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1 Abstract

2 Feral deer are some of Australia's worst emerging pest species. Recently, the Government of
3 South Australia launched a four-year program to reduce the populations of feral fallow deer
4 (*Dama dama*). The program will focus on coordinating landscape-scale aerial culls and seeks
5 to deliver the most efficient and humane approach to aerial culling. We sourced data from a
6 recent program trialling a new approach to aerial culling that incorporated advanced thermal
7 technology and a second shooter with a shotgun to target fallow deer. We reviewed available
8 video and audio records of 104 deer culled in the program to assess efficiency and welfare
9 outcomes. We collected information on the number of shotgun and rifle rounds fired per
10 animal, time between first shot with a shotgun and confirmed death, and pursuit time. We
11 completed field dissections of 20 individuals targeted in the program to assess the lethality of
12 wounds inflicted with shotgun pellets. We also compared program costs and efficiency
13 against published and unpublished data from ten other aerial-culling programs for feral deer
14 in South Australia since 2009. A total of 383 shotgun rounds and 10 rifle rounds were used

15 on 104 fallow deer in the focal program. We documented strong improvements to animal
 16 welfare for feral deer targeted with shotguns. The mean (\pm standard error) time between first
 17 shot and confirmed kill with a shotgun was 11.1 ± 0.7 seconds; mean pursuit time between
 18 detection and a confirmed kill was 49.5 ± 3.4 seconds. Pursuit time increased with
 19 subsequent deer controlled within a group; the maximum pursuit time for any individual was
 20 159.0 seconds. All autopsied animals had received lethal wounds from shotgun pellets, with
 21 100% receiving lung-penetrating damage and 70% also receiving heart-penetrating damage.
 22 While a program that uses a shotgun and rifle combined with a second shooter and
 23 thermographer can cost more to mobilise, the outcomes measured in cost deer⁻¹ made it the
 24 most cost-effective approach of any program we assessed. Control options that deliver
 25 improved animal welfare outcomes and increase efficiency are desirable for managing
 26 expanding populations of feral deer in South Australia and elsewhere.

27

28 **Keywords**

29 Aerial culling, animal welfare, Australia, cost-effectiveness, costs, culling, *Dama dama*, helicopters,
 30 management, non-native species, shooting, wildlife

31

32 **Introduction**

33 Feral deer are some of Australia's worst emerging pests. The total number of deer in
 34 Australia increased from an estimated 200,000 in 2000 (Moriarty 2004) to around 2 million
 35 animals by 2021 (i.e., a ten-fold increase) (Government of South Australia 2022). Their
 36 impacts are now severe and include damage to native plants, competition with native animals,
 37 economic losses to primary industries (crops, pastures, horticulture, plantations) (Bradshaw et
 38 al. 2021), and human safety risks from vehicle collisions. Feral deer are reservoirs and
 39 vectors of endemic animal diseases and have the potential to transmit exotic animal diseases,
 40 such as foot-and-mouth disease (Cripps et al. 2019). If left uncontrolled, within 30 years the
 41 economic impacts of feral deer are expected to cost billions of dollars annually (BDO
 42 EconSearch 2022; Frontier Economics 2022).

43 Australia has six species of feral deer — fallow (*Dama dama*), red (*Cervus elaphus*), hog
 44 (*Axis porcinus*), chital (*A. axis*), rusa (*C. timorensis*), and sambar (*Rusa unicolor*); of all the
 45 feral deer species, fallow deer are the most abundant and widespread (Centre for Invasive
 46 Species Solutions 2022b). They are also considered one of the most difficult deer species to
 47 shoot from a helicopter during aerial control programs, because they tend to hide in dense
 48 vegetation and run fast, darting quickly from side to side when being pursued (Hampton et al.

49 2022). These behaviours make accurate shots with a rifle difficult and can increase pursuit
50 times and duration of suffering relative to other deer species (Sharp et al. 2022).

51 Adopting new technologies could enhance the efficiency of aerial programs and welfare
52 outcomes for target animals. Recently, Pulsford et al. (2023) concluded that thermal-assisted
53 aerial culls were more effective than ground shooting when targeting sambar deer, and Cox et
54 al. (2022) demonstrated improvements in both efficiency and welfare outcomes for fallow
55 deer by incorporating thermal technology into their aerial programs. Government programs
56 across Australia are trialling new combinations of firearms for different terrain and species of
57 deer to improve the efficiency of culling operations. For example, programs have been
58 trialling the use of shotguns to target feral fallow deer in New South Wales and the
59 Australian Capital Territory (Hampton et al. 2022). While shotguns are routinely used by the
60 New Zealand Government for aerial culling of feral deer (Forsyth et al. 2013) and in
61 Australia for aerial culling of goats and pigs (Sharp 2012a, 2012b), they are not widely used
62 for the control of feral deer in aerial culling programs in Australia.

63 Fallow deer are also the most abundant deer species in South Australia and the population
64 is increasing despite the Government of South Australia supporting helicopter and ground-
65 based shooting programs for more than 15 years. Recently, the State Government and
66 Regional Landscape Boards launched a four-year program to reduce the populations of feral
67 fallow deer in South Australia. The program focusses on coordinating landscape-scale aerial
68 culls and aims to deliver the most efficient and humane approach to aerial culling. In that
69 context, the State Government recently did a trial program (henceforth, 'P1') to test a new
70 approach to aerial culling; it incorporated advanced thermal technology and a second shooter
71 with a shotgun to target feral fallow deer.

72 Our study assessed the outcomes from P1 to examine the efficiency of the shotgun-rifle-
73 thermal configuration compared to other configurations used in aerial culling programs
74 delivered in the same region and across South Australia. We predicted using the shotgun-
75 rifle-thermal combination could: (i) improve animal welfare outcomes for target animals by
76 minimising time between first shot with a shotgun and confirmed death and pursuit time, and
77 rapidly deliver fatal injuries to vital organs; and (ii) increase the efficiency and/or cost-
78 effectiveness of the program compared to other programs delivered in the same region and
79 across the State.

80

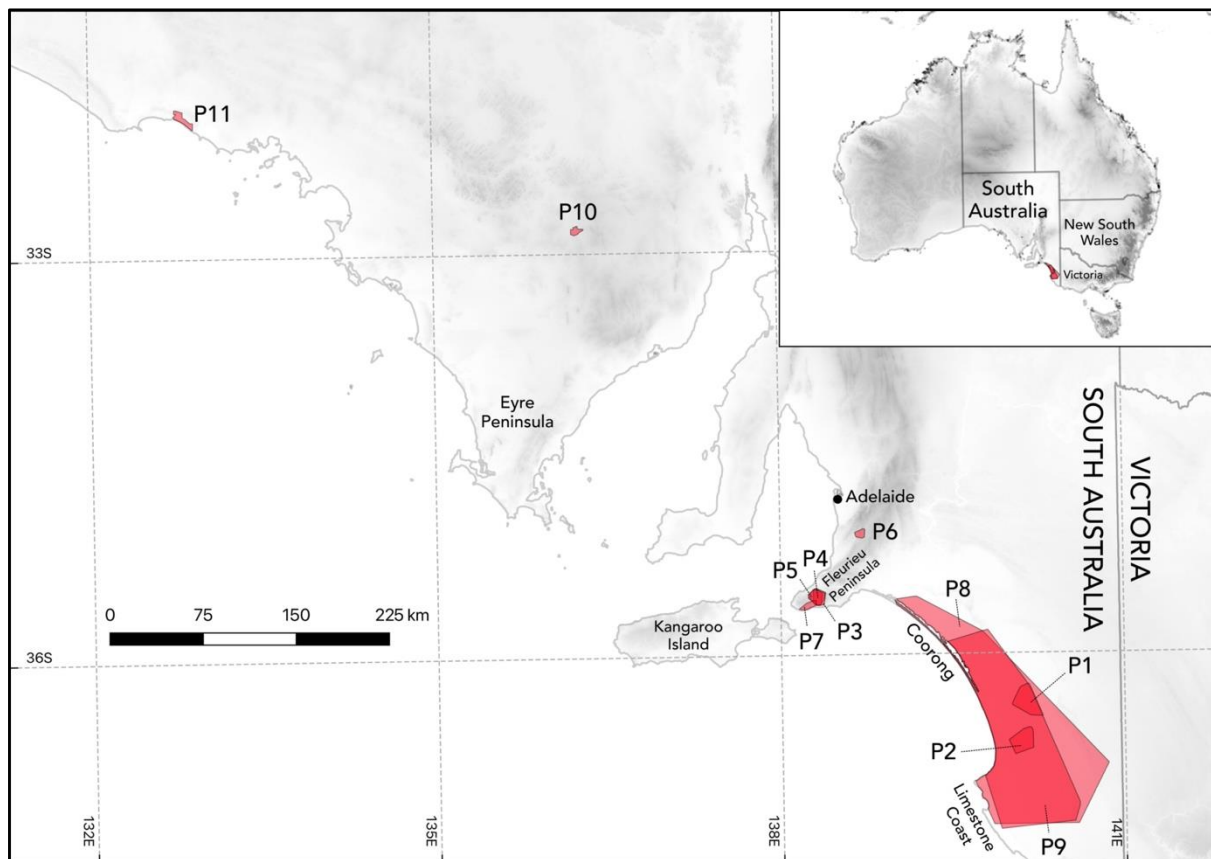
81 **Methods**

82 **Program location and target species**

83 The aerial culling trial program P1 occurred from 1–7 in October 2022, covering ~ 20,000 ha
 84 of private property in the Limestone Coast region of South Australia, about 300 km southeast
 85 of Adelaide (Fig. 1). The program targeted fallow deer — relatively small-bodied cervids
 86 with adult masses of 35–55 kg (females) and 50–97 kg (males) (West 2018). For comparison,
 87 sambar deer are Australia’s largest deer and weigh around 230 kg (females) and 300 kg
 88 (males) (Centre for Invasive Species Solutions 2022a). We reasoned that the small size of
 89 fallow deer would increase the likelihood of shotgun pellets effectively penetrating the thorax
 90 compared to larger-bodied species.

