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RESEARCH

Use of genetic mark-recapture to assess the efficacy of thermal aerial control in reducing deer density in mountainous forest

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Abstract: Invasive deer species pose significant ecological threats to New Zealand's indigenous forests. This study evaluated the effectiveness of a helicopter-based hunting technique, Thermal Aerial Control (TAC), in reducing red deer (*Cervus elaphus*) density in mountainous forest in Fiordland, New Zealand. Using DNA-based mark-recapture methods, the pre-control deer population was estimated at 79 deer (68–92, 95% CI). The TAC operation killed 60 deer over eight sorties totalling 10.65 hours, reducing density by 76% from 5.6 deer per km^2 to 1.3 deer per km^2, a level expected to allow regeneration of most deer-palatable plant species if maintained. Thermal Aerial Control detected ≥ 73% of deer within the catchment, of which 91% were shot. Analysis of habitat variables at kill sites showed deer were more likely to be detected and shot on steeper slopes (> 23°). Compared to ground-based hunting assisted by dogs in similar Fiordland forests nearby, TAC was more cost-effective at low deer densities, averaging NZ$595 per kill versus NZ$1428 for ground-based methods. These findings demonstrate that TAC, in the habitat evaluated, is a highly efficient tool for rapidly reducing forest-dwelling deer populations to levels that support conservation outcomes, with potential applicability across similar forest types and terrain throughout New Zealand.

Introduction

Historically, deer have been translocated far beyond their native ranges, mostly for hunting purposes (Nugent et al. 2025). However, conservationists in Australasia (Australia and New Zealand) now typically regard non-native deer as pests because of their unwanted effects on the native biota (Department of Conservation 2001; National Feral Deer Action Plan Working Group 2023). In New Zealand, deer browsing severely impacts regenerative processes, both in native forests and alpine grasslands (Coomes et al. 2003; Forsyth et al. 2010a; Latham & Nugent 2017; Wood & Wilmshurst 2019). Consequently, New Zealand has, since 1930, attempted to reduce the unwanted impacts of deer, but arguably with only modest success (Caughley 1983; Ramsey et al. 2018). However, from c. 1960, intensive commercial hunting (particularly using helicopters) resulted in major reductions in deer abundance (Challies 1991). Unfortunately, the economic viability of commercial hunting has waned in recent decades (Lawless et al. 2023) and deer abundance on public conservation land (PCL) has increased (Moloney et al. 2021). At the same time, governmental conservation spending has increasingly focussed on control or elimination of introduced mammalian predators, leaving limited resources for deer control (Leathwick & Byrom 2023). Despite increased funding for deer control in 2022 (New Zealand Treasury 2022), there remains an urgent and ongoing need to improve the efficiency of deer population control, particularly in the forests and shrublands that comprise 69% of PCL (Manaaki Whenua–Landcare Research 2020).

Deer control in New Zealand mainly involves helicopter-based (aerial) or ground-based hunting. Aerial hunting is highly effective in unforested areas, but far less effective in heavily forested areas (Nugent et al. 1987). Ground-based hunting is therefore used for deer control in forests but is expensive and more logistically difficult to deploy (GL, unpubl. data) and does not always deliver desired outcomes (Ramsey et al. 2018). The limited success of ground-based hunting has prompted efforts to increase the efficacy (the percentage of deer present that were killed) of aerial hunting by using thermal imagers to increase deer detection rates. From c. 2015, civilian grade thermal imagers were being trialled by commercial deer recovery operators in unforested habitats in New Zealand. These enabled operators to scan more terrain in less time with a high detection probability. In forested areas, however, deer were still often obscured by the canopy, resulting in few detections and limited ability to track detected animals. Higher resolution imagers have subsequently become available, improving in-forest detectability by capturing finer detail and enhancing the

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contrast of heat signatures from partially obscured animals. Following successful proof-of-concept trials in New Zealand during 2017 (N. MacDonald (deceased), DOC, unpubl. data), several teams are now operating across Australasia in a variety of landscape and vegetation types, targeting a range of species. This includes its successful use during aerial hunting of fallow deer (*Dama dama*) and feral pigs (*Sus scrofa*) in Australia (Cox et al. 2023), which is the only peer-reviewed study documenting the use of TAC to date. However, the efficacy and cost-effectiveness of TAC has not yet been quantified in terms of the actual reductions in deer density.

This study was undertaken to quantify the cost-effectiveness (NZ$ per kill) and efficacy of TAC in reducing the density of red deer (*Cervus elaphus*) in a densely forested mountainous catchment in Fiordland National Park (FNP), New Zealand. The TAC trial was conducted in June 2023. We used DNA-based mark-recapture to estimate deer population size (and therefore density) at the time of the trial and compared that to the number of deer killed in the trial. We also assessed the effects of habitat variables on deer kill probability and identified which metrics provided the best insight into TAC effectiveness. Lastly, we assessed the cost-effectiveness of TAC by comparing the cost per kill to similar historical data for conventional ground-based control.

