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Review

A systematic review of ground-based shooting to control overabundant mammal populations

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Abstract

Context. Ground-based shooting is widely used in management programs aiming to alleviate the impacts of invasive or overabundant wildlife populations. However, evaluations of individual shooting operations have shown variable results, and the effectiveness of ground-shooting as a population-management intervention has not been systematically examined.

Aims. Our review aimed to (1) assess the efficacy of shooting as a population management tool, and (2) identify commonalities among studies that will help managers identify situations where ground-shooting is most likely to be effective.

Methods. We systematically reviewed the literature to identify studies involving ground-shooting. From each study, we collated information about operational objectives, target taxa, geographic context, type of shooter used, effort, effectiveness, and use of additional control tools.

Key results. Most studies had no *a priori* quantifiable objectives. However, 60% of the 64 case studies produced a detectable reduction in population density and/or damage. The most common type of operation used unpaid or commercial harvest-oriented shooters to reduce herbivore density or damage. Only 30% of the operations that used volunteer shooters or recreational hunters achieved their objectives. Target taxa, geographic area or integration of shooting with other population-control methods had no detectable effect on the effectiveness of shooting operations. Common factors that hindered the effectiveness of shooting operations included immigration of target species from adjacent areas ($n = 13$), decreasing effort from shooters as the target population declined ($n = 7$) and selective harvesting ($n = 7$).

Conclusions. Ground-based shooting can be an effective management tool for overabundant wildlife populations, but many shooting operations did not achieve a notable decrease in animal abundance or damage. The source of failure could often be attributed to an inability to remove a sufficient proportion of the population to cause a population decline.

Implications. Managers contemplating using ground-based shooting to reduce the impacts or density of wildlife populations should (1) carefully consider whether this is a suitable management tool to achieve the desired outcomes, (2) establish clear objectives that aim to meet defined outcomes and allow for continuous improvement, and (3) ensure that operations are sufficiently resourced to achieve and maintain those objectives.

Additional keywords: hunting, human–wildlife interactions, sharp-shooting, vertebrate pest, wildlife management.

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Introduction

Populations of native or introduced mammals in many parts of the world occur at greater densities than land managers or other stakeholders desire. These populations are commonly termed ‘overabundant’, ‘pest’ or ‘problem’. All of these terms are value judgements that are applied to populations occurring at densities that (1) are believed to threaten human economic or health values, (2) depress the densities of favoured species, (3) are too numerous to maintain desirable levels of fecundity and health or (4) disrupt desirable ecosystem function (Caughley 1981). Often, the economic, environmental or social costs of overabundant mammal populations are important enough to motivate management that aims to reduce the population to a level that mitigates its impacts. This usually involves reducing the density of the target population because the extent of damage caused by overabundant mammals often, but not invariably, increases linearly with population density (Hone 2007; Norbury *et al.* 2015). However, the costs of control are often inversely related to density, such that at lower population densities they can outweigh the economic benefits (Moberly *et al.* 2004; Krull *et al.* 2016).

Many tools and methods have been used in control operations that aim to reduce the density of overabundant mammal populations. Lethal control by shooters operating in rotary- or fixed-wing aircraft or on the ground is a widely used method of reducing the density of mammal populations in many parts of the world (e.g. Reddiex *et al.* 2006; Nugent *et al.* 2011). Ground-based shooting (hereafter ground-shooting) is often used because it is perceived as a convenient and inexpensive means of reducing population densities. In many situations, it has been presented as the only viable option (e.g. Brown *et al.* 2000). In other cases, ground-shooting has been used to complement other control tools such as aerial shooting, trapping or poison baiting (e.g. Parkes *et al.* 2010).

Despite the longstanding and widespread popularity of ground-shooting as a population control tool, evaluations of the effectiveness of ground-shooting to control overabundant mammals have largely been limited to individual case studies (e.g. Doerr *et al.* 2001) or reviews, essays and opinion pieces discussing its application in specific situations (e.g. VerCauteren *et al.* 2011; Bengsen and Sparkes 2016). Animal welfare outcomes have been evaluated on a case-by-case basis (e.g. Lewis *et al.* 1997; Hampton *et al.* 2015). This diffuse literature makes it difficult for managers and decision-makers to determine how ground-shooting might best be used as a management intervention in new situations. Here, we systematically review the effectiveness of ground-shooting operations by using case studies describing the application of ground-shooting to control a wide variety of mammalian taxa and the damage that they are perceived to cause, around the globe. We aimed to (1) assess whether ground-shooting interventions can achieve objectives for the management of overabundant wildlife populations or their negative impacts, and (2) identify commonalities among studies that will help managers understand how best to use ground-shooting to reduce the density or impacts of overabundant populations.

Methods

We conducted a systematic review of published and unpublished literature describing or evaluating the effects of ground-shooting operations to reduce the impacts or density of overabundant mammal populations. The review process was guided by the PRISMA protocol (Moher *et al.* 2009), although not all items in the protocol were applicable to the present review.