91

92 **Figure 1.** Location of the feral deer aerial culling programs in South Australia from 2009 to 2022
 93 (P1–P11). See Table 1 for program descriptions. Red boxes are the minimum convex polygons
 94 enclosing all deer kills within each program (P1–P9), or the area searched by helicopters (P10–P11).
 95



96
 97

98 **Firearms, ammunition, and crew configuration**

99 In P1, one shooter (hereafter, the ‘primary’ shooter) was equipped with a Benelli M2 semi-
 100 automatic shotgun with a 26” barrel and a custom choke at full extension, which created a 25-
 101 cm pellet spread at 20 m and a 45-cm spread at 30 m. The primary shooter targeted deer in
 102 open areas, within a 30-m range. The shotgun was fitted with a red-dot scope (Sightron S30-5

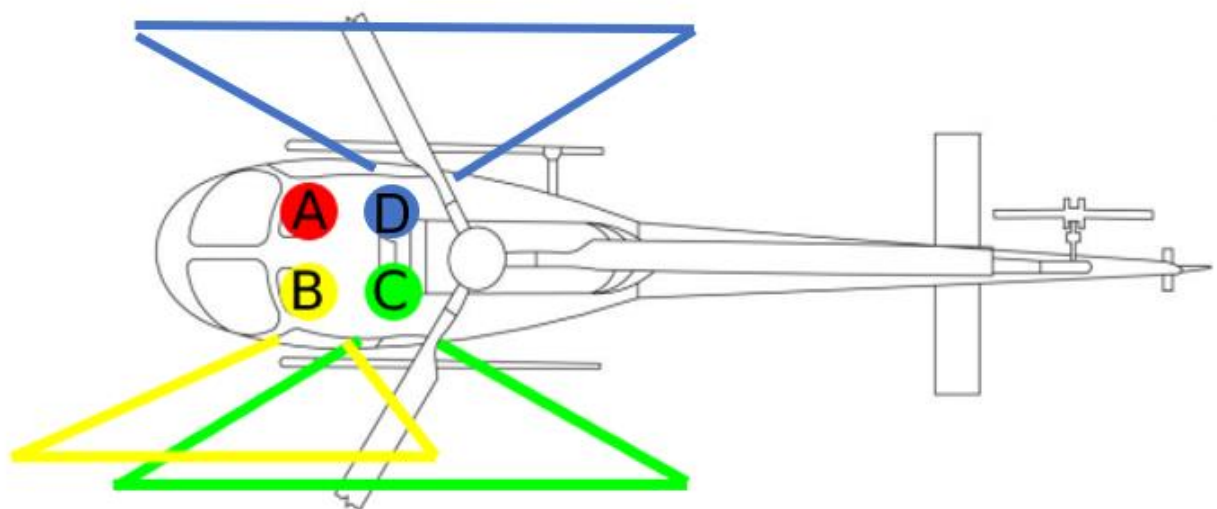
103 and Aimpoint 9000L™); it had a 12-shell tube magazine and was loaded with GB SSG 21-
 104 pellet buckshot and Winchester Super-X 16-pellet buckshot. The projectiles of the 21-pellet
 105 SSG cartridges have an average weight of 1.8 g, with an average total payload of 37 g. The
 106 projectiles in the Winchester Super-X 16-pellet SSG cartridges have an average weight of 2.3
 107 g and a total payload of 36 g. Professional shooters (Wildlife Resources Australia,
 108 Wangaratta, Victoria) did not observe any difference in the performance between the
 109 different rounds of buckshot. Both round types were mixed into the primary shooter's
 110 ammunition bags, and we did not distinguish between ammunition type during data
 111 collection. The primary shooter was positioned in the rear right-hand side of the helicopter
 112 behind the pilot (Fig. 2).

113 Another shooter ('secondary' shooter) was equipped with a Wedgetail WT25 semi-
 114 automatic, .308-calibre rifle with a variety of ammunition types. The secondary shooter
 115 targeted deer within vegetated areas and had a range of 70 m. The secondary shooter was
 116 positioned next to a thermal camera operator ('thermographer'; Fig. 2). The thermographer
 117 operated a Vayu HD uncooled microbolometer array with the Blackmagic Video Assist and
 118 Panasonic GH5 4K video camera and used a high-powered laser to assist the secondary
 119 shooter to locate deer in forested areas. The .308-calibre rifle was also equipped with a
 120 thermal scope (Pulsar Trail 2 LRF XQ50), so wounded deer in forested areas could be
 121 located quickly for follow-up shots and the thermographer could confirm death.

122

123 **Figure 2.** Seating configuration of the helicopter crew in P1: (A) pilot, (B) secondary shooter with
 124 rifle and thermal scope, (C) thermographer, and (D) primary shooter with shotgun and red-dot scope.
 125 Yellow and blue polygons show the indicative field of view for the shooters, and the green polygon
 126 shows the field of view for the thermographer.

127



128

129 Shooters made chest shots exclusively. For small deer species, especially those that move
 130 quickly and erratically such as fallow deer, chest shots are preferred for the best welfare
 131 outcomes (Sharp et al. 2022). P1 deployed a deliberate ‘overkill’ policy, which mandated that
 132 each deer was shot at least twice (following Hampton et al. 2022). If the target was not
 133 moving after a single shot, it would still receive at least one additional chest shot. Two crew
 134 members confirmed both visually and with the thermal equipment the insensibility/death of
 135 each target animal before moving to the next target (see signs for confirming death in ‘Data
 136 collection and analyses’). On average, the crew spent 5–10 seconds to confirm each death.
 137 The total flight time of P1 was 26.3 hours for a total of 611 feral deer culled.

138

139 **Data collection**

140 All P1 flights were recorded on the thermal camera and with a GoPro 3 camera. The thermal
 141 camera captured all vision from the thermographer’s perspective. The GoPro 3 camera was
 142 mounted to the rear firewall of the helicopter and recorded continuously; it captured the
 143 activities of all personnel in the helicopter and most of their field of view (Fig. 3). Both
 144 systems captured flight audio. The large video and audio files were overwritten every few
 145 days, so only a sub-sample of the 611 targeted deer was available for this assessment.

146 Based on the approach described by Cox et al. (2022), we reviewed all available video
 147 footage and audio from the first four hours of flight time on 2, 4, and 5 October 2022 and
 148 recorded: (i) number of shotgun and rifle rounds fired; (ii) time taken between the first shot
 149 fired at the target with a shotgun and a confirmed kill (with shotgun or rifle); at least two
 150 helicopter personnel confirmed time of death based on the thermographer observing hotspots
 151 indicating that the thorax (heart and/or lungs) had been pierced, and a complete absence of
 152 movement confirmed by any crew member with clear vision; (iii) time between first detection
 153 of the target and confirmation of its death; if a deer stayed with its group under pursuit,
 154 pursuit time was cumulative for each consecutive deer (i.e., last deer killed in the group was
 155 recorded as *pursued* for the entire time that other deer in the group were being culled); if the
 156 group dispersed and a subset of that group had to be re-located, pursuit time was started when
 157 the group was relocated.

158

159 **Figure 3.** A GoPro 3 camera, mounted to the rear firewall of the helicopter, captured the seating
 160 configuration of the personnel in the helicopter, their field of view, and four deer being pursued
 161 (circled in red).

162



163

164 **Analysis**

165 To test which components of an individual kill explained the most variation in the time from
 166 the start of the pursuit to the confirmed kill, we constructed a series of generalised linear
 167 models using the *glm* function in the *stats* R library (R Core Team 2022). Here, we tested
 168 whether the time between first and last/kill shots, number of rounds fired, and group size
 169 explained variation in the time from the start of the pursuit to the kill (with a shotgun). We
 170 applied a gamma error distribution and a log link function, and scaled the response and
 171 explanatory variables (except group size) using the *scale* function in R. We contrasted a total
 172 of eight models, including the three additive main effects, all combinations of two additive
 173 effects, single effects, and the intercept-only model. We compared the relative probability of
 174 the five models per response variable using Akaike’s information criterion corrected for
 175 small sample size (AIC_c) (Burnham and Anderson 2002). The bias-corrected relative weight
 176 of evidence for each model, given the data and the suite of candidate models considered, was
 177 the AIC_c weight (the smaller the weight, the lower the model’s probability) (Burnham and
 178 Anderson 2002). We also calculated the percent deviance explained (%DE) as a measure of
 179 goodness of fit. We examined model diagnostics using the *check_model* function in the
 180 *performance* R library (Lüdtke et al. 2021). All data and R code are available at
 181 github.com/cjabradshaw/deerCullShotgun.

182

183 **Field dissections to assess lethality of shotgun damage**

184 After the morning flights on 4 and 5 October 2022, 20 deer carcasses were located for
185 assessment. Field dissections were done to collect information on shotgun-pellet penetration
186 and spread and organ damage. Shotgun injuries were determined by cutting and peeling back
187 the pelt and visually assessing the external muscle tissue for bruising and penetration of
188 shotgun pellets on the impact and exit sides. Because damage from multiple projectiles to
189 either the heart or lungs is lethal, the number of projectiles that impacted the thorax was also
190 recorded for each carcass.