Methods

Study area

Our study area was part of a 518 km^2 area (the Murchison Mountains) within FNP in which deer have been intensively controlled (using ground and conventional aerial hunting) since the 1960s to help protect takahē (*Porphyrio hochstetterii*), a threatened native bird species. That ongoing control programme reduced deer density from 8.7 deer per km^2 in 1964 to 1.1 deer per km^2 in 2008 (Tanentzap et al. 2009), and provides insight into the hunting effort and expenditure required to maintain the low deer densities (c. 1 deer per km^2) considered necessary to permit regeneration of deer-preferred plant species (Tanentzap et al. 2009).

Our overall 28 km^2 study area included forest and alpine grassland habitats comprising much of the upper Snag Burn Valley, a steep U-shaped glaciated valley ranging from c. 400–1400 m a.s.l. (Fig. 1). The TAC trial was conducted within a 14.2 km^2 treatment area of dense southern beech forest (*Lophozonia menziesii* and *Fuscospora cliffortioides*) spanning c. 400–1000 m a.s.l. Mean canopy cover (foliage and stems > 1.35 m above ground), derived from thirteen 20 × 20 m forest assessment plots (Hurst & Allen 2007) located in or

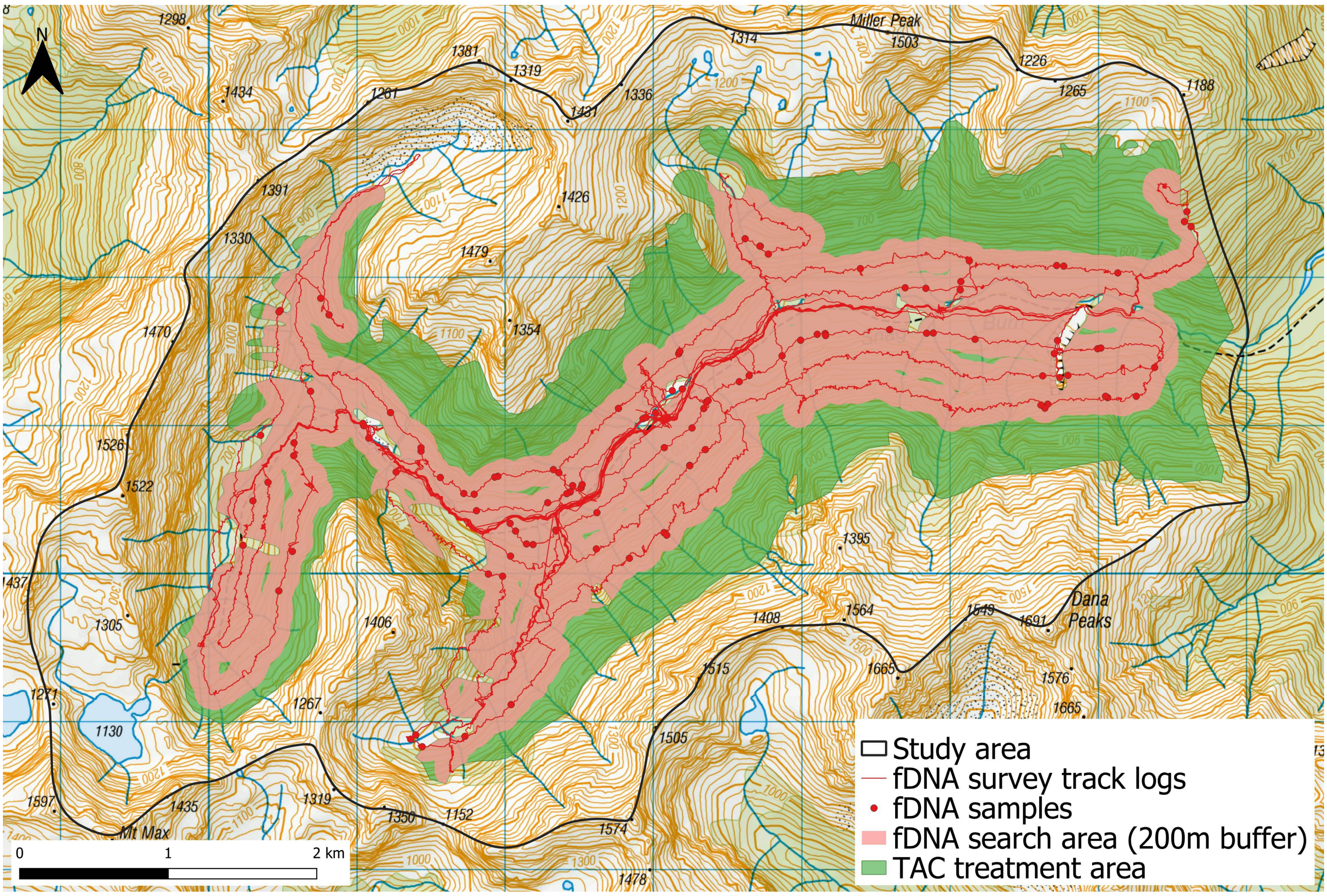

Figure 1. Map of the treatment area displaying tracklogs from the faecal DNA survey. Red points are individual faecal DNA (fDNA) sample collection locations. Pink areas represent the effective area searched in the fDNA survey (tracklogs buffered by 100 m either side of the track) clipped to the forested Thermal Aerial Control (TAC) treatment area (green). Intensive tracking of the main valley floor was due to the repeated use of the main valley track to access transects. Basemap: NZ Topo50 Basemap (LINZ Data Service. https://data.linz.govt.nz; accessed 29 July 2025).

near the study area was 65%. The terrain and forest type are broadly representative of the southern beech forest associations that comprise about half of New Zealand's indigenous forests (Schindler et al. 2021). No other ungulates were present other than the occasional chamois (*Rupicapra rupicapra*).

The catchment was selected because there are extensive unforested alpine areas between the Snag Burn and adjoining catchments, which allows easy detection and killing of most deer utilising such areas. Deer avoid areas of high aerial hunting pressure (Latham et al. 2018), so we attempted to establish a 'landscape of fear' (Proudman et al. 2020) by aerially hunting deer in the alpine buffer control areas surrounding the forested parts of the catchment on three dates (14th and 24th March, and 9th May 2023) before the TAC trial. A handheld thermal imaging monocular was used to help detect deer. In total, 24 deer were killed, all of them on the first day. We believe that this will have greatly reduced the immigration or emigration of deer from the forest in the study area, effectively creating a largely closed deer population in the forested treatment area.

Thermal Aerial Control (TAC) trial