We addressed the first aim of the study by positing the following question: 'How consistently do ground-shooting operations achieve management objectives?' This guided our search locations, terms and criteria for including or excluding studies. Three online databases were searched for relevant case studies on 6 March 2017 and 26 November 2018. The Web of Science was searched using the following search criteria: topic = (hunt OR shooting) AND topic = (pest OR over NEAR/1 abundant), refined by publication type = (article, proceedings paper, review, editorial) AND category = (environmental studies, environmental sciences, ecology, veterinary sciences, zoology) AND timespan = 1980–2017. This database was chosen to provide access to a broad range of journals. Four BioONE journals (*Journal of Wildlife Management*, *Mammal Study*, *Wildlife Monographs*, *Wildlife Research*) were searched using the criterion 'hunting OR shooting' in Title OR Abstract. These journals were chosen to provide access to wildlife management journals based in North America, Asia and Australasia. The *European Journal of Wildlife Research* was searched using the search term 'hunting OR shooting AND pest OR 'over abundant' OR overabundant'. This journal was chosen to provide access to European studies. We also searched our personal bibliographic databases for relevant studies, including unpublished works that could help reduce reporting and publication bias. However, we recognise that unsuccessful operations are likely to remain under-represented in our sample. Further studies were found by examining reference lists in studies identified through the methods described above.

Studies were accepted for review only if they met the following criteria: (1) the target population was a terrestrial mammal species that was considered overabundant; (2) the management aim was to reduce the impacts and/or abundance of the target species; (3) ground-shooting was an important part of the operation; (4) the study reported outputs of shooting operations; and (5) the study was reported in English. To identify commonalities among disparate studies, we sought to determine whether the effectiveness of ground-shooting operations varied according to the operational objective, the status and motivations of the shooters involved, the target taxa, whether shooting was integrated into a management strategy that also used other control methods, and the geographic scale of operations. These questions guided the data extraction and study-classification processes.

The following information on shooting effectiveness and its assessment were extracted from each relevant study, where possible: whether a measurable management objective was stated (yes/no); the type of objective (eradication, density reduction, population growth rate reduction, damage reduction); whether the objective was achieved (yes/no); whether the study authors perceived the operation as having been effective (yes/no); whether a reduction in population density or damage was reported (yes/no); the type of shooters involved, based on the shooters' main objectives and their source of remuneration (five levels, Table 1); the trophic category and taxonomic details of the species targeted; whether the target species was native or introduced; the geographic location, landscape type (biome, fragmented agricultural, peri-urban) and area (km^2) of operations; and the start and end year of operations. Importantly, reported reductions in metrics such as population density or damage were not necessarily statistically, biologically or economically significant. Differences in estimation and reporting methods, and the timescales over which effects were estimated, made it impossible to compare studies consistently. We, therefore, accepted reported reductions in a target metric at face value and expect that some or many of these apparent benefits may be trivial or short-lived.

Where numerical data were not reported in the text, they were inferred from digitised plots using WebPlotDigitiser (Rohatgi 2018). Additional information extracted or inferred included the broad aim of the operation (if no measurable objective was defined, e.g. density reduction), the type of study design (including spatial and temporal replication), other management tools that were used, and any other factors noted by the study authors to have helped or hindered the effectiveness of the operation.

We used multiple correspondence analysis (Husson and Josse 2014) to reduce the dimensionality of the dataset and create a typology of ground-shooting operations based on operational objectives, the types of shooter used, target taxa, geographic scale and whether other control tools were used in the broader program. However, no combination of these traits provided a clear grouping or explained more than 35% of the variance in the data. We, therefore, used a three-factor classification based on the trophic category of the target species, the aim of management operations, and the motivation of the shooters used. These factors were chosen because they represented three categorical conditions that described different aspects of shooting operations and existed before operations commenced. As such, we expected them to highlight similarities and differences among individual studies.

Table 1. A typology of shooter types, based on shooter motivations for participation (population control or harvest) and their remuneration

The 'volunteer' category includes shooters operating on their own or other peoples' properties to control overabundant animals, without a direct financial reward. Commercial wildlife-management contractors are normally remunerated using performance-based contracts, whereas commercial harvesters are typically paid by weight of animals submitted for processing. NA, not applicable

Remuneration	Motivation	
	Population control	Harvest
Unpaid	Volunteer	Recreational hunter
Commercial	Commercial wildlife-management contractor	Commercial harvester
Government	Government	NA

We used contingency tables to examine associations between categorical variables and the success or failure of operations in (1) achieving *a priori* objectives and (2) achieving a detectable reduction in a target metric, such as population density. We used Fisher's exact test to test the hypothesis of no association between each of the two variables describing the success or failure of operations and (1) the operational objective, (2) the main type of shooter used, (3) target-species taxonomic family, (4) native or introduced status and (5) whether additional control methods such as trapping or aerial shooting were used. We used logistic regression to evaluate the relationships between the size of the area of operations and success in achieving objectives or achieving a reduction in a target metric.

Results

Data scope

The literature search provided 489 potential studies (Web of Science = 269, European Journal of Wildlife Research = 88, BioOne = 53, authors' databases = 79). After removing 23 duplicated articles and 413 articles that did not meet our inclusion criteria, we identified 64 useful cases from 56 journal articles, book chapters and technical reports. These included a further three cases found within reference lists of selected articles. Some articles included more than one case study. All five technical reports were found in personal bibliographical database searches. Most cases were from Australasia (52%), North America (22%) and Europe (22%) (Fig. 1). Our inclusion criteria excluded several cases that could have filled large geographic or taxonomic gaps in our sample because the reports did not provide sufficient information to contribute to this review.