191 Following inspection of the muscle tissue and sites of pellet impact, the chest cavity was
192 opened below the sternum using a bone saw. The heart and lungs were removed and
193 inspected for tissue damage, wound channels, bleeding, and blood coagulation to determine
194 whether pellets penetrated the heart and/or the lungs. The heart and lungs were dissected to
195 establish the extent of the wounding by shotgun pellets, if not obvious externally. The chest
196 cavity was also inspected for pooling of blood. All damage was recorded photographically,
197 and the sites assessed for evidence of struggle or distress (such as kicking or disturbance of
198 surrounding ground).

199

200 **Cost-effectiveness**

201 We compared the economic costs and outcomes of P1 to those of 10 other aerial culling
202 programs (P2–P11) completed between June to November 2022. All programs targeted deer
203 in the same region (Limestone Coast) or elsewhere in South Australia, and varied in crew
204 configuration, firearms, equipment, deer density, area covered, and landscape (Table 1). P3,
205 P4 and P5 were part of one large program, but we treated them separately based on their
206 different configurations. We compared the programs according to the following metrics: (i)
207 costs associated with delivering each program, (ii) costs per number of deer culled, and (iii)
208 costs per flight hour and area covered.

209 Staff costs were included in the assessment because they are necessary to plan and deliver
210 all aerial culling programs. This approach is consistent with ‘competitive neutrality’
211 requirements for government agencies in South Australia, which ensure government
212 businesses compete fairly in the market (Government of South Australia 2023a). Staff costs
213 were estimated to be \$150 per hour for all agencies.

214 To contextualise any landscape-scale differences among the programs that could have
215 affected cost effectiveness, we also calculated the dominant landcover classes within the area
216 of each program using the South Australia Land Cover raster (2010–2015) at a resolution of

217 25 m × 25 m (available from data.sa.gov.au/data/dataset/sa-land-cover). We compared the
218 land cover classes in which kills occurred to ‘available’ land cover classes within a minimum
219 convex polygon defined by the locations of all kills in the program. Additionally, we
220 calculated the mean human population density (persons km⁻²) within 50 km of the program’s
221 minimum convex polygon to assess the relative likelihood of human visitors to a program
222 area during culls (when near to larger human populations, personnel costs increase — see
223 Results).

224 **Table 1.** Summary details of 11 feral deer aerial culling programs, including the recent trial (P1), to compare program efficiency. F = fallow deer (F); R = red deer
 225 (R); S = sambar deer (S); TAAC = thermal-assisted aerial cull (crew has a dedicated thermographer). All programs used .308 centrefire rifles exclusively except for
 226 P1 and P5 that also used a shotgun. The lead South Australian Government agency for each program was: PIRSA (P1–P5); Hills and Fleurieu Landscape Board
 227 (P6–P7); Limestone Coast Landscape Board (P8–P9); Eyre Peninsula Landscape Board (P10–P11).
 228

No.	Region and location	Land use	Area (km ²)	Deer species	Deer density	Helicopter	Primary shooter	Secondary shooter	TAAC	Shotgun	Notes
P1	Limestone Coast, Willalooka	rich agricultural area, isolated patches of vegetation	150	F, R, S	high	B2 Squirrel	✓	✓	✓	✓	current trial; fallow most common species
P2	Limestone Coast, Taratap	coastal agricultural area, linear vegetation remnant and dunes	100	F, R	high	B3 Squirrel	✓		✓		first trial of TAAC for deer in South Australia; fallow most common species
P3	Fleurieu Peninsula, Parawa	undulating peri-urban area mixed	60	F	high	B2 Squirrel	✓		✓		Programs 3-5 delivered as part of a single program, but separated based on crew configuration, area covered, firearm type
P4	Fleurieu Peninsula, Parawa	agricultural/rural with abundant vegetated creek lines and vegetation	30	F	high	B2 Squirrel	✓	✓	✓		
P5	Fleurieu Peninsula, Parawa	pockets	110	F	high	B2 Squirrel	✓	✓	✓	✓	
P6	Adelaide Hills, Mt Bold	peri-urban water reservoir, undulating land covered in native and pine forest	20	F	high	R44	✓				goats also targeted
P7	Fleurieu Peninsula, Deep Creek	national park – undulating landscape with thick vegetation	40	F	high	B2 Squirrel	✓				
P8	Limestone Coast, Salt Creek to Taratap	coastal agricultural area, linear vegetation remnant and dunes	1200	F, R, S	high	2 × R44	✓				2 helicopters, single shooter in each; fallow most common species
P9	Limestone Coast, Salt Creek to Taratap	coastal agricultural area, linear vegetation remnant and dunes	1200	F, R, S	high	2 × R44	✓				2 helicopters, single shooter in each; fallow most common species
P10	Eyre Peninsula, Buckleboo	open, dry-land cropping country, isolated vegetation patches	160	R	low	R44	✓				no individual coordinates
P11	Eyre Peninsula, Chadinga	remote conservation reserve, squat coastal vegetation	100	no deer culled	low	R44	✓				no individual coordinates

230 **Results**

231 **Number of rounds**

232 We reviewed all available footage from P1, which included 20% of the 611 fallow deer culled ($n = 104$).
 233 Of these, 92% were killed with a shotgun only ($n = 96$) and 8% with a shotgun-rifle combination ($n = 8$).
 234 Shooters used a total of 383 shotgun rounds and 10 rifle rounds (Table 2).

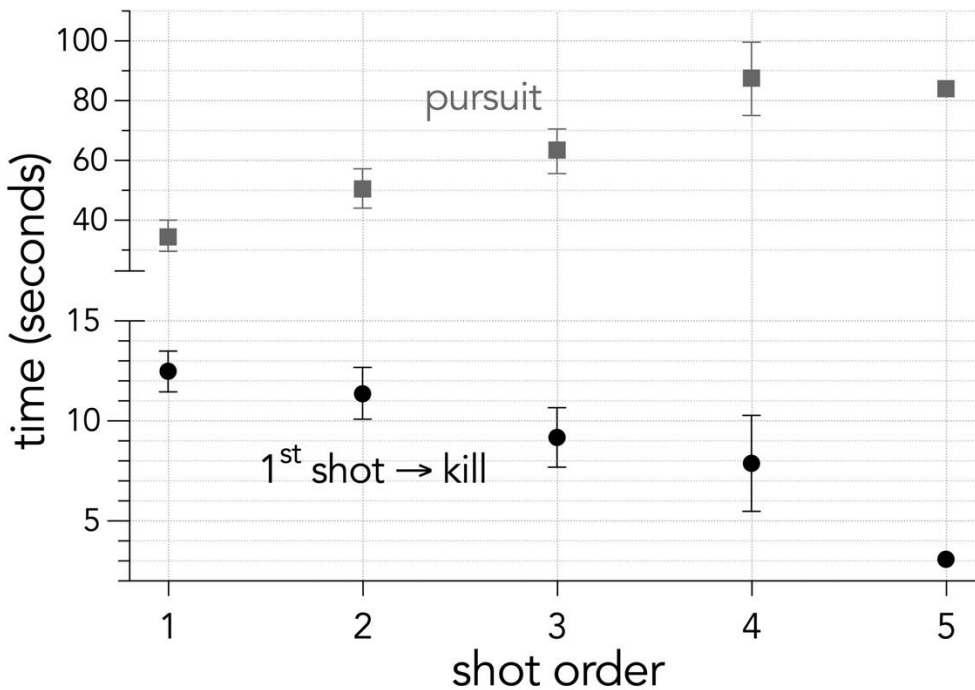
235
 236 **Time between first shot with a shotgun and confirmed death**

237 The mean time between first shot with a shotgun and confirmed death was 11.1 seconds (± 0.7 ; $n = 104$).
 238 Individual deer, or the first deer shot in a group, had the greatest mean time between first shot and
 239 confirmed death, but this time decreased with subsequent individuals targeted within the group (Fig. 4).
 240 The maximum time recorded between first shot and a confirmed death for any individual deer was 35.9
 241 seconds (Table 2).

242
 243 **Pursuit time**

244 Mean time between first detection and confirmed death was 49.5 seconds (± 3.4 ; $n = 104$). Pursuit time
 245 increased with subsequent deer shot within a group (Fig. 4). The maximum pursuit time for any deer was
 246 159.0 seconds. See summary data from the analysis of footage in Table 2.

247
 248 **Figure 4.** Mean (\pm standard error) time (seconds) between first shot and confirmed kill (black circles) and mean (\pm
 249 standard error) pursuit time (seconds) between first detection and confirmed kill (grey squares) as a function of shot
 250 order (either singularly or in groups of 1 to 5).



253 **Table 2.** Summary statistics from footage of 104 deer killed with a combination of firearms, a secondary shooter, and thermal-imaging technology.

summary statistic	order of deer shot					total	mean
	first ^a	second	third	fourth	fifth ^b		
sample size (no. deer)	45	29	21	8	1	104	-
shotgun rounds fired	169	114	64	34	2	383	-
mean \pm s.e. shotgun rounds per deer	3.8 \pm 0.3	3.9 \pm 0.3	3.0 \pm 0.4	4.3 \pm 0.6	2.0	-	3.7 \pm 0.2
rifle rounds fired	4	6	-	-	-	10	-
min-max time between first shot with shotgun and confirmed kill (seconds)	2.9–35.9	2.6–32.0	2.6–33.2	4.0–14.1	3.1	-	-
mean \pm s.e. time between first shot with shotgun and confirmed kill (seconds)	12.5 \pm 1.0	11.4 \pm 1.3	9.2 \pm 1.5	7.9 \pm 2.4	3.1	-	11.1 \pm 0.7
min-max pursuit time (seconds)	13.9–83.1	16.0–89.4	14.5–120.2	46.3–159.0	84.2	-	-
mean \pm s.e. pursuit time (seconds)	34.9 \pm 5.2	50.7 \pm 6.5	63.1 \pm 7.6	87.4 \pm 12.3	84.2	-	49.5 \pm 3.4

254 ^a first deer includes isolated individual deer as well as the first deer targeted within a group; data also collected for subsequent deer shot from the same group for up to five deer.255 ^b sample size = 1, no standard error (s.e.), mean, or range calculated.

