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Quantitative analysis of animal-welfare outcomes in helicopter shooting: a case study with feral dromedary camels (*Camelus dromedarius*)

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Abstract

Context. Helicopter shooting is a common and effective tool for reducing overabundant wildlife populations. However, there is little quantitative information on the humaneness of the method, leading to uncertainty in wildlife-management policy. There is, subsequently, a need for an improved understanding of the welfare implications of helicopter shooting.

Aim. A study was undertaken to infer the humaneness of helicopter shooting for a case study species, the feral dromedary camel (*Camelus dromedarius*).

Methods. Seven post-mortem studies ($n = 715$) and one ante-mortem study ($n = 192$) were undertaken during routine helicopter shooting programs of free-ranging camels. In these studies, we measured four animal-welfare parameters to allow inference on the humaneness of the technique. These parameters were time to death, instantaneous death rate (proportion of animals for which time to death = 0), wounding rate and location of bullet-wound tract. We also modelled these welfare variables against hypothesised explanatory variables to assist improvement of future programs.

Key results. The mean wounding rate was 0.4%, and the killing efficacy of the technique was 99.6%. Mean time to death was 4 s, and mean instantaneous death rate was 83%. Each animal displayed a mean 2.4 bullet-wound tracts, with 75%, 63% and 35% of animals shot at least once in the thorax, cranium and cervical spine, respectively. Regression analysis revealed that the identity of the shooter and the nature of the local vegetation were the most important factors associated with an animal experiencing an inferred instantaneous death or not.

Conclusions. Helicopter shooting of feral camels produces a very low wounding rate and rapid time to death. Shooter identity is the most important consideration for determining animal-welfare outcomes. Improvements to the humaneness of programs can be made by increasing the rigour of shooter selection and training.

Implications. Wildlife killing methods must be demonstrated to be humane to receive public support; however, few shooting methods are objectively examined. Helicopter shooting can be independently examined and operators assessed. Adoption of this examination template may allow continual improvement by industry as well as increasing societal acceptance of helicopter shooting.

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Introduction

Helicopter shooting or culling has been employed worldwide as a management tool for the control of large invasive mammals for several decades (Tustin and Challies 1978; Campbell *et al*. 2010). The efficacy of the technique has been demonstrated, particularly for high-density populations of large invasive herbivores and in remote or inaccessible situations in which alternative control methods have proven ineffective (e.g. Smith *et al*. 1986). Several studies have examined factors affecting the efficacy of helicopter shooting techniques (e.g. Hone 1990; Saunders 1993; Bayne *et al*. 2000), but a quantitative study of relevant animal-welfare parameters has not been published for the helicopter shooting of any species. Consequently, perception rather than scientific evaluation has driven helicopter shooting policy. Increasingly contentious perceptions of the animal-welfare implications of the technique have seen its use discontinued in the management of some species in some jurisdictions (e.g. Nimmo and Miller 2007).

The importance of animal welfare in wildlife management is receiving increasing recognition. The two most important determinants of welfare outcome for any killing method are widely accepted as the duration and intensity of suffering experienced by the animal (Mellor and Littin 2004). Because of the difficulty and subjectivity inherent in assessing intensity of suffering, quantification of duration of suffering has been recognised as the most practical approach for the assessment of animal-welfare outcomes for killing methods (Mellor and Littin 2004; Knudsen 2005). Several recent studies have assessed the duration of suffering associated with trapping (e.g. Warburton *et al*. 2008), poison baiting (e.g. Cowled *et al*. 2008) and drowning (e.g. Ludders *et al*. 1999), but very few have assessed shooting (Knudsen 2005). Recent studies have highlighted the general absence of scientifically rigorous examinations of wildlife-shooting outcomes (Caudell 2013) and the poor scientific rigour of the existing literature (Daoust *et al*. 2014). A template for the empirical assessment of terrestrial shooting programs was developed for the present study, using parameters developed for the assessment of whale-killing methods (Kestin 1995; Knudsen 2005; Brakes and Donoghue 2006). The template requires a combination of ante- and post-mortem observations to elucidate time to death (TTD), instantaneous death rate (IDR), wounding rate (WR) and anatomical locations of bullet-wound tracts. We are unaware of any published examples of studies to subject helicopter shooting to rigorous animal-welfare assessment and these parameters have remained unquantified for the technique.