The 19 mammalian species subject to ground-shooting were from seven families, and ranged in body mass from 2 kg (European rabbit, *Oryctolagus cuniculus*) to >200 kg (sambar deer, *Cervus unicolor*) (Table S1, available as Supplementary material to this paper). Most were herbivores (84%). The studies spanned the years 1944–2015, and the median study length was 5 years (range = 1–55 years).

Study designs

Most case studies were observational in nature, commonly reporting estimates of the effects of single (28) or repeated (23)

Fig. 1. Locations of the 64 ground-shooting case studies.

shooting operations, without comparison to different treatments such as experimental controls of different levels of effort. A further seven comparative studies examined multiple levels of management intervention repeated at different sites or years. Only six studies were classified as manipulative experiments in which treatments were deliberately allocated. Four of these six studies used random treatment allocation to reduce the risk of selection bias, whereas one other study used a cross-over design in which each site received each treatment at different times. Treatment allocation was not randomised for the remaining study (S. Comte, pers. comm.).

Objectives

Twenty-seven case studies stated a quantifiable objective that allowed the effects of shooting operations to be assessed against a desired target. Eradication was the single most commonly stated objective (56%), followed by reducing density to a target level >0 (19%), reducing population growth (19%) and reducing damage (7%). Expanding the sample to include those cases without a quantifiable objective, reducing population density was inferred to be the most common aim (48%), followed by eradication (23%), reducing population growth (19%) and reducing damage (9%).

A three-level classification of cases according to the stated or inferred operational aim, shooter type and target trophic class identified 12 different types of shooting operation. The most common type (25%) used harvest-oriented shooters to try to reduce the density of herbivores. Using a two-level classification based on shooter type and target taxa, the same proportion of case studies involved recreational hunters targeting deer (Cervidae) populations.

Effectiveness

Among those cases with a measurable objective, we found no clear evidence that the ability of shooting operations to achieve the stated objective varied by objective type (Fisher's exact test, $n = 23$, $P = 0.085$; damage category excluded because of small sample size). A small majority of case studies (59%) that stated a measurable objective actually achieved that objective (Fig. 2*a*). Including the 37 operations that did not state a measurable objective, more than half (67%) of the case studies reported a reduction in a target metric such as population density or an index of density or damage. We found no evidence that the odds of achieving a reduction in a target metric varied among case studies with different reported or inferred aims (Fisher's exact test, $n = 64$, $P = 0.34$; Fig. 2*b*).

Nearly half of the cases (42%) used unpaid recreational hunters as their main type of shooter. This was the most common category of shooter in all regions except Australasia, where shooters employed by government agencies were most frequent (45% of Australasian cases). Cases that had a quantifiable objective used all five types of shooter, but government-agency staff were the single most frequent type. The frequency of cases that achieved their objective (hereafter, objective effectiveness) varied among the types of shooter used (Fisher's exact test, $n = 24$, $P = 0.021$; commercial harvesters were removed because of scarcity of data). Most (72%) cases that used government-agency shooters or commercial wildlife-management contractors

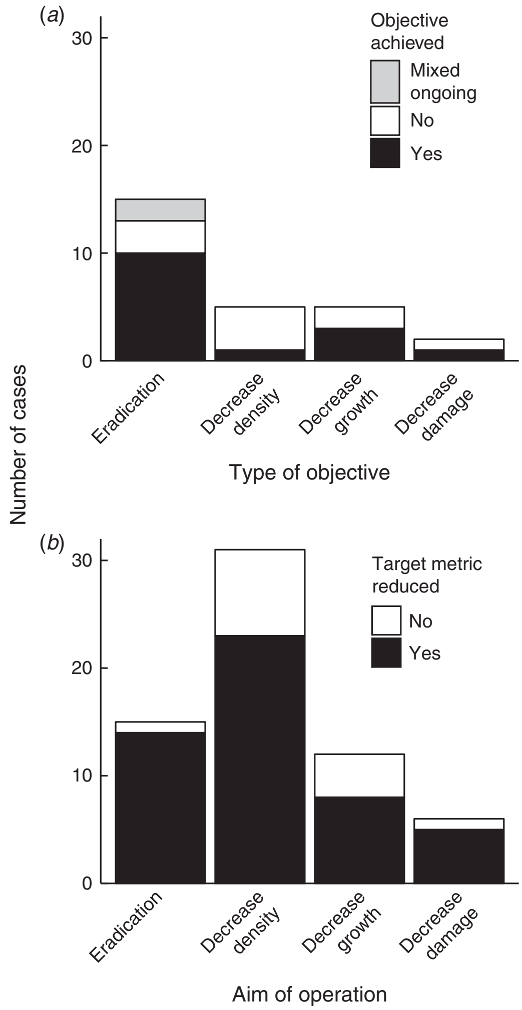

Fig. 2. Number of cases in which (*a*) a measurable objective was achieved, not achieved, or was ongoing ($n = 27$) and (*b*) the operation was reported to have produced a detectable reduction in a target metric such as population density, growth or damage ($n = 64$) in shooting operations with different objectives or inferred aims.

met their stated objectives, and 30% of cases that relied on unpaid recreational hunters or volunteers did (Fig. 3*a*). The ability of shooting operations to achieve a reduction in a target metric such as population density did not vary among studies using different types of shooter (Fisher's exact test: $n = 62$, $P = 0.42$; commercial harvesters removed because of scarcity of data; Fig. 3*b*).