256 **Model results**

257 There was a positive effect of deer group size and number of shotgun rounds fired on the total time
 258 elapsed since start of pursuit to death (Table 3). These two variables explained ~ 43% of the variation in
 259 the response. However, there was no evidence for an effect of the time between the first and last shot and
 260 total time elapsed since start of pursuit to death.

261

262 **Table 3.** Generalised linear model results testing the effects of time between first and last/kill shots (*t1stLast*),
 263 number of rounds fired (*rnds*), and group size (*grpSize*) on the time from the start of the pursuit to the kill with a
 264 shotgun (response). *k* = number of model parameters; ℓ = -log likelihood; AIC_c = Akaike’s information criterion
 265 corrected for small sample size; $wAIC_c \approx$ model probability; %DE = percent deviance explained.
 266

model	<i>k</i>	ℓ	AIC_c	$wAIC_c$	%DE
<i>~grpSize + rnds</i>	3	-24.770	57.945	0.529	42.7
<i>~t1stLast + grpSize + rnds</i>	4	-23.859	58.330	0.436	43.7
<i>~t1stLast + grpSize</i>	3	-27.489	63.383	0.035	39.7
<i>~grpSize</i>	2	-32.480	71.201	0.001	33.8
<i>~rnds</i>	2	-50.879	107.997	<0.001	6.9
intercept-only	1	-54.745	113.610	<0.001	-
<i>~t1stLast + rnds</i>	3	-50.356	109.116	<0.001	7.8
<i>~t1stLast</i>	2	-54.603	115.446	<0.001	0.3

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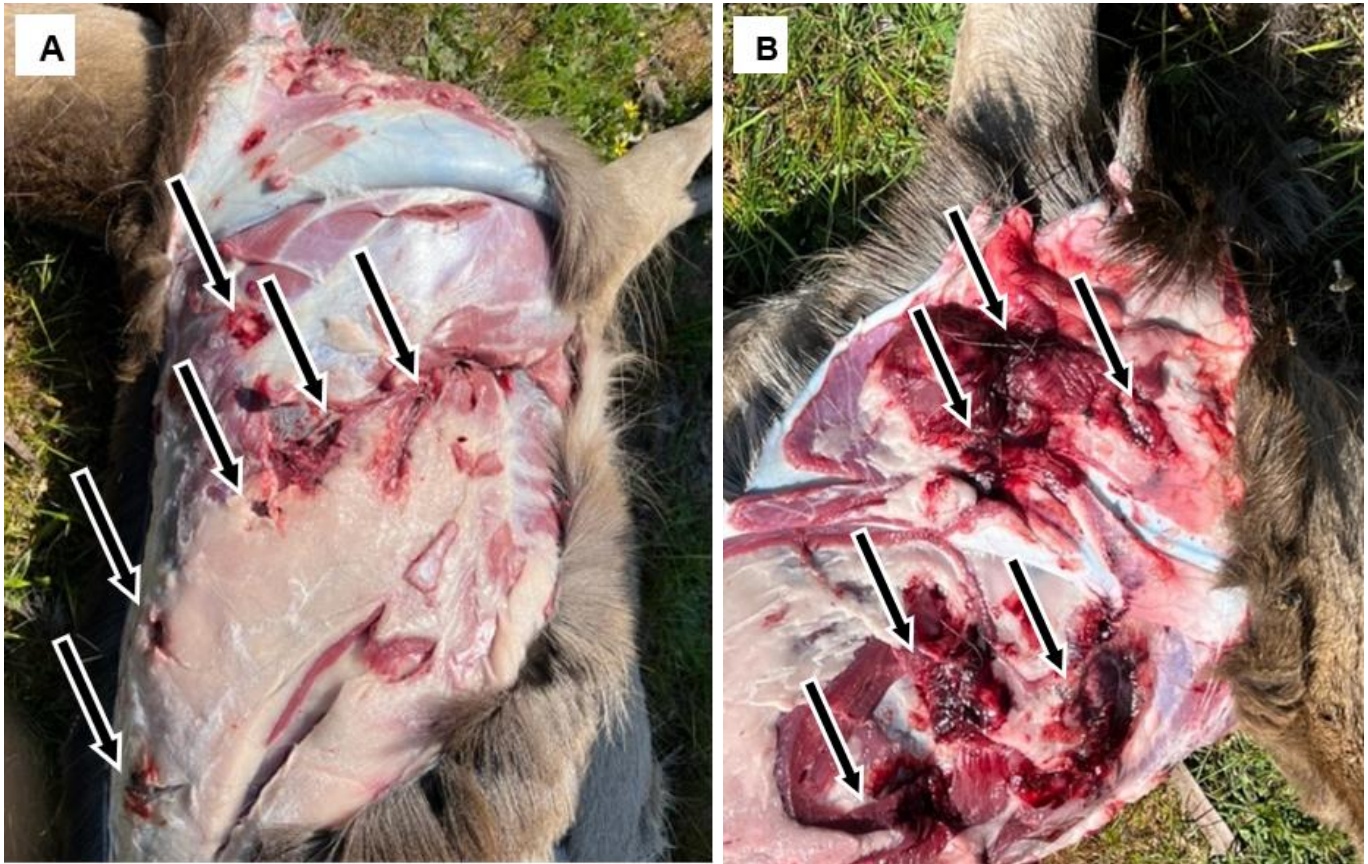
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269 **Dissection to assess shotgun damage**

270 The 20 carcasses were recovered and dissected within six hours of being culled in P1. All carcasses had
 271 received shotgun wounds only and were located using GPS data collected during the flight. A total of 116
 272 shotgun pellets had penetrated the thorax of the 20 deer (5.8 ± 0.6 pellets per deer; range: 3–13 pellets
 273 deer⁻¹). Lethal lung-penetrating wounds were recorded in all 20 animals; 14 (70%) also recorded lethal
 274 heart-penetrating wounds. The wounds and their classification are shown in Figures 6–10. Carcasses
 275 showed no indication of struggle or distress or movement from the location at which they were shot and
 276 confirmed killed by the helicopter crew.

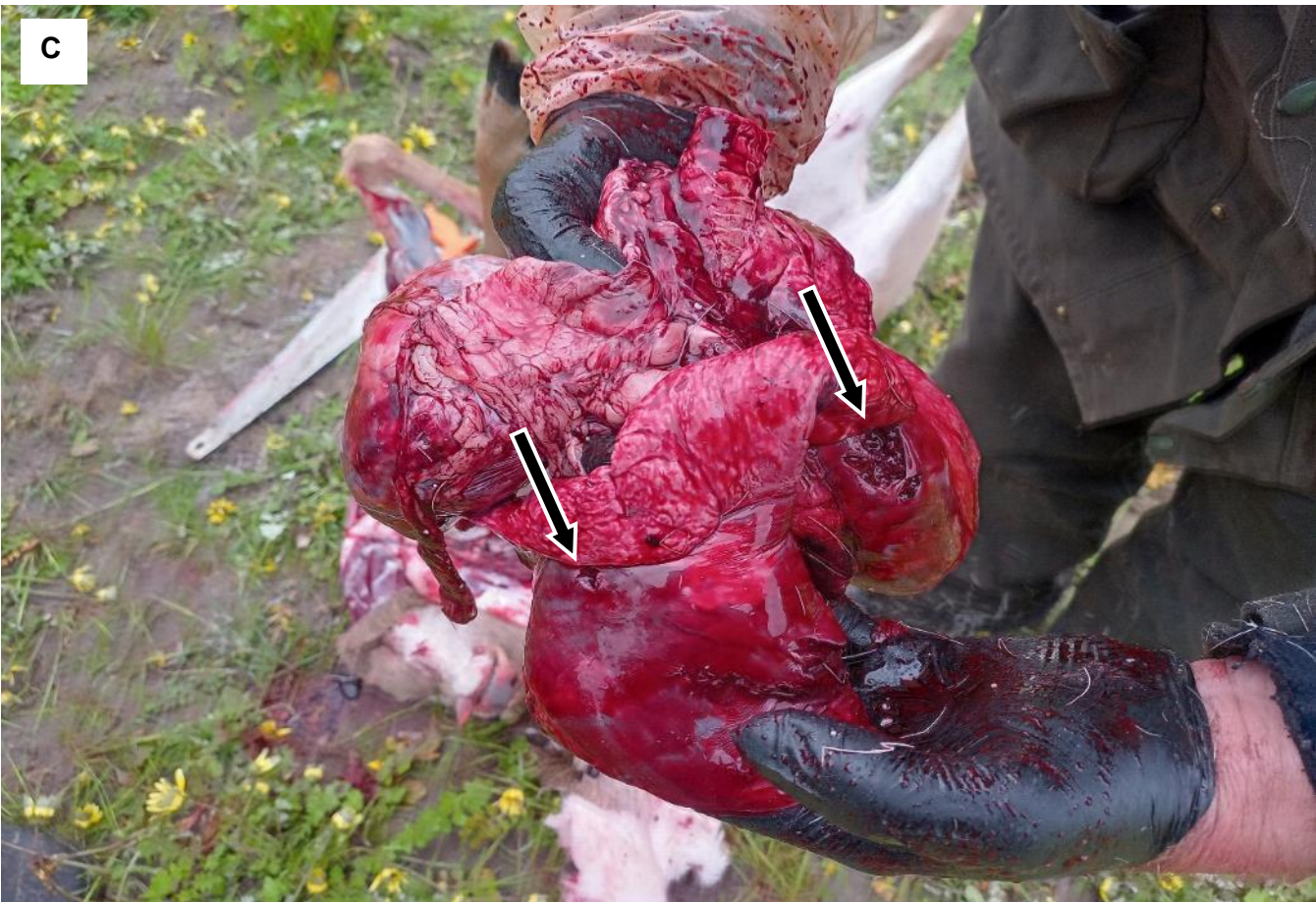
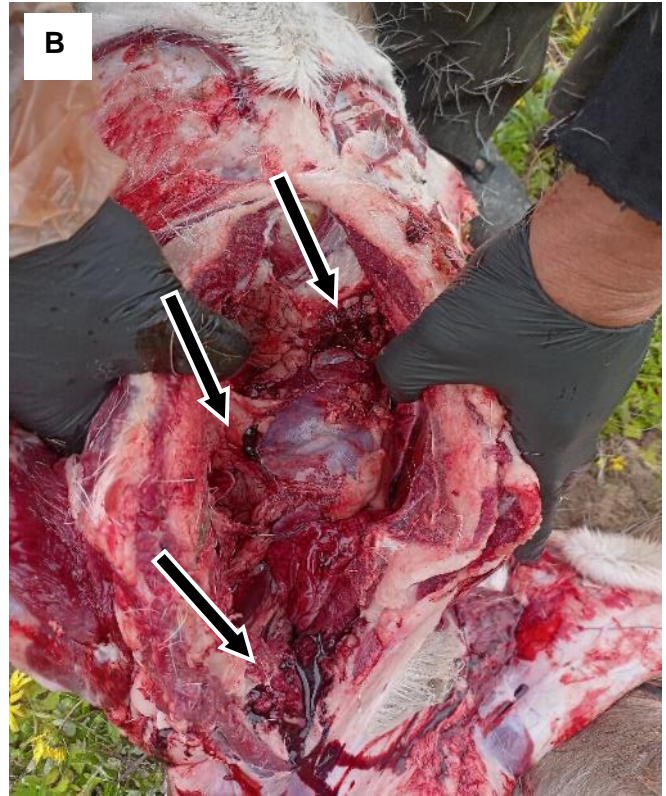
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278 **Figure 6.** Deer VI, killed with the shotgun; pelt is removed to show the difference between shotgun-pellet wounds
279 on the entry (A) and exit (B) sides of the carcass. Arrows indicate the wounds described in each image: (A) entry
280 wounds with minimal bruising or bleeding; (B) exit wounds with extensive bleeding, bruising, and coagulation of
281 blood.
282