Feral camels (*Camelus dromedarius*) are an invasive species found only in arid areas of Australia. Although their populations have existed for decades (Edwards *et al*. 2001), recent appreciation of their environmental, cultural and agricultural impacts (see Edwards *et al*. 2010; Vaarzon-Morel and Edwards 2012) has led to population-management programs being implemented. The Australian Feral Camel Management Project (AFCMP) was initiated in 2009 to provide a coordinated national approach for the management of the species (Vaarzon-Morel and Edwards 2012). Although ground shooting and live capture have been used as removal tools at a local scale (see Pople and McLeod 2010), remoteness and low animal density have dictated that helicopter shooting has been the primary component of management efforts (Edwards *et al*. 2004*b*; Drucker *et al*. 2010). A model national standard operating procedure (Sharp 2010) exists for helicopter shooting in Australia, and the AFCMP set contractual requirements for qualified government helicopter shooters to comply with this. A process of ongoing verification and feedback was implemented to assess compliance, and these provided an opportunity for the collection of data relevant to animal-welfare outcomes. The aim of the present study was to provide an objective, quantitative assessment of the humaneness of feral-camel helicopter shooting operations through a combination of ante- and post-mortem observations.

Materials and methods

Shooting practices

Helicopter shooting operations are highly regulated in Australia, and all shooting operations under the AFCMP were required to comply with the current model national standard operating procedure (Sharp 2010) and Civil Aviation Safety Authority regulations. Shooters operated from Robinson® 44 (R44) helicopters (Robinson Helicopter Co., Torrance, CA, USA), flown by pilots with low-level flying experience, as per Sharp (2010). Two types of semi-automatic firearms were used, namely, an M1A (Springfield Armory, Geneseo, IL, USA), and an LR-308 (DPMS Panther Arms, St Cloud, MN, USA). Both rifles were chambered in 0.308 Winchester® (7.62 × 51 mm NATO) calibre. Ammunition used was 150 grain Winchester® Power-Point soft-nose (Winchester, Morgan, UT, USA) or 150 grain Federal® soft-point (Federal Premium Ammunition, Anoka, MN, USA). Rifles were fitted with open sights, electronic Eotech® holographic sights (L-3 Communications, Eotech, Ann Arbor, MI, USA) or electronic Aimpoint® red-dot sights (Aimpoint AB, Malmö, Sweden). Shooting procedures were specified by Sharp (2010) and consisted of cranium and thorax aim points, repeat shooting of animals and the performance of a 'fly-back' procedure after shooting, as a means of reducing the risk of non-fatal injury to the animal (Sharp 2010). Shooting distances for this procedure were estimated as 2–10 m. Fly-back procedures observed consisted of returning to all animals, to fire additional shots (Sharp 2010).

Ante-mortem observations

One helicopter shooting operation was examined in May 2013, in central Australia (Fig. 1). An independent observer stationed in a separate R44 helicopter timed ante-mortem events for the shooting of feral camels. The observing helicopter flew as close to the shooting helicopter as was reasonably possible to allow the observer the clearest and nearest line of sight to the shooting event. This generally consisted of the observing helicopter flying ~30 m directly above the shooting helicopter. From this proximity, all pursuit and shooting events were able to be observed

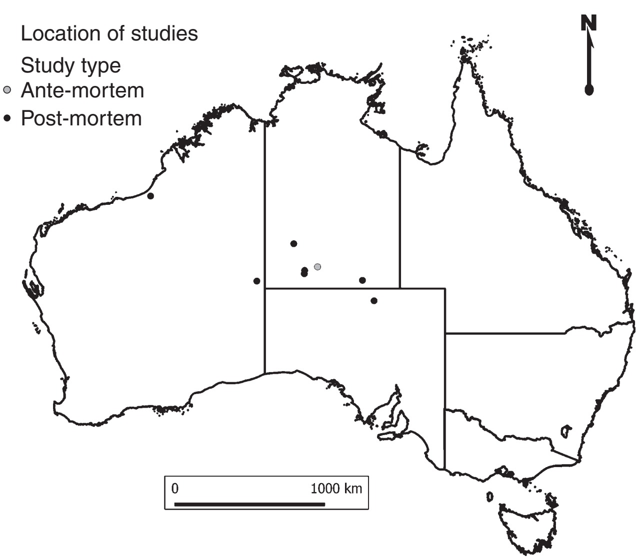

Fig. 1. Location of the seven post-mortem study sites (black dots) and one ante-mortem study site (grey dot) used to assess the helicopter shooting of dromedary camels (*Camelus dromedarius*) in Australia between November 2011 and May 2013.