There was no evidence that the odds of shooting operations achieving their objectives or reducing a target metric differed among taxonomic families (Fisher's exact test: objective effectiveness (cervids, bovids, suids, felids only): $n = 24$, $P = 0.27$; target metric reduction (excluding leporids): $n = 62$, $P = 0.22$). Most shooting operations (61%) targeted introduced species. We found no evidence that the odds of success in achieving objectives or reducing target metrics varied between introduced and native species (Fisher's exact test: objective effectiveness $n = 26$, $P = 0.23$; target metric reduction $n = 63$, $P = 0.12$).

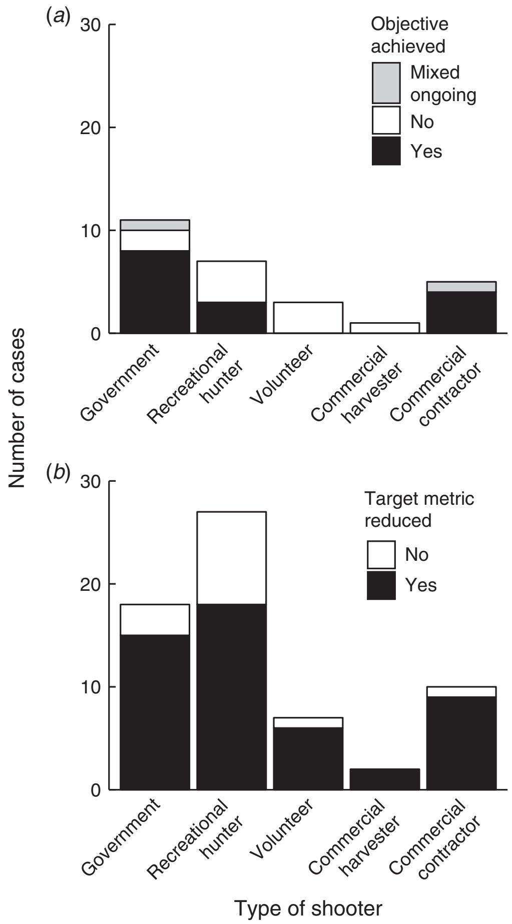

Fig. 3. Number of cases in which (*a*) a measurable objective was achieved, not achieved, or was ongoing ($n = 27$) and (*b*) a reduction in population density, growth or damage was reported ($n = 64$) in shooting operations using five types of shooter.

Twenty-five case studies (39%) combined ground-shooting with another control tool or method. Ground-shooting was usually the primary control tool (84%), but this was probably an artefact of our study selection criteria. When ground-shooting was used with at least one other control method, it was most commonly used concurrently (68% of cases). Trapping was the most commonly used additional method (22%). Fencing (13%) was mainly used to facilitate the spatial concentration of animals for shooting in eradication programs, rather than to protect assets from pest damage. Other tools used to help reduce population densities or damage were aerial shooting (11%), poison baiting (11%) and supplementary feeding (4%). There was no indication that the inclusion of control methods other than ground-shooting affected the odds of a shooting operation achieving its objectives (Fisher's exact test, $n = 26$, $P = 0.42$) or producing a decline in a target metric (Fisher's exact test, $n = 63$, $P = 0.19$).

The geographic scale considered by case studies varied from single properties to entire states, but most cases were at the scale of single or multiple properties or reserves. Average treatment area for each case ranged from 0.5 km^2 to 83 454 km^2 (median = 58 km^2). Twelve case studies were on islands or other enclosed systems, ranging in size from 0.5 km^2 (Domm and Messersmith 1990) to 4450 km^2 (Masters *et al.* 2018). There was no linear relationship between average treatment area and success in meeting objectives of the shooting operations (logistic regression: McFadden's $R^2 = 0.11$, $P = 0.46$) or the ability of operations to achieve a reduction in a target metric (logistic regression: McFadden's $R^2 = 0.09$, $P = 0.58$). Inconsistencies in reporting meant that it was not possible to standardise effort by study area, so area effects could be confounded by variation in effort among studies.