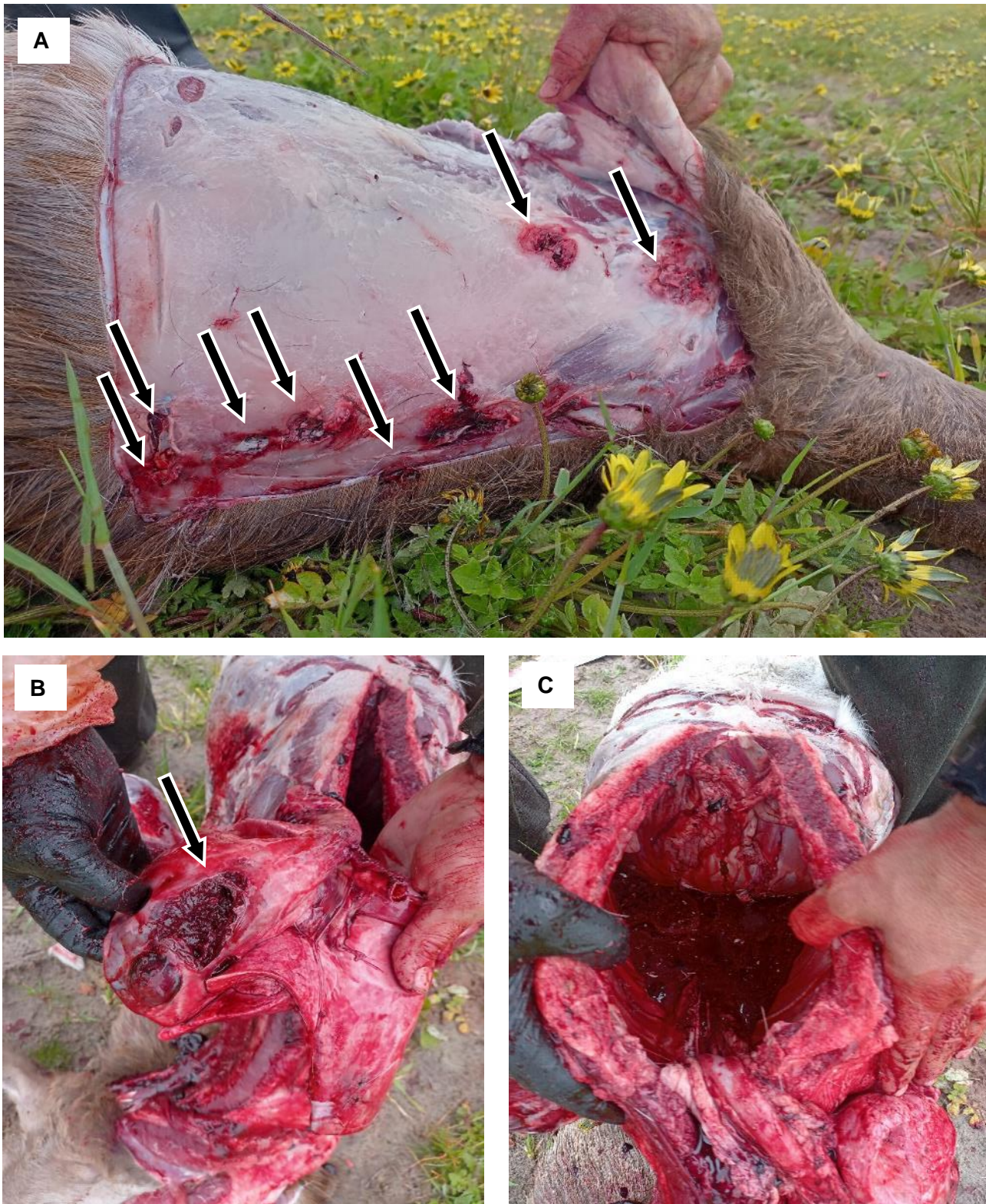
283

284 **Figure 7.** Deer XV, showing typical wounds and mode of death for fallow deer culled with shotguns in this trial.
285 Arrows point to wounds described in each image: (A) four thorax-penetrating pellet entry wounds, showing
286 bleeding and bruising at the end of the wound channel; (B) chest cavity with old oxygenated, congealing blood in
287 multiple areas around the heart and lungs; (C) example of removed heart and lungs with penetrating wounds to the
288 lungs.