and accurately timed. Observer bias was minimised by observing all shooting events that could be clearly seen. For each animal, the observer recorded the interval between the first shot being fired at an animal and the moment the animal fell and did not move (TTD), as per convention (Lewis *et al*. 1997; Knudsen 2005; Parker *et al*. 2006; Cockram *et al*. 2011). As this methodology does not permit observation of physiological responses (e.g. Warburton *et al*. 2008), insensibility owing to neurotrauma (e.g. Knudsen and Øen 2003) can be confused with death. Assuming that repeat shooting is performed, animals are unlikely to experience a return to sensibility (as per Grandin 2002), ensuring that this measure of TTD provides an accurate estimate of duration of suffering. The proportion of animals for which TTD was zero (IDR) was also determined, as per Kestin (1995).

Post-mortem examinations

Seven separate helicopter shooting operations, defined as 1–2-week management programs, were examined between November 2011 and May 2013, in different areas of Australia (Fig. 1). Eleven different shooters were assessed, ranging from two to three for each shooting operation. Post-mortem investigations, and the recording of several variables, were made by three independent veterinarians within 4 h of shooting. A non-random sampling strategy was employed, whereby large social groups were selected for observation after shooting. All animals from each selected social group were examined. Observers, not shooters, selected animal groups to be inspected, to reduce the possibility for changed shooting behaviour related to the presence of the observer.

Because of the inspection of animals *in situ*, the open nature of the vegetation (see Fig. 2) and the presence of manipulable substrate, environmental parameters were also recorded from the immediate proximity of each animal. The presence or absence of 'blood trails' and evidence of 'paddling' or 'thrashing' in manipulable substrate was recorded. Blood trails were defined as pools or drops of blood removed from the animal's final resting place, consistent with the animal travelling after having first been shot, as per Causey *et al*. (1978). Blood-trail length was measured using a Leupold® RX 600 range finder (Leupold, Beaverton, OR, USA). Paddling was defined as visible disturbance of sand, soil or vegetation around the animals' feet or head, or surrounding blood spray, consistent with recumbent, immobile, conscious pre-mortem flailing or thrashing. We also recorded GPS location, approximate age (body size), sex, recumbency position and the size of the social group for inspected animals. GPS coordinates were recorded with a Garmin® Etrex H handheld GPS receiver (Garmin, Kansas City, MO, USA). The vegetation type in which each animal was found was attributed to one of the following three broad categories: woodland, grassland or open (sand dune or clay pan).

Gross pathology of vital and non-target organs attributable to injuries of the bullet-wound tract were recorded following the principles of Hollerman *et al*. (1990) and Di Maio (1999). Bullet wound-tract locations were recorded as per Urquhart and McKendrick (2003, 2006), by assigning tracts to the anatomical zone displaying the most damage. As per previous ungulate shooting studies, fatal target zones were considered to be the cranium, cervical spine and thorax (Urquhart and McKendrick 2003, 2006; Cockram *et al*. 2011; Stewart and Veverka 2011). Quantification of the number of fresh bullet-wound tracts has been demonstrated for carcasses skinned and suspended in controlled *ex situ* conditions (e.g. RSPCA Australia 2002; Urquhart and McKendrick 2003, 2006). Such quantification is more difficult for large, entire animals inspected *in situ*, but avoids the problems of shooter selection of carcasses and removed body parts (e.g. RSPCA Australia 2002; Urquhart and McKendrick 2003). Wounding rate (WR) was defined as the proportion of animals shot but not killed (*sensu* Stormer *et al*. 1979) and was elucidated as per Divljan *et al*. (2011), as the proportion of immobile animals found alive. This methodology may under-estimate WR, because it does not account for mobile, wounded animals and is dependent on the duration of the interval between shooting and observation. Killing efficacy was defined