Several key themes were repeatedly raised by study authors as having contributed to or detracted from the success of individual shooting operations, although their impacts were seldom explicitly estimated. The most common of these themes was the importance of tools or methods to increase efficiency (47% of studies). The most commonly used tools were dogs (31% of studies) and spotlights or night-vision equipment (19% of studies) to help locate or kill animals. It was not always possible to determine whether the dogs used in a study were indicator dogs or dogs that were used to pursue, flush, restrain or otherwise prevent the escape of target animals. Most cases that used dogs achieved their *a priori* objectives (89%), whereas 47% of operations that did not use dogs achieved theirs. Similarly, 83% of operations that used spotlights or night-vision devices were objectively successful, whereas 55% of operations that did not use them were. However, there was no strong evidence to support the hypotheses that the use of dogs or night-vision devices (including spotlights) improved the odds of an operation achieving its objectives (Fisher's exact test: dogs, $n = 26$, $P = 0.09$; night vision, $n = 26$, $P = 0.35$). A further five studies reported that dividing the area of operations into distinct management units was helpful for concentrating effort, and three studies reported that a formal process to facilitate learning from previous experience was helpful for improving performance of multi-year operations. Common factors that were thought to hinder the effectiveness of shooting operations included immigration of target species from adjacent areas ($n = 13$), decreasing effort by recreational hunters, commercial harvesters and volunteers as target animals became scarcer ($n = 7$), and selective harvesting of adult male deer and pigs by trophy-oriented hunters ($n = 6$) or commercial harvesters targeting pigs with the greatest body mass ($n = 1$).

Discussion

Our review has shown that ground-shooting has been used in a wide variety of ways to attempt to reduce the density or impacts of many different species of mammals, in landscapes ranging from suburbs to sub-Antarctic islands. This diversity, combined with the scarcity of measurable objectives in the studies we reviewed, made it difficult to answer the question of how consistently ground-shooting operations achieved their objectives. Nonetheless, 41% of operations that stated a measurable objective failed to achieve it. A similar failure rate occurred using a much less rigorous scale of success of whether there was a decrease in population density, growth or damage, rather than a particular percentage decrease.

Influence of shooter types

The only factor that showed a relationship with the ability of shooting operations to achieve stated objectives was the type of shooter used. Although some operations using volunteers were able to achieve measurable reductions in population density, population growth or damage, none achieved their stated objectives. More than two-thirds of operations using recreational hunters also failed to meet their predefined objectives. The high failure rate of cases using unpaid or harvest-oriented shooters could be due to at least three problems that may be most likely to manifest in this type of operation.

The first problem is that the motivations of unpaid or harvest-oriented shooters to participate are not always aligned with operational objectives, so shooter participation can end before the objective is achieved. Harvest-oriented shooters typically seek meat or trophies. They can be expected to display a strong functional response (*sensu* Holling 1959) to declining numbers of the target species (Van Deelen and Etter 2003). As the density of the target population declines, the effort required to harvest an animal increases to a value where it becomes unrewarding and shooters will quit or move to more profitable areas. If the population density at which shooters quit is greater than the target density, the objective will not be achieved (e.g. McDonald *et al.* 2007; Williams *et al.* 2013). All seven studies that identified shooters' functional response to declining populations as an impediment to effectiveness used unsubsidised volunteers, recreational hunters or commercial harvesters. In another example of conflicting aims, some studies found that harvest-oriented shooters declined opportunities to take females or juveniles, preferentially targeting adult males that made little contribution to population growth and recovery. All these studies involved recreational hunters or commercial harvesters (e.g. Forsyth 1999; Martin and Baltzinger 2002; Toïgo *et al.* 2008). In some cases, harvest-oriented shooters may even resist management objectives that are perceived to threaten their resource or are in conflict with their hunting ethic (e.g. Holsman *et al.* 2010; Kaji *et al.* 2010).

Second, operations using unpaid shooters often relied on an inconsistent pool of shooters, with varying levels of skill and motivation. Differences in effort, skill or personal beliefs meant that not all shooters were equally effective at contributing towards management objectives (e.g. Nugent 1988; Doerr *et al.* 2001; Holsman and Petchenik 2006). Ground-shooting is an inherently inefficient method of achieving initial knock-down of a target population; numbers of animals killed per unit effort are often much lower than can be achieved using other control tools such as aerial shooting (e.g. Husheer and Robertson 2005; Banko *et al.* 2014; Macdonald *et al.* 2019) or poison baiting (Newsome *et al.* 2014), and the area over which intensive control can be applied is often much smaller. Operations that fail to remove animals from a population faster than they are replaced by births and immigration cannot achieve more than a trivial and short-lived reduction in population density; so, outcomes such as damage mitigation will not be achieved. Operations that rely on an inconsistent labour source may remove fewer animals per unit time than those that use a small cadre of shooters with local experience and a proven commitment to operational objectives (Williams *et al.* 2013). Several case studies reported that the efficiency of shooters increased after they had become familiar with an area (e.g. Hygnstrom *et al.* 2011; Krull *et al.* 2016) and some studies took or suggested steps to retain unpaid shooters with local experience to increase the combined effectiveness of all shooters (Hygnstrom *et al.* 2011; Williams *et al.* 2013). The constraints of low or inconsistent efficiency are likely to be strongest in widespread, well established populations that occur at densities close to environmental carrying capacity. These populations can be expected to have a greater capacity to compensate for increased mortality from shooting operations by increasing reproductive output or survival (Bartmann *et al.* 1992). Given the low efficiency of ground-shooting, variability in the effort and effectiveness of shooters is likely to be an important determinant of the total shooting mortality rate (Bengsen and Sparkes 2016).