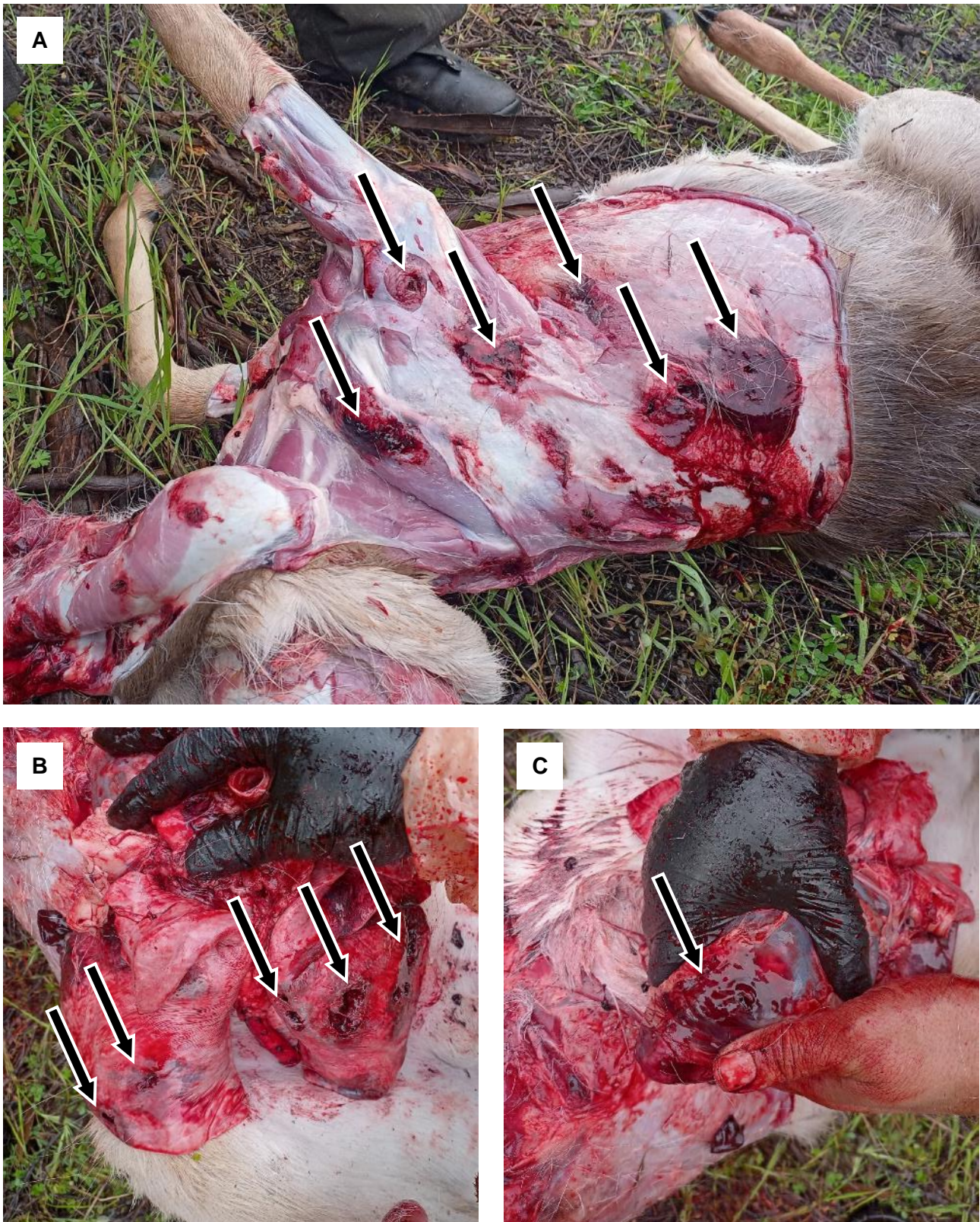


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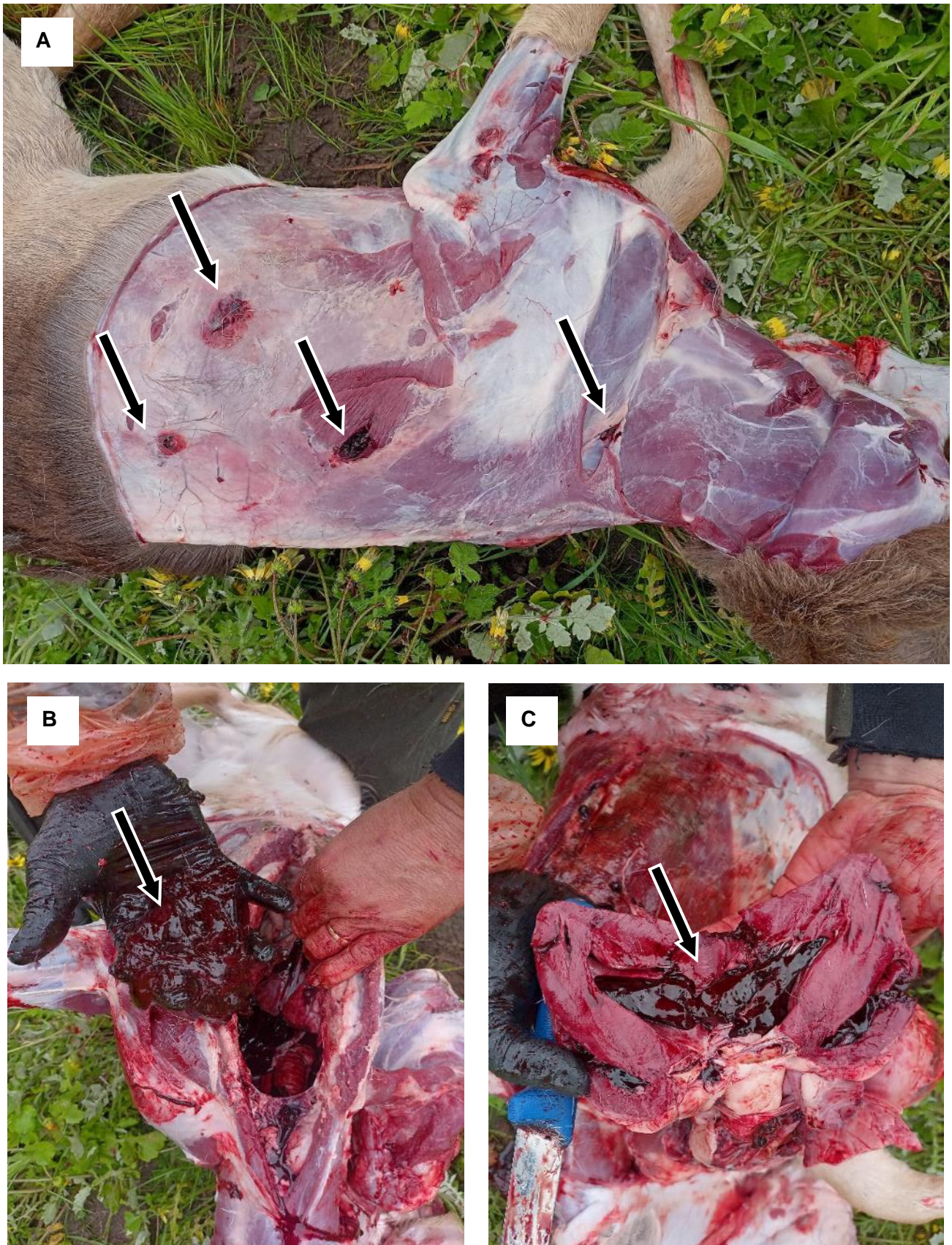
291 **Figure 8.** Deer IX, showing typical wounds and mode of death for fallow deer culled with shotgun in this trial.
292 Arrows point to wounds: (A) eight pellet entry wounds across the side and back of this fallow deer;
293 (B) damage to lung tissue with blood clotting inside the lungs;
294 (C) blood pooling in the chest cavity, following removal of the heart and lungs; bleeding is from the wounds to the heart, lungs, and other tissue.



295 **Figure 9.** Deer XII, showing typical wounds and mode of death for fallow deer culled with shotgun in this trial.
296 Arrows point to wounds: (A) six pellet exit wounds on the thorax, showing blood loss, bruising, and clotting; (B)
297 multiple penetrating wounds to the lungs; (C) bleeding from a penetrating wound to the heart.



298 **Figure 10.** Deer XIV, showing typical wounds and mode of death for fallow deer culled with shotgun in this trial.
299 Arrows point to: (A) four thorax-penetrating entry wounds; (B) blood clot from pooling of blood in chest cavity;
300 (C) dissection of heart showing clotting of blood along a wound channel.



301 **Cost effectiveness**

302 In 2022, the cost of delivering 11 aerial culling programs for feral deer in South Australia exceeded \$1.1
303 million (Table 4); the mean \pm s.e. cost per program was \$100,461 \pm \$13,385; individual program costs
304 ranged from \$45,000 for one component of a larger program (P3) to over \$160,000 for P8. As expected,
305 the most expensive component of running any program was associated with helicopter operations, which
306 comprised 54% of all costs.

307 Operating staff costs accrued by various agencies (South Australian Department of Primary Industries
308 and Regions; Regional Landscape Boards of the Hills and Fleurieu, Limestone Coast, and Eyre Peninsula;
309 National Parks and Wildlife Service; Department for Environment and Water; SA Water; Forestry SA)
310 varied considerably among programs. These costs were largely associated with the location of the
311 operations. P3–P7 occurred on public lands (e.g., parks) near metropolitan areas, so additional staff were
312 required to supervise entrances and prevent public access during the operations. Staff costs for all
313 agencies for all programs combined exceeded \$330,000, or 30% of all costs. P6 had the highest staff
314 costs, exceeding \$45,000, which comprised 54% of all costs associated with the project. This program
315 required many multi-agency staff to supervise gates and entrances to the operations area, which is a high-
316 profile, peri-urban site on public land (Fig. 1).

317 From the 11 programs, a total of 3,609 feral deer (at least 90% fallow deer) were culled during 486
318 flight hours (see Table 5). In terms of the program cost per feral deer controlled, P1 was the most cost-
319 effective at \$199 deer⁻¹. The least cost-competitive programs were P10 and P11, which operated in areas
320 with low deer densities (Table 1). Seven animals were culled in P10, costing more than \$10,000 deer⁻¹;
321 P11 cost \$27,000 and no animal was destroyed. Excluding P1, the cost per deer controlled in areas with
322 high deer densities (P2–P9) ranged from \$210 to \$447 deer⁻¹. The cost per flight hour ranged from around
323 \$1,720 (P9) to \$8,440 (P7); the mean was \$4,526 \pm \$604 flight hour⁻¹; P1 cost around \$4,950 flight
324 hour⁻¹. The cost per area covered ranged from around \$130 (P9) to \$6,800 (P6) km⁻² of program
325 delivered; the mean was \$1,445 \pm \$570 km⁻²; P1 cost \$868 km⁻².

326 Deer were most commonly killed in native woody vegetation > 1 m in height (64% of all kill locations
327 across all programs) (Table 5), and in all programs except P7 (Fig. S1h), this land cover class was
328 proportionally less-available (20% of area flown) (Fig. S1). Sparse native vegetation was the second-most
329 common land cover class in which deer were killed overall (18%), which compares to an availability of
330 only 1% (Fig. S1a). Dryland crops was the third-most common land cover class in which deer were killed
331 overall (11%), but this was relatively low compared to an availability of 55% (Fig. S1a). Contrary to
332 expectation, there was no apparent relationship between mean human population density within 50 km of
333 a program and either the total personnel costs or personnel costs flight⁻¹ hour⁻¹ area⁻¹ animal⁻¹; however,
334 the Limestone Coast and Fleurieu Peninsula programs had separate clusters within this cost-population
335 density relationship (Fig. S2).

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338**Table 4.** Cost summary for 11 deer culling programs completed in South Australia between June and November 2022. P3, P4, and P5 are separate components of a large program; all staff hours were costed at \$150 per hour. All costs in AU\$ and include goods and services tax.