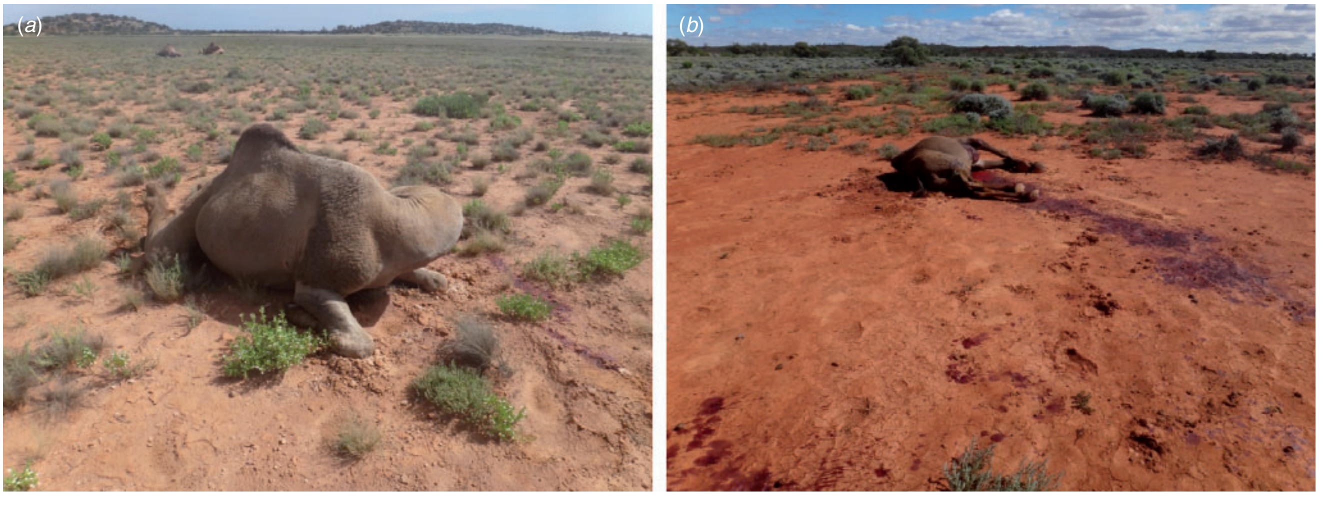

Fig. 2. *In situ* post-mortem evidence from dromedary camels (*Camelus dromedarius*) shot from a helicopter with 150 grain soft point bullets from a 0.308 calibre rifle in Australia between November 2011 and May 2013. (*a*) Evidence of inferred instantaneous death, and (*b*) inferred non-instantaneous death. Note the presence of other dead feral camels in the background (*a*) and the presence of a 'blood trail' leading to the animal (*b*).

as the proportion of targeted animals that were killed (*sensu* Dolbeer *et al*. 1991), and in this context, it was defined as 1 – WR.

Statistical analysis

Analyses of post-mortem data were performed to determine the influence of several recorded variables on the likelihood of an animal being killed instantaneously (humaneness). Shooting outcomes were dichotomised to those animals experiencing an inferred instantaneous death (IID) and those that were not. Animals deemed to have experienced an IID were considered to be those that satisfied all of the following four criteria: (1) dead when examined, (2) absence of a blood trail, (3) absence of paddling, and (4) at least one bullet-wound tract to the cranium, thorax or cervical spine. Several explanatory variables were collected that were considered potentially important to the occurrence of IID or might have been confounders of any observed statistical relationship. These included:

(1) individual shooter (11 shooters),
(2) estimated age of camel (juvenile or adult),
(3) camel herd size (number of camels),
(4) vegetation (three vegetation types: open, grassland, woodland),
(5) sex of animal (male or female), and
(6) number of bullet wounds (count).

In addition, the distance between nearest neighbours was calculated as a Euclidean distance between all non-solitary camels. Bivariable analyses were conducted to describe the association between each variable and humaneness. Additionally, several multivariable models were implemented, with each model representing additional plausible *a priori* hypotheses. These multivariable models modelled associations between explanatory variables and outcome IID, while controlling for potentially confounding variables. All models (bivariable and multivariable) were generalised linear models with a log odds link function. All models (bivariable and multivariable) were then assessed using information-theoretic approaches, to determine which models (hypotheses) were best supported by the data (Burnham and Anderson 2002; Burnham *et al*. 2011). Akaike information criterion (AIC) values and model weights (w_i) were used to compare relative support for each model. All models in the set were used to estimate parameters with model averaging. The natural-average method (Burnham and Anderson 2002) was used, whereby the parameter estimate for each predictor is averaged only over models in which that predictor appears and is weighted by the summed weights of those models (Grueber *et al*. 2011). This was implemented with the MuMin package in R (Barton 2013). Relative variable importance was calculated for each variable by summing the AIC weights across all models in the set where the variable occurs.

