendered insensible, but were not killed, and fly back was not performed. Second, three deer were hit, remained mobile and disappeared under dense rubber vine (*Cryptostegia grandiflora*) thickets where they could not be seen by the shooter. In the latter situations, fly-back procedures were performed but did not prevent non-fatal wounding. To avoid these outcomes, deer may need to be flushed (chased) into more open areas, which would come with an animal welfare trade off, whereby duration of stress during pursuit would be increased to reduce the likelihood of an adverse event during shooting.

Observations of non-fatal wounding are likely to be related to most animals being shot only once in Operation A, whereas repeat shooting occurred almost always in the other two operations, and the probability of being shot in the thorax or head was much lower for Operation A than for the other operations. Non-fatal wounding was detected in two different ways in Operation A: (1) via helicopter-based observations (mobile deer; $n = 3$) and (2) via ground-based observations (immobile deer; $n = 4$). This finding indicates that some deer for whom TTI was censored were not killed. Given that ground-based observations showed that all animals assessed in Operations B and C were dead, it seems reasonable to assume that deer for whom TTI was known were actually killed. However, the average interval between shooting and inspection was also much shorter in Operation A, increasing the likelihood of finding wounded animals during ground-based observations (Hampton *et al.* 2017). Repeat shooting has been added to many aerial shooting procedural documents in Australia in an attempt to reduce the frequency of non-fatal wounding (Hampton *et al.* 2016a), but the procedural documents used in Queensland operations did not require repeat shooting (Standing Committee on Agriculture Animal Health Committee 2002). The imposition of fly back and repeat shooting to the thorax or head would likely reduce the number of deer that are killed per hour; i.e. better animal welfare outcomes would likely come at the cost of increased flying time and ammunition per deer killed (Sharp 2012).

The animal welfare outcomes reported here for deer can be compared with those for aerial shooting of feral camels

(Hampton *et al.* 2014) and horses (Hampton *et al.* 2017). The proportion of deer seen that were shot (~75%) was lower than the 100% reported for feral camels and horses in central Australia (Hampton *et al.* 2014; Hampton *et al.* 2017). TT was similar for deer and horses, but was not quantified for feral camels (Hampton *et al.* 2016a). In the present study, the mean number of bullet wounds was similar for Operations B and C and camels and horses (~2.4 wounds), but lower for Operation A. The frequency of immediate insensibility from shooting was relatively low (<20%) for all deer operations, in contrast to feral camels and horses, whereby a majority of animals were rendered immediately insensible via 'head shooting' (Hampton *et al.* 2016a).

The animal welfare outcomes observed for deer in aerial shooting operations are likely to be lower than those observed for larger ungulates in flat and treeless environments for several reasons. First, there are large size differences between the two deer species in the present study and camels and horses; thus, the head of a fallow or chital deer is a substantially smaller target than that of a camel or horse, and the probability of successfully killing an animal with an attempted head shot is likely to be lower for a deer than for a camel or horse. Consequently, shooters targeting fallow or chital deer may be more likely to shoot at the thorax to incapacitate a deer rather than attempting a head shot (Sharp 2012; Feral Animal Aerial Shooting Team 2020). Second, there are important differences in running speed and escape behaviour (Linklater and Cameron 2002). Deer typically run at maximum speed and zigzag (Stankowich and Coss 2007) to escape the pursuing helicopter (M. Leeson and S. Boyd-Law, pers. comm.). In contrast, horses run in straight lines (Linklater and Cameron 2002) and camels display little consistent escape behaviour in response to the presence of helicopters (Hampton *et al.* 2014). Third, the presence of tall trees in all three deer operations precluded low-level flight, making follow-up shooting of wounded but mobile deer more difficult. The presence of tall trees has been shown to reduce the probability of detecting similar-sized ungulates (feral goats and sika deer) during helicopter-based shooting operations (Bayne *et al.* 2000; Latham *et al.* 2018).

The methods used in the present study could be refined to improve the quality of the data collected. In particular, the position of the observer in the helicopter meant that the proportion of events that could not be observed (and for which TTI was censored) was ~30% for all operations. Our estimates of the duration of suffering, a critical parameter for many animal welfare assessment frameworks (Baker *et al.* 2016), could have been biased if the sample of observed animals somehow differed from the unobserved animals. One solution would be to mount a video camera behind and above the shooter (inside the helicopter), or to the helmet of the shooter, as has been used to estimate time-to-event data in helicopter-based wildlife capture studies (Latham *et al.* 2020a).