Third, operations that are poorly conceived or do not have sufficient funding in place to achieve stated objectives may be more likely to rely on cheap or readily available labour provided by volunteers, hunters or commercial harvesters. Such projects may fail for many reasons, not just because of the type of shooter they use. Braysher (2017) identified seven elements of best practice for overabundant-animal management that helped control operations achieve better results than would otherwise have been possible, including using operators who are trained in population-management methods. Many operations in the present review showed other indicators of best practice, such as using the latest knowledge available (e.g. Rodríguez *et al.* 2006), applying ecological principles (e.g. Tapper *et al.* 1996), using a strategic approach and following population-management principles (e.g. Masters *et al.* 2018) and sound governance (e.g. Hygnstrom *et al.* 2011). Having an effective monitoring program based on *a priori* objectives is one of the key principles of population management (Kaji *et al.* 2010; Braysher 2017), and an indicator of best practice that should be clearly discernable in reports on shooting operations. Whereas 34% of the case studies that used unpaid or harvest-oriented shooters stated a measurable objective, 61% of cases that used paid shooters did, suggesting that operations using unpaid shooters may have been more likely to suffer from other shortcomings.

Problems relating to low or inconsistent effectiveness arising from the functional response of unpaid or harvest-motivated shooters have been addressed by a range of methods. One operation that used a commercial harvester to reduce the density of western grey kangaroo (*Macropus fuliginosis*) in a peri-urban environment paid a subsidy to the harvester once the population density declined to an uneconomic level (Mawson *et al.* 2016). Smart incentives such as this can reduce the threshold on the functional response curve at which diminishing returns become unacceptable to commercial harvesters. By reducing the number of animals that need to be removed per unit time for a profit to be realised, the harvester can continue removing animals at a lower population density than would otherwise be possible (Fig. 4*a*). Modelling studies have suggested that similar subsidies could sometimes deliver more cost-effective population reductions by harvesters than do operations using government-agency shooters or commercial wildlife-management contractors (Nugent and Choquenot 2004). Another classic example of smart incentives is the performance bonuses paid to trappers for the successful coypu

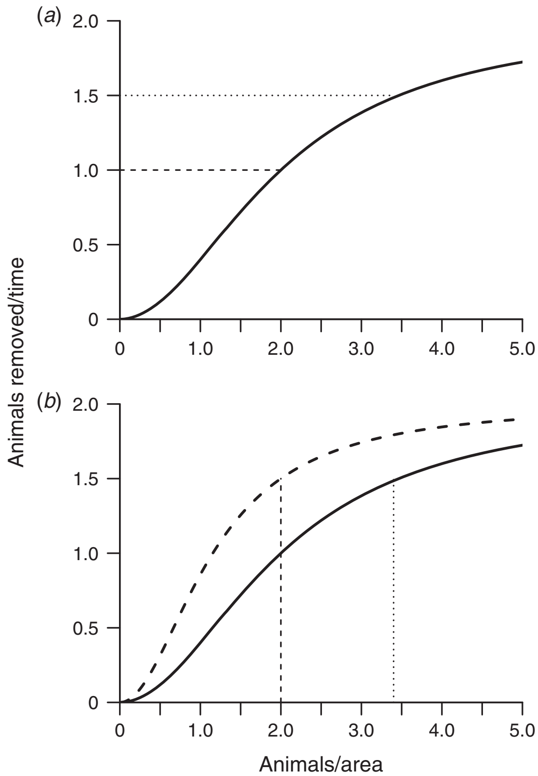

Fig. 4. Hypothetical functional-response curves for harvest-motivated shooters. (*a*) The graph shows how reducing the threshold at which harvesting becomes unprofitable allows a harvester to kill animals at lower population densities. Here, if unprofitability forces a harvester to quit at 1.5 animals per unit time (dotted line), they will quit harvesting at a population density of ~3.4 animals per unit area. If they can continue to be profitable until they harvest 1.0 animals per unit time (dashed line) with the same level of efficiency, then they can continue harvesting until population density reaches 2.0 animals per unit area. (*b*) The graph shows functional-response curves with harvest efficiencies of 0.5 animals per unit time (solid line) and 1.5 animals per unit time (dashed line). If the profitability threshold is fixed at 1.5 animals per unit time, then the more efficient harvesting rate allows harvesters to continue harvesting until population density reaches 2.0 animals per unit area (dashed vertical line), whereas the less efficient harvesting rate requires them to quit at a population density nearer to 3.4 animals per unit area (dotted vertical line).

(*Myocastor coypus*) eradication program in Britain during the 1980s. Funding for the eradication campaign was fixed at 10 years, and trappers were to be paid a sliding bonus starting at 3 years' annual salary if eradication was achieved in less than 6 years. Eradication was effectively achieved in just under 8 years and the trappers received a substantial bonus (Gosling and Baker 1989). However, recreational hunters and volunteers are not primarily motivated by profit maximisation. Indeed, hunters often incur considerable expense to be able to hunt and to improve their hunting experience (Finch *et al.* 2014; Kerr and Abell 2016). Factors such as time constraints, ideology, the conservation of animals to hunt and the quality of hunting experiences are often more likely to prevent hunters or volunteers from taking more animals than are economic concerns (Nugent and Choquenot 2004; MacMillan and Leitch 2008; Kerr and Abell 2016). Unsophisticated financial incentives such as broadscale bounties cannot, therefore, be assumed to increase the number of animals taken by recreational hunters and volunteers (e.g. Ditchkoff *et al.* 2017).