The following *a priori* multivariable hypotheses were examined using multivariable logistic regression models:

Hypothesis 1: shooter identity

Some shooters are more skilled than others, resulting in better animal-welfare outcomes. However, vegetation type may confound observed associations, with more highly skilled shooters in less optimal landscapes likely to have less optimal shooting outcomes than expected (e.g. Bayne *et al*. 2000). The number of bullet wounds may also confound an association, because a less highly skilled shooter may be more cautious and use more shots to ensure that all animals are killed humanely. Conversely, less experienced shooters may have been overconfident and used fewer shots than is optimal. The model used had the form:

$$\log_e \frac{P}{1-P} = B_0 + B_1\text{Shooter} + B_2\text{Vegetationtype} + B_3\text{Wounds},$$

where P = probability of outcome and $B_{i\text{–}j}$ are the estimated coefficients for the model.

Hypothesis 2: vegetation type

Vegetation type influences animal-welfare outcome because some high-canopied vegetation types (e.g. woodland) can make it difficult to shoot camels humanely, for example, because of increased shooting distance between the camels and the helicopter. However, vegetation type may also influence camel-group structure, which also affects welfare outcomes (e.g. older male camels are harder to shoot humanely because their thicker bone structure provides greater resistance to bullet penetration). Hence, camel biological measures such as sex, age and herd size were included to control confounding. The model used had the form

$$\log_e \frac{P}{1-P} = B_0 + B_1\text{Vegetation type} + B_2\text{Sex} + B_3\text{Age} + B_4\text{Herd Size}.$$

Hypothesis 3: group size and structure

Group structure is an interaction between sex and age, and is most important to welfare outcomes. Older male camels are more difficult to kill humanely, so sex and age were included. An interaction term for sex and age was also tested for inclusion in the model. However, the number of animals in a herd also influences the behaviour of the shooter and, hence, is included to control confounding. The model used had the form

$$\log_e \frac{P}{1-P} = B_0 + B_1\text{Sex} + B_2\text{Age} + B_3\text{Herd Size} + B_4\text{Sex} \times \text{Age}.$$

Hypothesis 4: combined

A combination of camel herd structure, shooter type and vegetation type affects success of shooting and, hence, welfare outcomes. All variables are included in the model. The model used had the form

$$\log_e \frac{P}{1-P} = B_0 + B_1\text{Sex} + B_2\text{Age} + B_3\text{Shooter} + B_4\text{Herd Size} + B_5\text{Wounds} + B_6\text{Vegetation} + B_7\text{Sex} \times \text{Age}.$$

Results

Ante-mortem observations

TTD was recorded for camels subjected to helicopter shooting (n = 192) and ranged from 0 to 242 s (mean; 4 s, 95% CI: 1–6 s).

Mean IDR (95% CI) was 83% (77–88%). Mean TTD for non-instantaneously killed animals ($n = 32$) was 22 s (95% CI: 11–33 s).

Post-mortem examinations

Of 715 animals subjected to post-mortem examination, 712 (99.6%) were dead and three (0.4%) were found alive when examined within 4 h of shooting. Killing efficacy was hence 99.6% (95% CI: 99.1–100.0%) and WR 0.4% (95% CI: 0–0.9%). Seventy per cent of camels were shot in grassland vegetation (95% CI: 66–73%), 21% were shot in open vegetation (95% CI: 18–24%), and 9% where shot in woodland vegetation (95% CI: 7–11%). The proportion of examined camels shot by each individual shooter varied from 3% to 15%. More females than males (52 : 48) and more adults than juveniles (68 : 32) were present in the sample, and mean (mean $\pm$ s.d.) mob size was 16 ± 11 animals. Pairwise Euclidean distance between each dead camel and its nearest neighbour within a social group ($n = 703$) was 28 m (95% CI: 25–30 m). The number of bullet-wound tracts per animal was 2.4 ± 0.9, with a range of one and eight bullet-wound tracts.