Detailed costs	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11
helicopter operations	81,999	46,620	52,851	28,959	83,257	28,216	27,390	104,247	106,904	28,875	14,300
ammunition	7,500	1,868	2,802	1,535	4,413	2,756	2,200	4,051	3,221	0	0
professional shooters	7,200	3,000	3,842	2,105	6,053	6,916	4,500	27,000	27,000	4,200	1,780
PIRSA costs	20,625	26,149	18,010	9,869	28,371	6,450	0	0	0	0	0
Landscape board costs	5,625	970	1,890	701	2,659	29,100	21,375	16,950	9,000	31,000	6,750
NPWS costs	0	0	750	0	900	11,600	23,415	0	0	450	750
DEW costs	0	0	0	0	0	0	655	1172	1609	0	0
SA Water costs	0	0	0	0	0	47250	0	0	0	0	0
Forestry SA costs	0	0	2,500	1,500	3,000	0	0	0	0	0	0
community engagement	2,500	2,710	2,401	1,316	3,783	1,800	2,250	0	0	2,550	1,575
other logistics (car hire, travel, food, etc.)	4,700	2,460	2,145	1,175	3,379	1,900	2,600	6,846	6,978	3,100	2,200
Total costs	\$130,149	\$83,777	\$87,190	\$47,160	\$135,816	\$135,988	\$84,385	\$160,266	\$154,712	\$70,175	\$27,355

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Table 5. Cost effectiveness of 11 feral deer culling programs done in South Australia between June and November 2022. P3, P4, and P5 are separate components of a large program. All costs in AU\$ and include goods and services tax.

Program outcomes	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11
total animals culled	655	190	195	179	645	347 ^a	243	645	503	7	0
total flight hours	26	16	18	10	29	20	10	87	90	21	9
animals/flight hour	25	12	11	18	22	17	24	7	6	< 1	0
cost/animal	\$198.70	\$440.93	\$447.13	\$263.46	\$210.57	\$391.90 ^d	\$347.26	\$248.47	\$307.58	\$10,025	-
cost/flight hour	\$4,948.63	\$5,404.97	\$4,777.58	\$4,716.00	\$4,724.05	\$6,799.40	\$8,438.50	\$1,842.14	\$1,719.02	\$3,341.67	\$3,073.60
cost/area (km ²)	\$867.66	\$837.77	\$1,453.17	\$1,572.00	\$1,234.69	\$6,799.40	\$2,109.63	\$133.56	\$128.93	\$483.59	\$273.55
dominant vegetation in program area	dry cropland	dry cropland	dry cropland	dry cropland	dry cropland	woody native > 1 m	woody native > 1 m	dry cropland	dry cropland	woody native ^c > 1 m	woody native ^d > 1 m
dominant vegetation in which deer were culled	dry cropland	woody native > 1 m	woody native > 1 m	woody native > 1 m	woody native > 1 m	woody native > 1 m	woody native > 1 m	woody native > 1 m	woody native > 1 m		
mean human pop density within 50 km (persons km ⁻²)	0.47	0.52	69.70	75.76	68.64	58.05	59.50	4.71	3.96	0.10	negligible

^a total animals culled for Program 6 at Mt Bold Shoot includes 61 goats

^b the cost/animal adjusted to include the 61 goats is \$333.30

^c no individual kill locations available; value indicates dominant land cover class available (64% of area searched)

^d no deer killed; value indicates dominant land cover class available (83% of area searched)

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349 Discussion

350 Aerial culling

351 Aerial culling can be an effective, rapid, and humane means for removing large numbers of feral deer
352 (Bengsen et al. 2022; Husheer and Robertson 2005; Pulsford et al. 2023), feral pigs (Cox et al. 2022), and
353 other pest species in vast, remote, and inaccessible landscapes. Over the last three years, South
354 Australia's aerial culling programs have removed approximately 3,000 feral deer per year (BDO
355 EconSearch 2022). In addition to aerial culling, some programs have used ground shooting by
356 professional shooters, volunteers and landholders, and commercial harvesting operations (Government of
357 South Australia 2023b). Recreational hunting and culling by private landholders are estimated to remove
358 about 8,300 feral deer annually. With all control approaches combined, approximately 11,300 feral deer
359 are removed per year from South Australia (BDO EconSearch 2022).

360 Unfortunately, a large proportion of the population of feral deer must be removed each year to drive
361 population decline. For example, at least 34% of the population of fallow deer must be removed each year
362 just to avoid population increase, and even higher culling proportions are required for other deer species
363 (hog: 52%; chital: 49%; rusa: 46%; sambar: 40%) (Hone et al. 2010). The number of feral fallow deer
364 removed annually from the estimated population of 40,000 in South Australia is around 28% (BDO
365 EconSearch 2022), so the population has continued to grow.

366 Large-scale, intensive, and coordinated control programs are therefore necessary to drive population
367 declines of feral deer. Improved efficacy of aerial culling programs is clearly needed if management goals
368 to arrest the impacts of feral deer are to be realised. However, the adoption of new approaches and
369 technologies first requires examination to ensure high animal welfare standards are met, in addition to
370 operational cost effectiveness. Analysis of the outcomes from a recent trial program that used shotguns
371 and thermal equipment, in combination with a rifle, provided insight into the humaneness and
372 effectiveness of a new approach to controlling feral deer in South Australia.

374 Animal welfare

375 In pest control operations, welfare is generally evaluated in terms of the duration and intensity of
376 suffering (Littin et al. 2004), which inform humaneness assessments of control tools that are common
377 practice in Australian (Sharp & Saunders 2008) and New Zealand (Littin et al. 2004). We used 'time
378 between first shot with a shotgun and confirmed death' and 'pursuit time' as indicators of duration of
379 suffering and penetration and severity of shotgun pellets as indicators of intensity of suffering. The time
380 recorded by Cox et al. (2022) between first shot and confirmed death of deer using a rifle was 22 seconds;
381 Hampton et al. (2022) reported that 95% of deer were dead within 57 seconds of the first shot in their
382 program using rifles. In this trial, the average time between first shot with a shotgun and confirmed death
383 was 11 seconds, a markedly improved animal welfare outcome.

384 Individual deer, or the first deer shot in a group, had the longest mean time between first shot and
385 confirmed kill, and this interval decreased if targeting subsequent individuals in a group. This decrease is
386 because of the relatively longer time taken to pursue a group of deer after first being sighted, before the
387 first deer is shot. Once the group of deer was engaged, the pursuit time of the remaining deer in the group
388 was usually shorter. The maximum time recorded between first shot and a confirmed kill for any deer was
389 35.9 seconds, which is an improvement on programs that have used a rifle exclusively (Hampton et al.
390 2022).

391 Unlike Cox et al. (2022), our study assessed the metrics of a program that targeted deer with shotguns
392 in relatively open terrain. Shotguns have not been trialled in densely vegetated areas, and so additional
393 trials will be required to determine their efficacy in such terrain. Clearly, different vegetation densities
394 and terrain will affect the outcomes of aerial culling program. The dominant vegetation class of several
395 programs was ‘dry cropland’ (P1–P5, P8–P9), but only P1 also recorded this vegetation type as dominant
396 where deer were killed. Unlike the other programs, outcomes from P1 included a subset of the overall
397 program and selected for shotgun kills, which only occurred in open areas. We found similar proportions
398 of available and kill-location land cover classes in P3–P4 (i.e., including P1, each had 50–60% dry
399 cropland and deer were killed in 30–40% dry cropland; see S1), but the dominant land cover class where
400 deer were killed for most programs was woody native vegetation (i.e., P2–P9) that harbour deer in the
401 landscape.

402 Other influences such as proficiency of shooters, type of helicopter used, and weather conditions will
403 also affect time between first shot (with shotgun or rifle) and confirmed death. In their study, Cox et al.
404 (2022) measured the ‘time from first shot impact to death’, a potentially useful metric for assessing
405 shooter proficiency. We were unable to differentiate impact shots from non-impact shots because the
406 thermographer was not on the same side of the helicopter as the primary shooter with the shotgun. The
407 GoPro footage was not of sufficient quality to assess individual shot impacts. However, we were able to
408 assess overall pursuit time, and time between first shot and confirmed kill. Cox et al. (2022) and Hampton
409 et al. (2022) recorded pursuit times of around 150 seconds and 90–200 seconds, respectively. The average
410 pursuit time from 104 animals in our study was just 50 seconds, and the maximum pursuit time for any
411 individual was 159 seconds.

412 In most jurisdictions, procedures and guidelines for aerial culling programs of feral deer dictate that a
413 shot with a rifle is not taken until the shooter has a clear shot of the chest or head, and that there is no risk
414 of the a wounded animal escaping to somewhere where a follow-up shot cannot be taken. The spread
415 pattern of the shotgun pellets requires less precision for pellets to hit the thorax of the animal. Hence,
416 using a shotgun reduces the time required to ‘line up’ an accurate and humane shot.

417 In terms of the intensity of suffering, all animals assessed had received rapid and lethal impacts from
418 shotgun pellets. The average number of thorax-penetrating wounds delivered with the shotgun was higher

419 than in some autopsies of deer culled with a rifle (Hampton et al. 2022). All animals recorded lethal
420 damage to their lungs, and most to their hearts as well. Wounds to the lungs and the pooling and/or
421 clotting of blood in the chest cavity indicated a pneumothorax (collapse of lung) and/or a hemothorax
422 (collapse of lung because of blood in chest cavity). The wounds to the heart are expected to have caused
423 rapid decrease in blood pressure, rapid loss of consciousness, and rapid death by exsanguination. In
424 combination, these injuries lead to hypovolaemic shock, causing unconsciousness due to inadequate
425 cerebral perfusion pressure, and resultant rapid death from lack of blood supply to the brain (Stokke et al.
426 2018).