Ground-based shooting, trapping and fencing are also commonly used to reduce the impacts of deer (Bennett *et al.* 2015; Forsyth *et al.* 2017; Bengsen *et al.* 2020), but the animal welfare outcomes of these methods have seldom been reported (Hampton *et al.* 2019b). An evaluation of ground-based shooting for culling red deer (*Cervus elaphus*) in England found that

93% of deer were killed within 2 minutes of being shot and 2% escaped wounded (Bradshaw and Bateson 2000), similar to the results of the present study. Further assessments of alternative deer control methods are required for meaningful comparison of those methods with aerial shooting. Assessments of the animal welfare outcomes of helicopter-based shooting are also needed for other deer species and in other locations (e.g. red deer and sika deer in New Zealand; Latham *et al.* 2018; Warburton *et al.* 2018). Finally, manipulative (rather than observational) studies of aerial shooting could be performed in the future to assess species-specific differences through standardising variables such as helicopter and ammunition type.

Conclusion

Helicopter-based shooting of deer produced variable animal welfare outcomes, likely reflecting key procedural differences. The best animal welfare outcomes were achieved when helicopter-based shooting operations followed a fly-back procedure and required repeat shooting in the thorax or head.

Data availability statement

The data that support this study cannot be publicly shared due to ethical or privacy reasons, but may be shared upon reasonable request to the corresponding author if appropriate.

Conflict of interest

The authors declare no conflicts of interest.

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References

- ACT Government GeoHub (2018). 'Vegetation Communities.' (ACT Government: Canberra, Australia.)
- Aebischer, N. J., Wheatley, C. J., and Rose, H. R. (2014). Factors associated with shooting accuracy and wounding rate of four managed wild deer species in the UK, based on anonymous field records from deer stalkers. *PLoS One* **9**, e109698. doi:10.1371/journal.pone.0109698
- Ahrestani, F. S., Van Langevelde, F., Heitkönig, I. M., and Prins, H. H. (2012). Contrasting timing of parturition of chital *Axis axis* and gaur *Bos gaurus* in tropical south India – the role of body mass and seasonal forage quality. *Oikos* **121**, 1300–1310. doi:10.1111/j.1600-0706.2011.20244.x
- Armstrong, R. C., Turner, K. D., McDougall, K. L., Rehwinkel, R., and Crooks, J. I. (2013). Plant communities of the upper Murrumbidgee catchment in New South Wales and the Australian Capital Territory. *Cunninghamia* **13**, 125–265. doi:10.7751/cunninghamia.2013.13.003
- Baker, S. E., Sharp, T. M., and Macdonald, D. W. (2016). Assessing animal welfare impacts in the management of European rabbits (*Oryctolagus cuniculus*), European moles (*Talpa europaea*) and Carrion crows (*Corvus corone*). *PLoS One* **11**, e0146298. doi:10.1371/journal.pone.0146298
- Bayne, P., Harden, B., Pines, K., and Taylor, U. (2000). Controlling feral goats by shooting from a helicopter with and without the assistance of ground-based spotters. *Wildlife Research* **27**, 517–523. doi:10.1071/WR99059
- Bengsen, A. J., Forsyth, D. M., Harris, S., Latham, A. D. M., McLeod, S. R., and Pople, A. (2020). A systematic review of ground-based shooting to control overabundant mammal populations. *Wildlife Research* **47**, 197–207. doi:10.1071/WR19129
- Bennett, A., Haydon, S., Stevens, M., and Coulson, G. (2015). Culling reduces fecal pellet deposition by introduced sambar (*Rusa unicolor*) in a protected water catchment. *Wildlife Society Bulletin* **39**, 268–275. doi:10.1002/wsb.522
- Bentley, A. (1995). Fallow deer. In 'The Mammals of Australia'. (Ed. R. Strahan.) pp. 732–733. (Australian Museum / Reed New Holland: Sydney, Australia.)
- Bradshaw, E., and Bateson, P. (2000). Welfare implications of culling red deer (*Cervus elaphus*). *Animal Welfare* **9**, 3–24.
- Brooks, S. P., and Gelman, A. (1998). General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* **7**, 434–455.
- Burgin, S., Mattila, M., McPhee, D., and Hundloe, T. (2015). Feral deer in the suburbs: an emerging issue for Australia? *Human Dimensions of Wildlife* **20**, 65–80. doi:10.1080/10871209.2015.953274
- Challies, C. (1985). Commercial hunting of wild red deer in New Zealand. In 'Game Harvest Management'. (Eds S. L. Beasom and S. F. Robertson.) pp. 279–287. (Caesar Kleberg Wildlife Research Institute: Kingsville, USA.)
- Chapple, R. (2005). The politics of feral horse management in Guy Fawkes River National Park, NSW. *Australian Zoologist* **33**, 233–246. doi:10.7882/AZ.2005.020
- Davis, N. E., Bennett, A., Forsyth, D. M., Bowman, D. M., Lefroy, E. C., Wood, S. W., Woolnough, A. P., West, P., Hampton, J. O., and Johnson, C. N. (2016). A systematic review of the impacts and management of introduced deer (family Cervidae) in Australia. *Wildlife Research* **43**, 515–532. doi:10.1071/WR16148
- DeNicola, A. J., Miller, D. S., DeNicola, V. L., Meyer, R. E., and Gambino, J. M. (2019). Assessment of humaneness using gunshot targeting the brain and cervical spine for cervid depopulation under field conditions. *PLoS One* **14**, e0213200. doi:10.1371/journal.pone.0213200
- Denwood, M. J. (2016). Runjags: an R package providing interface utilities, model templates, parallel computing methods and additional distributions for MCMC models in JAGS. *Journal of Statistical Software* **71**, 1–25. doi:10.18637/jss.v071.i09
- English, A. W. (1992). Management strategies for farmed chital deer. In 'The Biology of Deer'. (Ed. R. D. Brown.) pp. 189–196. (Springer-Verlag: New York City, USA.)
- Feral Animal Aerial Shooting Team (2020). 'The FFAST Manual. Version 2.3 (August 2020).' (National Parks & Wildlife Service, NSW Local Land Services and NSW Department of Primary Industries, on behalf of the NSW Government: Sydney, Australia.)
- Forsyth, D. M., Wilmschurst, J. M., Allen, R. B., and Coomes, D. A. (2010). Impacts of introduced deer and extinct moa on New Zealand ecosystems. *New Zealand Journal of Ecology* **34**, 48–65.
- Forsyth, D. M., Ramsey, D. S., Veltman, C. J., Allen, R. B., Allen, W. J., Barker, R. J., Jacobson, C. L., Nicol, S. J., Richardson, S. J., and Todd, C. R. (2013). When deer must die: large uncertainty surrounds changes in