Seventy-five per cent (95% CI: 72–78%) of animals displayed at least one bullet-wound tract in the thorax, 63% (95% CI: 59–68%) in the cranium, and 35% (95% CI: 32–39%) in the cervical spine. Ninety-eight per cent (95% CI: 97–99%) of animals displayed at least one bullet-wound tract affecting the cranium and/or thorax and/or cervical spine. Of non-target anatomical zones, 12% (95% CI: 9–14%) of animals displayed at least one bullet-wound tract in the forelimbs, and 9% (95% CI: 7–11%) in the abdomen. All animals shot in these non-target zones also displayed at least one bullet-wound tract affecting a target zone. Fifteen per cent (95% CI: 12–18%) of animals were found in a position of sternal recumbency (Fig. 2*a*) and 85% (95% CI: 82–88%) in lateral recumbency (Fig. 2*b*). Blood trails (see Fig. 2*b*) were associated with 3% (95% CI: 2–4%) of animals, with a mean length of 27 m (95% CI: 11–42 m) and a range of 1–140 m. Twenty-one per cent (95% CI: 18–24%) of camels displayed evidence of pre-mortem paddling. Seventy-seven per cent (95% CI: 74–80%) of camels were assessed under these criteria as IID, generating an inferred post-mortem IDR of 77% (74–80%). There was close similarity between the inferred post-mortem IDR and the observed ante-mortem IDR (83%; 77–88%).

Predictors of instantaneous death

The following three models were well supported: the bivariable shooter model, the multivariable shooter identity and combined models (see Table 1). 'Model averaging' indicated that the individual-shooter variable was the most important variable across all models. Additionally, some covariates were assumed to be associated with the outcome when model-averaged odds ratios were calculated (with 95% confidence intervals) for all covariates. These were individual shooters, vegetation (wooded) categories, being male and the interaction term between sex and age (Table 2). The presence of woodland vegetation, in particular, was interesting (Table 2; odds ratio 0.50; 0.26–0.97).

Discussion

The present paper provides the first detailed assessment of the animal-welfare implications of helicopter shooting, an important wildlife-management tool worldwide. Through combining ante- and post-mortem observations, we were able to quantify the critical parameters of killing efficacy (99.6%), wounding rate (0.4%), time to death (4 s), observed instantaneous death rate (83%) and bullet wound-tract locations, for the helicopter shooting of feral camels. The elucidation of shooter identity and the nature of the local vegetation as important parameters in determining the animal-welfare outcome for any individual are useful to allow improvements to future helicopter shooting programs.

Shooter identity was found to be the most important factor determining the humaneness of individual animal outcomes. Shooter identity is likely to reflect a combination of shooter selection, training, experience and skill. The critical importance of shooter training has been demonstrated by various studies in wildlife management (e.g. Daoust and Caraguel 2012) and military performance (e.g. Tharion *et al*. 2003). Standard operating procedures guiding helicopter shooting practices also stress the critical importance of shooter training and experience (Sharp 2010). The implications for future improvements to the technique of helicopter shooting are positive. Shooter performance has a very large impact on

Table 1. Values of Akaike information criterion (AIC) and other model comparison parameters for model selection, using information-theoretic approaches (Burnham and Anderson 2002; Burnham *et al*. 2011)

The probability of the bivariable shooter and multivariable shooter identity and combined models are high and, clearly, the data support these three models. Models are listed from most supported to least supported

Hypothesis (model)	Number of estimated parameters (K)	Bias corrected AIC (AICc)	AICc differences (Δ)	Probability (Akaike weight)
Shooter	11	704.8	0	0.514
Combined	18	706.3	1.48	0.245
Shooter identity	14	706.3	1.52	0.241
Vegetation type	3	762.6	57.8	0
Vegetation type	6	766.2	61.44	0
Age	2	767.3	62.47	0
Number of wounds	2	767.6	62.85	0
Herd size	2	767.8	62.97	0
Group size and structure	5	768.6	63.84	0
Sex	2	769.2	64.41	0