427 A potential shortcoming of our study is that the death of the target animals in P1 was confirmed in the
428 air by the pilot, and at least one other crew member, rather than landing the helicopter to have a
429 veterinary surgeon make a formal assessment (e.g., Hampton et al. 2022). Instead, a veterinary surgeon
430 (A.D.) and a medical doctor (J.D.) were available for consultation for our study. Future research into the
431 use of different firearms to cull deer could benefit from additional veterinary oversight, including work to
432 ensure that culled deer do not have spinal injuries, which could render the animal unresponsive, but alert
433 for some time. In addition, high-resolution photos taken from the helicopter could be used to compare the
434 exact location and position of culled deer with photos subsequently taken from the ground. These records
435 could be used to determine whether there were any signs of movement, distress, or disturbance of the
436 surrounding ground after each deer was killed from the helicopter.

437 **Cost effectiveness**

438 Helicopter-based aerial shooting is a cost-effective tool for feral deer control (Bengsen et al. 2022).
439 However, few studies have assessed the efficiency of different crew and equipment configurations. We
440 assessed a trial program (P1) that used the same pilots, aircraft, and thermal technology as Cox et al.
441 (2022) in their feral pig and deer control research. The main difference was the inclusion of a second
442 shooter armed with a shotgun; it is only the second time (after P5) a program has used a shotgun for
443 targeting feral deer in South Australia.

444 The largest expense associated with aerial culling is helicopter flight time (Bengsen et al. 2022),
445 largely driven by the cost of aviation fuel. The approximate \$2,500 cost hour⁻¹ of flight time for a B2/B3
446 Squirrel helicopter is nearly double that of the R44 (approximately \$1,000). As such, when using the
447 larger and more expensive helicopters in aerial culling of high-density deer populations, our results
448 indicate that efficiency is maximised by the addition of a thermographer and second shooter with a
449 shotgun. While cost per flight hour and area is relatively high for P1, the efficiency of the configuration
450 was unmatched (25 deer hour⁻¹ at < \$200 deer⁻¹). Crew configurations would be amended to suit program
451 objectives. For example, a second shooter or thermographer might not be necessary when targeting
452 exclusively open areas where deer densities are high. However, the additional crew members reported

454 other benefits, including (i) additional safety benefits because shooters had opportunities to take brief
455 breaks during each flight; (ii) shooters had the opportunity to change roles when a magazine needed to be
456 changed; (iii) shooters had the opportunity to alternate between using the shotgun and the rifle between
457 flights; (iv) the thermographer had more opportunity to monitor welfare outcomes of targeted animals
458 using the high-resolution thermal camera to confirm death and to locate wounded deer in forested areas;
459 and (v) the thermographer provided a strategic approach to targeting feral deer and enables searching and
460 scanning areas harbouring deer that might otherwise be missed. The flight crew also reported an increase
461 in the rate of detections of target animals because of the extra spotting capacity from an additional shooter
462 equipped with thermal optics (Rob Matthews, Heli Surveys, Jindabyne, New South Wales, pers. comm.).

463 Program costs and efficiency will vary with location and density of deer. For example, the cost of
464 targeting sambar deer at low densities in alpine environments exceeded \$1,000 deer⁻¹ (Pulsford et al.
465 2023). We compared 11 aerial culling programs that varied in location, planning, staffing, and logistic
466 requirements. P10 and P11 occurred in remotes areas with low deer densities. The goal of those programs
467 was to eradicate small satellite populations before they established. The relatively high costs of programs
468 in areas with low deer densities should not discourage land managers, particularly where eradication is
469 possible. Of the programs delivered in areas with high deer densities, program costs ballooned for peri-
470 urban programs because additional staff were required to restrict public access to popular recreation
471 areas. Programs should continue to document the inputs, configurations, and outcomes of their efforts to
472 inform future aerial culling programs of feral deer.

474 Conclusions

475 We found that the use of a suitable shotgun could improve welfare outcomes for culled deer, compared to
476 programs that used .308-calibre rifles only. Improved welfare outcomes included reduced pursuit time
477 and reduced time between the first shot and death. Furthermore, all deer dissected were shot more than
478 once, and received multiple thorax-penetrating wounds, resulting in lethal injuries to either the lungs
479 and/or heart, and ensuring a short time until death. These findings are at least as good as the best welfare
480 outcomes reported from aerial culling programs in Australia to date (e.g., Hampton et al. 2022).

481 We found that a two-shooter crew configuration, with the addition of a thermal camera operator and a
482 primary shooter with a shotgun, resulted in increased program operational efficiency and cost
483 effectiveness when compared to more conventional crew configurations. These changes to the format of
484 the aerial operation appeared to increase efficiency independently, but the addition of the shotgun appears
485 to have made the biggest single difference. These results are likely to be applicable to areas with similar
486 deer densities, canopy cover, and terrain to the Limestone Coast region of South Australia. Control
487 options that deliver improved animal welfare outcomes and increased efficiencies are urgently needed to
488 manage expanding populations of feral deer in South Australia.

489

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497 Research and Experimentation licence number is 176.

498

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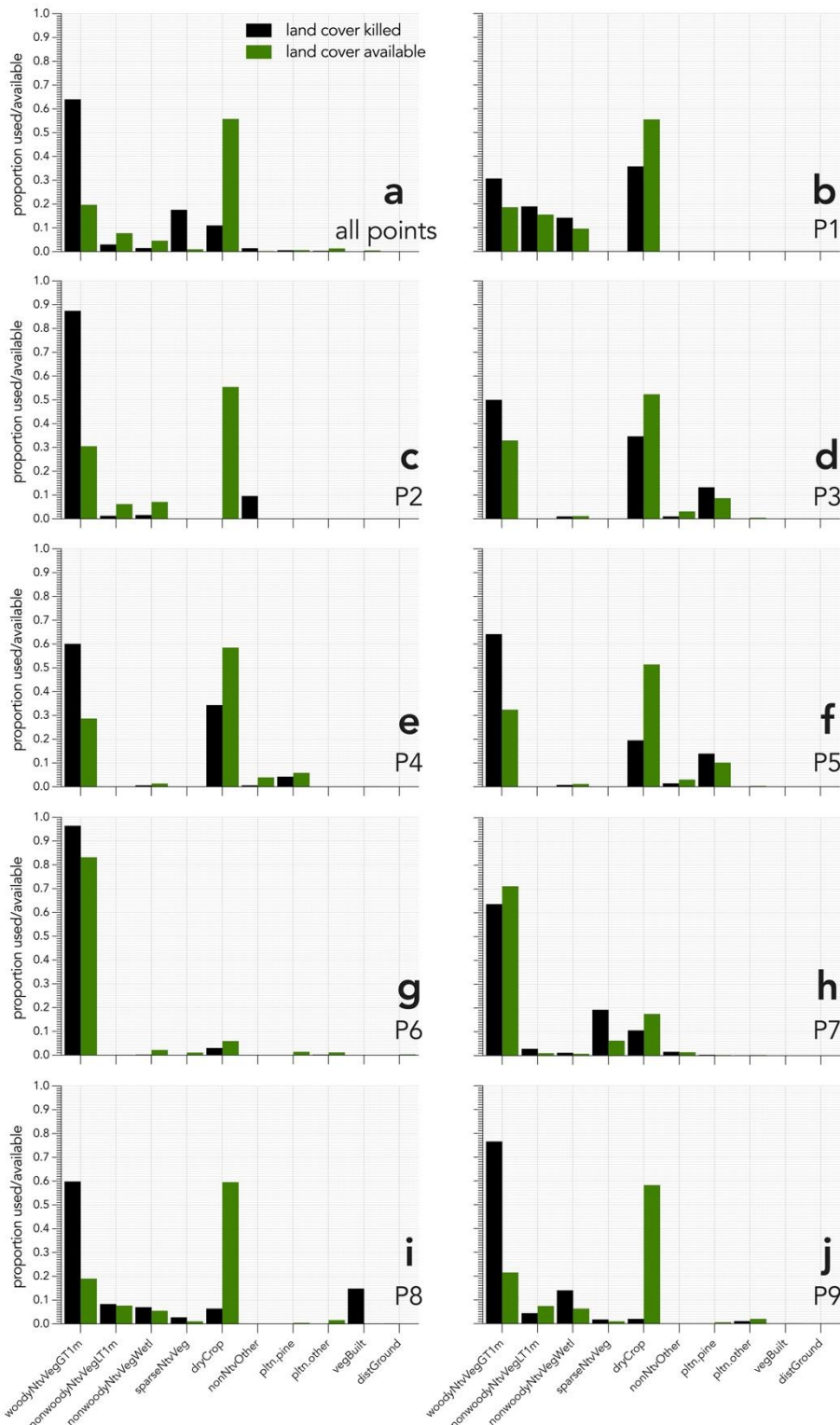
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Supplementary Information

Supplementary Figure S1. Proportion of deer killed per major land cover class (black bars) relative to availability (proportional coverage within a minimum convex polygon defined by the kill locations per program; green bars) for (a) all kill locations combined and (b–j) P1–P9. Data for P10 and P11 not shown (kill locations unavailable for P10, and no deer shot in P11). Most-common land cover classes in which deer were killed given in Table 5.



Land cover classes shown: **woodyNtvVegGT1m** = woody native vegetation > 1 m height; **nonwoodyNtvVegLT1m** = non-woody native vegetation < 1 m height; **nonwoodyNtvVegWell** = non-woody native vegetation associated with wetlands; **sparseNtvVeg** = sparse native vegetation; **dryCrop** = dryland crops; **nonNtvOther** = non-native vegetation not otherwise classified; **pltn.pine** = pine-dominated plantation; **pltn.other** = plantation dominated by other species; **vegBuilt** = combination of vegetation and built-up areas; **distGround** = disturbed ground.

Supplementary Figure S2. Mean human population density within 50 km of the minimum convex polygon defined from kill locations per program (top panel). Bottom two panels show personnel costs, and personnel costs/flight time/animal, as a function of the mean population densities, respectively. See also Tables 4 and 5.