- deer abundance achieved by helicopter-and ground-based hunting in New Zealand forests. *Wildlife Research* **40**, 447–458. doi:10.1071/WR13016
- Forsyth, D., Pople, T., Page, B., Moriarty, A., Ramsey, D., Parkes, J., Wiebkin, A., and Lane, C. (2017). '2016 National Wild Deer Management Workshop Proceedings, Adelaide, Australia.' (Invasive Animals Cooperative Research Centre: Canberra, Australia.)
- Forsyth, D. M., Pople, A., Woodford, L., Brennan, M., Amos, M., Moloney, P. D., Fanson, B., and Story, G. (2019). Landscape-scale effects of homesteads, water, and dingoes on invading chital deer in Australia's dry tropics. *Journal of Mammalogy* **100**, 1954–1965. doi:10.1093/jmammal/gyz139
- Graf, W., and Nichols, L. (1966). The axis deer in Hawaii. *Journal of the Bombay Natural History Society* **63**, 629–734.
- Gregory, G. (2017). Vertebrate scavengers on deer carcasses in the Australian Capital Territory, south-eastern Australia. Honours thesis, University of Canberra, Canberra, Australia.
- Hampton, J. O., and Forsyth, D. M. (2016). An assessment of animal welfare for the culling of peri-urban kangaroos. *Wildlife Research* **43**, 261–266. doi:10.1071/WR16023
- Hampton, J. O., Cowled, B. D., Perry, A. L., Miller, C. J., Jones, B., and Hart, Q. (2014). Quantitative analysis of animal-welfare outcomes in helicopter shooting: a case study with feral dromedary camels (*Camelus dromedarius*). *Wildlife Research* **41**, 127–135. doi:10.1071/WR13216
- Hampton, J. O., Jones, B., Perry, A. L., Miller, C. J., and Hart, Q. (2016a). Integrating animal welfare into wild herbivore management: lessons from the Australian Feral Camel Management Project. *The Rangeland Journal* **38**, 163–171. doi:10.1071/RJ15079
- Hampton, J. O., Hyndman, T. H., Laurence, M., Perry, A. L., Adams, P., and Collins, T. (2016b). Animal welfare and the use of procedural documents: limitations and refinement. *Wildlife Research* **43**, 599–603. doi:10.1071/WR16153
- Hampton, J. O., Edwards, G. P., Cowled, B. D., Forsyth, D. M., Hyndman, T. H., Perry, A. L., Miller, C. J., Adams, P. J., and Collins, T. (2017). Assessment of animal welfare for helicopter shooting of feral horses. *Wildlife Research* **44**, 97–105. doi:10.1071/WR16173
- Hampton, J. O., MacKenzie, D. I., and Forsyth, D. M. (2019a). How many to sample? Statistical guidelines for monitoring animal welfare outcomes. *PLoS One* **14**, e0211417. doi:10.1371/journal.pone.0211417
- Hampton, J. O., Finch, N. A., Watter, K., Amos, M., Pople, T., Moriarty, A., Jacotine, A., Panther, D., McGhie, C., Davies, C., Mitchell, J., and Forsyth, D. M. (2019b). A review of methods used to capture and restrain introduced wild deer in Australia. *Australian Mammalogy* **41**, 1–11. doi:10.1071/AM17047
- Latham, A. D. M., Latham, M. C., Herries, D., Barron, M., Cruz, J., and Anderson, D. P. (2018). Assessing the efficacy of aerial culling of introduced wild deer in New Zealand with analytical decomposition of predation risk. *Biological Invasions* **20**, 251–266. doi:10.1007/s10530-017-1531-0
- Latham, A. D. M., Davidson, B., Warburton, B., Yockney, I., and Hampton, J. O. (2020a). Efficacy and animal welfare impacts of novel capture methods for two species of invasive wild mammals in New Zealand. *Animals (Basel)* **10**, 44. doi:10.3390/ani10010044