When unpaid shooters are motivated to maximise the number of animals taken, their functional response to declining harvests can also be manipulated by increasing their efficiency, expressed as the number of animals harvested per unit of time (Fig. 4*b*). Studies in the present review used dogs (e.g. Gürtler *et al.* 2017; Quirós-Fernández *et al.* 2017), spotlighting from vehicles (e.g. Bennett *et al.* 2015) and shooting over bait (e.g. Doerr *et al.* 2001; DeNicola and Williams 2008) to increase either the rate at which animals were encountered or the rate at which encounters were converted to kills. Other studies suggested using night-vision equipment (e.g. thermal imagers, light intensification optics) or firearms fitted with muzzle blast suppressors to help increase efficiency (e.g. Williams *et al.* 2013). Some studies used suppressors (Frost *et al.* 1997; DeNicola and Williams 2008), but none specifically reported any efficiency benefits of night-vision equipment or suppressors. Spotlighting, night-vision equipment and suppressors were most commonly used by government-agency staff or contract shooters in our sample of studies, but are also commonly used by unpaid shooters in some parts of the world (e.g. Heydon and Reynolds 2000). The use of shooting teams was also found to be useful in some studies because it reduced the number of animals that escaped the initial encounter with shooters (e.g. Fraser *et al.* 2003; Crouchley *et al.* 2011). Reducing escapes is important because animals that have been exposed to shooting can become more evasive and, hence, more difficult to locate and kill later (Williams *et al.* 2008; Thurfjell *et al.* 2017).

The problem of harvest-oriented shooters selecting for adult males has commonly been addressed by regulation or education. Regulations that require recreational hunters to take antlerless deer before they can harvest an antlered male can be effective at shifting the sex ratios of harvested deer away from adult males (Holsman and Petchenik 2006; Hygnstrom *et al.* 2011; Boulanger *et al.* 2012). However, they also risk reducing hunter satisfaction and motivation to participate if hunters do not believe that such regulations are in their own best interests (Van Deelen *et al.* 2010). One operation required unpaid shooters to participate in orientation activities that encouraged practices conducive to population reduction, such as the harvesting of females and young males, through education and incentives (Hygnstrom *et al.* 2011). Other operations directly involved recreational hunters in the process of adaptive management, thereby encouraging ownership and responsibility for the control of overabundant populations (Hothorn and Müller 2010; Hagen *et al.* 2018).

Other variables

Although we found no simple relationship between the geographic size of shooting operations and their effectiveness, case study results indicate that the size and spatial configuration of operations can be important. One in five studies reported that the effects of shooting were undermined by rapid immigration from nearby areas or by dispersal from refugia within the area of operations (AO). Substantial immigration from outside the AO indicates that the area targeted for control was too small or was poorly defined, relative to the connectivity of the population (e.g. Hanson *et al.* 2009; Lieury *et al.* 2015). One study reported that control efforts were hindered by immigration from a neighbouring hunting reserve where feral pigs were deliberately released (Engeman *et al.* 2014). However, if the AO is too large, it can be impossible to concentrate enough shooting effort to offset *in situ* reproduction (Simard *et al.* 2013). Several studies have addressed this dichotomy by dividing the AO into smaller management units based on geographic barriers to immigration (e.g. Parkes *et al.* 2010; Barron *et al.* 2011; Masters *et al.* 2018). Dispersal from refugia within an AO can arise from several sources, including non-participation from landholders within the AO (e.g. Williams *et al.* 2013), the presence of areas where shooting is impractical because of public safety or other limitations (e.g. Hygnstrom *et al.* 2011), or spatial concentration of shooters in easily accessed areas (e.g. Simard *et al.* 2013). The combined effort of recreational hunters, for example, is often greatly diminished away from easy access points or in areas where the topography or vegetation is difficult to traverse or provides poor visibility (e.g. Nugent 1988; Millspaugh *et al.* 2000). The importance of population recovery through immigration shows that the spatial area covered by shooting operations is an important contributor to the probability of success. However, size effects are probably mediated by other factors such as the presence of refugia, landscape connectivity, the mobility of the target species and frequency and intensity of control efforts.

Given the diversity of case studies, the small sample size, and the wide range of biological, geographic and social variables that could potentially influence the effectiveness of shooting operations, it is perhaps unsurprising that we found no univariate relationships between program effectiveness and our remaining variables, namely, type of aim or objective, target taxa, whether the target population was native or introduced, or whether other control tools were used in the broader management program. Ideally, future examinations of shooting operations should address a more specific question than we could, specifying a target taxon and type of shooting operation, and assessing effectiveness in terms of achieving predefined objectives. However, our search results suggested that there is insufficient literature available at present. One-quarter of the case studies in our sample described or evaluated the effects of recreational hunting on native or introduced deer populations, but only four of these stated an objective against which success could be measured.