Table 2. 'Model-averaged' parameter estimates

Coefficient	Estimate	s.e.	Odds ratio 95% CI	Relative variable importance
(Intercept)	0.74	0.38	2.09 (1.00–4.38)	
ShooterB (Referent A)	–0.46	0.54	0.63 (0.22–1.81)	1
ShooterC	2.02	0.69	7.52 (1.94–29.08)	1
ShooterD	1.69	0.81	5.40 (1.11–26.19)	1
ShooterE	0.55	0.39	1.74 (0.81–3.70)	1
ShooterF	0.26	0.38	1.30 (0.62–2.73)	1
ShooterG	0.36	0.54	1.44 (0.49–4.12)	1
ShooterH	1.56	0.67	4.78 (1.28–17.89)	1
ShooterI	2.59	0.79	13.39 (2.87–62.42)	1
ShooterJ	0.12	0.37	1.13 (0.55–2.31)	1
ShooterK	2.25	0.52	9.51 (3.41–26.51)	1
Vegetation TypeO (Referent G)	–0.50	0.34	0.60 (0.31–1.17)	0.49
Vegetation TypeW	–0.69	0.33	0.50 (0.26–0.97)	0.49
Number of bullet wounds	0.02	0.11	1.02 (0.82–1.27)	0.49
Sex (referent male)	–0.50	0.25	0.61(0.37–0.99)	0.24
Age (referent juvenile)	–0.11	0.29	0.90 (0.51–1.57)	0.24
Herd size	–0.02	0.01	0.98 (0.96–1.01)	0.24
Interaction (sex : age)	1.00	0.44	2.72 (1.14–6.50)	0.24

animal-welfare outcomes and this is potentially manipulable through shooter selection and training. The performance of the helicopter pilot is a potentially important variable relating to the stability and proximity of the shooting platform that we were unable to assess in the present study because of confidentiality concerns. We recommend consideration of the influence of pilot and aircraft identity for future helicopter shooting studies.

Woodland vegetation was associated with relatively poor animal-welfare outcomes. The association between woodland (high-canopied vegetation) and poor animal-welfare outcomes is unsurprising, given the paramount importance of visibility and proximity in helicopter shooting (Bayne *et al*. 2000). Helicopter shooting programs in areas of high-canopied vegetation have been shown to be less efficient in detecting animals and less time-efficient in killing detected animals than those in areas of low-canopied vegetation (Choquenot *et al*. 1999; Bayne *et al.* 2000). Avoiding shooting animals while they are in high-canopied vegetation is likely to improve the humaneness of helicopter shooting. Some uncontrollable factors that cannot be manipulated, such as animal age and sex, were found to be significantly associated with welfare outcome. Overall, the results of our study suggested that shooter management and vegetation type are the two areas that require consideration for future improvements to be made to animal-welfare outcomes.

The potential to wound and not kill animals is inherent in all remote-killing methods (Knudsen 2005). Our estimated wounding rate of 0.4% was considerably lower than those reported for other hunting methods. The best documented wounding rates are to be found in waterfowl hunting ('crippling rate' e.g. Noer *et al*. 2007; Schulz *et al*. 2013), marine-mammal hunting ('struck and lost rate' e.g. Kestin 1995) and bow hunting (e.g. Gregory 2005). Daoust *et al*. (2014) argued that 'struck and lost' rates should not be compared with 'wounding' rates, because 'lost' (non-recovered) animals may be dead or permanently insensible. In addition, several studies of terrestrial rifle shooting have relied on hunter-reported wounding rates (e.g. Bradshaw and Bateson 2000). However, the studies of Nieman *et al.* (1987) and Schulz *et al.* (2013) demonstrated that hunters tend to underestimate their wounding rate, compared with that estimated by an independent observer. These findings highlighted the difficulty in attempting to make direct comparisons between studies employing different methods to assess animal-welfare outcomes.