- Latham, A. D. M., Latham, M. C., Norbury, G. L., Forsyth, D. M., and Warburton, B. (2020b). A review of the damage caused by invasive wild mammalian herbivores to primary production in New Zealand. *New Zealand Journal of Zoology* **47**, 20–52. doi:10.1080/03014223.2019.1689147
- Linklater, W. L., and Cameron, E. Z. (2002). Escape behaviour of feral horses during a helicopter count. *Wildlife Research* **29**, 221–224. doi:10.1071/WR01063
- McTee, M., Young, M., Umansky, A., and Ramsey, P. (2017). Better bullets to shoot small mammals without poisoning scavengers. *Wildlife Society Bulletin* **41**, 736–742. doi:10.1002/wsb.822
- New Zealand Government (2018). 'Deer Code Of Welfare.' (New Zealand Government: Wellington, New Zealand.)
- Nugent, G., and Choquenot, D. (2004). Comparing cost-effectiveness of commercial harvesting, state-funded culling, and recreational deer hunting in New Zealand. *Wildlife Society Bulletin* **32**, 481–492. doi:10.2193/0091-7648(2004)32[481:CCOCHS]2.0.CO;2
- Office of Environment and Heritage (2017). 'The NSW State Vegetation Type Map: Methodology for a Regional-Scale Map of NSW Plant Community Types.' (Office of Environment and Heritage: Sydney, Australia.)
- Pecorella, I., Ferretti, F., Sforzi, A., and Macchi, E. (2016). Effects of culling on vigilance behaviour and endogenous stress response of female fallow deer. *Wildlife Research* **43**, 189–196. doi:10.1071/WR15118
- Plummer, M. (2017). 'JAGS Version 4.3.0 User Manual.' (International Agency for Research on Cancer: Lyon, France.)
- Pople, A., Clancy, T., Thompson, J., and Boyd-Law, S. (1998). Aerial survey methodology and the cost of control for feral goats in western Queensland. *Wildlife Research* **25**, 393–407. doi:10.1071/WR97123
- R Core Team (2020). 'R: a Language and Environment for Statistical Computing. V 4.0.3.' (R Foundation for Statistical Computing: Vienna, Austria.)
- Rutberg, A. T. (1997). The science of deer management: an animal welfare perspective. In 'The Science of Overabundance: Deer Ecology and Population Management'. (Eds W. J. McShea, H. B. Underwood and J. H. Rappole.) pp. 37–54. (Smithsonian Institution Press: Washington, DC, USA.)
- Sharp, T. (2012). 'Standard Operating Procedure GOA002: Aerial Shooting of Feral Goats.' (Centre for Invasive Species Solutions: Canberra, Australia.)
- Standing Committee on Agriculture, Animal Health Committee (2002). 'Model Code of Practice for the Welfare of Animals: Feral Livestock Animals: Destruction or Capture, Handling and Marketing: SCARM Report 34.' (CSIRO Publishing: Melbourne, Vic., Australia.)
- Stankowich, T., and Coss, R. G. (2007). Effects of risk assessment, predator behavior, and habitat on escape behavior in Columbian black-tailed deer. *Behavioral Ecology* **18**, 358–367. doi:10.1093/beheco/arl086
- Stokke, S., Arnemo, J. M., Brainerd, S., Söderberg, A., Kraabøl, M., and Ytrehus, B. (2018). Defining animal welfare standards in hunting: body mass determines thresholds for incapacitation time and flight distance. *Scientific Reports* **8**, 13786. doi:10.1038/s41598-018-32102-0
- Tuckwell, C. D. (2003). 'The Deer Farming Handbook.' (Rural Industries Research and Development Corporation: Canberra, Australia.)
- Warburton, B., Anderson, D., and Nugent, G. (2018). Economic aspects of New Zealand's wild venison recovery industry. In 'Advances in Conservation through Sustainable Use of Wildlife'. (Eds G. Baxter, N. Finch, and P. Murray.) pp. 265–271. (University of Queensland: Brisbane, Qld, Australia.)

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