Management implications

Ground-shooting has traditionally been an important tool for managing introduced and native mammal populations and is likely to remain so for the foreseeable future. Case studies examined in the present review have shown that it can be effective, either on its own or as a complement to other control tools. However, the high proportion of cases that failed to meet their objectives shows that there are important constraints on the ability of ground-shooting to reduce population densities or impacts to desirable levels. Objectives, therefore, need to be realistic. Furthermore, ineffective or inefficient ground-shooting can result in many animals being killed for no apparent benefit, or more animals being killed than would otherwise be necessary to achieve population- or damage-reduction objectives. This could jeopardise further operations because of animal-welfare concerns (Warburton and Norton 2009). The disturbance of populations by ineffective shooting operations can also make existing problems worse, for example, by increasing the risk of disease transmission (Comte *et al.* 2017), increasing local population densities (Wäber *et al.* 2013) or rendering survivors more difficult to control (Thurfjell *et al.* 2017).

Shooting programs have tended to fall along a continuum between (1) well planned operations with clear and meaningful objectives that were designed to maximise efficiency and generate reliable information that could be used to improve future iterations (e.g. Crouchley *et al.* 2011) and (2) *ad hoc* operations that relied on convenient resources such as unpaid shooters and assessed their efficacy in terms of whether they achieved a noticeable short-term reduction in animal numbers or an increase in participant satisfaction (e.g. Ditchkoff and Mitchell 2009). Managers considering the use of ground-shooting to help reduce overabundant populations should strive to position their operations towards the first end of this continuum by addressing the three key points below.

First, in common with any population-management program, managers must establish clear, meaningful and measurable objectives that allow for performance assessment, operational learning and continuous improvement. Ideally, objectives should be specified in terms of outcomes, such as damage mitigation, net economic benefit or population health (Moberly *et al.* 2004; Reddiex and Forsyth 2006; Morellet *et al.* 2007; Braysher 2017). However, this is not always possible and a strict focus on local damage alone is not always desirable, particularly for populations that have wide-ranging and variable impacts (Bengsen *et al.* 2014) or those that produce emigrants that cause damage elsewhere (Wäber *et al.* 2013). It will sometimes be difficult to identify objectives that have agreement from all important stakeholders (Rutberg 1997; Holsman *et al.* 2010), and objectives may need to change over time in response to variation in the state of the target population and its interactions with the environment (Morellet *et al.* 2007). Nonetheless, clear, measurable and meaningful objectives are critical for designing effective management operations, determining whether operations are useful, improving effectiveness and efficiency over time and minimising unnecessary killing (Warburton and Norton 2009).

Second, once objectives have been established, managers should consider how ground-shooting can help them achieve those objectives given the geographic, ecological and social contexts. Ground-shooting is sometimes used because it is seen as convenient or cheap (Gentle and Pople 2013), or because established practice or doctrine promotes a 'business-as-usual' approach (Rutberg 1997; Holsman 2000). The types of shooters (Table 1), methods and incentives most likely to achieve the objectives need to be identified (e.g. Parkes *et al.* 2010). Our review has indicated that experienced commercial wildlife management contractors or government-agency shooters are more likely to achieve objectives, and more quickly, than are other types of ground-shooters.

Third and, finally, the logistical and financial resources must be sufficient to achieve the objectives, given the types of shooters that will be used and the timeframe over which they are likely to be needed. Many management programs have failed because of an inability to remove a sufficient proportion of the population to achieve a population decline. We believe that these failures often could have been averted by investing more resources at the start of the program such that a larger initial knock-down was achieved, with fewer resources subsequently required to maintain the population at a low density. Conversely, eradication programs may need to ensure that sufficient resources are available for protracted operations after the initial knock-down (e.g. Macdonald *et al.* 2019). Several studies have reported a history of insufficiently resourced and ineffectual attempts to manage populations (e.g. Parkes 1990; Banko *et al.* 2014; Masters *et al.* 2018). Others have shown that a higher intensity of control was needed to achieve desired outcomes (Husheer and Robertson 2005). Collecting information on the relationship between control effort, susceptibility of target animals to control and outcomes can help managers assess the cost-effectiveness of shooter types and allocate resources more appropriately in future years (Hone *et al.* 2017; Latham *et al.* 2018). For example, parameterising the effort–outcome relationship has shown that using ground-based commercial wildlife-management contractors to control introduced deer in steep New Zealand forests was less cost-effective than using helicopter-based shooters (Forsyth *et al.* 2013).

Conclusions

Ground-shooting can be an effective tool for reducing the densities of wildlife populations that are having unwanted ecological, economic or social impacts, but many shooting operations did not achieve a reduction in animal numbers or damage that was perceived to be useful. The most common source of failure was an inability to remove a sufficient proportion of the population to cause anything other than a small, short-lived population decline. Given high monetary costs and the necessity of killing animals, it is essential to maximise the chance that a control operation will achieve its stated objectives. Using commercial wildlife-management contractors or government-agency shooters will typically cost more than does using other shooter types, but is more likely to achieve management objectives.

Conflicts of interest

The authors declare no conflicts of interest.

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