The mean time to death of 4 s reported in the present study is indicative of the duration of suffering from shooting. Time to death does not quantify the duration of stress owing to helicopter pursuit (e.g. Dexter 1996; Linklater and Cameron 2002) before death, as per Sharp and Saunders (2011). This could not be recorded in our study. Feral camels have been observed to display subdued flight responses to the presence of helicopters when compared with other large herbivore species (Sharp 2010). The criteria used to estimate time to death were those used in published studies of terrestrial shooting (Lewis *et al*. 1997; Parker *et al*. 2006; Cockram *et al*. 2011). Estimates of time to death from an aerial platform, as in our study, are likely to be more accurate than for ground-based observers, because of superior visibility (Knudsen 2005). However, the inability of visual observations to assess an animal's physiological responses (e.g. Warburton *et al*. 2008) means that the method employed may underestimate time to death. For a discussion of the criteria used to assess death and insensibility, see Knudsen (2005). The mean duration of suffering associated with helicopter shooting is much lower than for other wildlife-killing methods, including infectious agents (e.g. Saunders *et al*. 2010), transport and slaughter (e.g. Sharp and Saunders 2011), poison baiting (e.g. Cowled *et al*. 2008), fumigation (Marks 2009), kill traps (e.g. Warburton *et al*. 2008) and drowning (e.g. Ludders *et al*. 1999).

There is inherent instability involved in helicopter shooting, because a moving target is shot from a moving platform. This instability dictates that helicopter shooting may be considered imprecise when compared with shooting methods employing a stable platform to fire at a stable target. This is reflected in our observed instantaneous death rate (83%) being lower than those reported for some professional ground shooting methods (e.g. Lewis *et al*. 1997; 93%). However, the helicopter platform offers several advantages that offset the loss in precision, including superior proximity, manoeuvrability, visibility and ease of repeat shooting (Wade 1976). Darting wildlife from helicopters, a technique requiring comparable precision levels to shooting, is widely practiced and accepted as humane (e.g. Ballard *et al*. 1982; Golden *et al*. 2002; Woolnough *et al*. 2012). Although repeat shooting has been inferred as evidence of non-instantaneous death by some studies (e.g. Butterworth and Richardson 2013), it is encouraged in many forms of hunting (Knudsen 2005) and is a mandatory practice for helicopter shooting as a means of reducing the risk of non-fatal injury (Sharp 2010). Repeat-shooting practices using semi-automatic firearms in our study resulted in a mean of 2.4 bullet-wound tracts per animal, a mean minimum distance between cohort animals of 28 m and a mean time to death of 4 s.

Shooting methods utilising a stable platform, such as ground shooting, may have the capacity for increased precision, but are subject to other factors that may hinder animal-welfare outcomes. Ground shooting methods involving rifles often require shooting over long distances, reducing the capacity for repeat shooting, and contributing to the potential for escape of wounded animals (Bradshaw and Bateson 2000; Sharp and Saunders 2011). Ground shooting methods are generally poorly regulated and their outcomes are consequently highly variable (e.g. Lewis *et al*. 1997; RSPCA Australia 2002; Noer *et al*. 2007). In the context of management, helicopter shooting is utilised as a landscape-scale population-reduction tool in which all detected animals are targeted (Edwards *et al*. 2004*a*; Forsyth *et al*. 2013), whereas ground shooting involves the targeting of a selected number of individual animals. This selectivity may improve the ability of ground shooting to achieve high animal-welfare outcomes for selected animals in some contexts (e.g. Lewis *et al*. 1997), but severely limits its utility as a tool for population management (Campbell and Long 2009; Forsyth *et al*. 2013). There is currently a lack of rigorous data available pertaining to ground shooting methods (e.g. Ben-Ami *et al*. 2014), reducing potential for meaningful comparisons to be made between ground and helicopter shooting methods (e.g. Forsyth *et al*. 2013). We encourage the adaption of our study methods for the assessment of animal-welfare outcomes from contentious ground shooting programs.

We conclude that animal-welfare parameters can be quantified for helicopter shooting. By combining ante- and post-mortem observations, we were able to benchmark humaneness standards and explanatory factors associated with them. Helicopter shooting of feral camels generated a comparatively low mean wounding rate and time to death through the advantages of close proximity, high manoeuvrability, high visibility (owing to open vegetation and large animal size), and the practice of repeat shooting. The technique is associated with a shorter average duration of suffering than for most methods of lethal population control. The identification of important variables affecting the animal-welfare outcomes of helicopter shooting is instructive for the refinement of standard operating procedures and the improvement of future outcomes. Our study has provided a template that can be applied to assess other helicopter shooting programs, including those targeting contentious species such as wild horses (*Equus caballus*).

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