The TAC trial was conducted in early winter 2023. Due to budget limitations, the intent was to remove as many deer as possible over 10 hours of TAC or to cease operations if > 60 minutes was flown with no deer detections. Five aerial hunts (sorties) of 84–105 min were conducted in the first three days (7–9 June), another on 27 June (100 min), and two more on 29 June (41 and 19 min respectively). No deer were detected during the last 82 cumulative minutes across the final three sorties, so the trial was terminated. Weather conditions were clear and windless with air temperatures ranging between 0–7 °C (NIWA 2024). Sorties were flown in the mornings and/or evenings to minimise non-target thermal interference. Quoted search speeds from the four suppliers engaged in the procurement process ranged from approximately 40–80 km h^{-1}. We aimed to complete multiple fast (> 60 km h^{-1}) search speed) sweeps of most of the treatment area, assuming that the fast sweeps were likely to result in more detections of deer than slower intensive sweeps because briefly stationary but obscured deer were likely to be missed regardless of helicopter speed. Full technical details of equipment and crew configuration used in buffer and TAC control flights are summarised in Appendix S1 in the Supplementary Material. The time and location of each deer shot was recorded, along with the flight tracklog, using a GPSMAP 64s (Garmin, Olathe, USA) Global Positioning System.

Deer population size

Overview

Deer population size was estimated using two genetic (DNA-based) mark-recapture methods. Our primary approach used the capwire method (Miller et al. 2005; Pennell et al. 2013) and involved a single five-day field survey in mid-February 2023 in which faecal pellet material was located and collected (described in detail below). Faecal DNA (hereafter fDNA) genotypes were later obtained from the samples. The number of times each unique genotype was identified in the set of samples was used to estimate the number of deer present in the surveyed area. The second, corroborative, method used a classical Lincoln-Petersen mark-recapture approach in which the fDNA genotypes above were used to represent marked deer. Tissue-based DNA (tDNA) from a subsample of the deer shot during the TAC trial in June 2023 was then used to determine the number of fDNA genotypes that were recaptured during the TAC trial. The Chapman mark-recapture estimator (Chapman 1954) for sampling without replacement from closed populations was then used to estimate the pre-trial population size.

fDNA survey and genotyping

The fDNA survey involved the location and swabbing of freshly deposited faecal material and subsequent extraction and genotyping of DNA from that material. Methods are described briefly here and in more detail in Appendix S2. Success in obtaining genotypes from faecal pellets declines quickly after exposure to sunlight and/or rainfall (Woodruff et al. 2015; Agetsuma-Yanagihara et al. 2017), so we collected pellets during a fine weather window with little precipitation in the preceding five days. Unfortunately, forecast rain on the sixth day (when only 59% of the area had been sampled) halted further sampling.

The faecal pellet survey was conducted along transects spaced about 200 m apart (as per MacDonald 2019; Ebert et al. 2021). In total, 109 groups of pellets were located and swabbed. DNA was later extracted from the fDNA swabs and profiled by amplification of ten microsatellite markers. A final fDNA profile for each sample was recorded where alleles were observed at each marker in at least two or more replicate profiles. Profiles were grouped based on genotype similarity per marker with each identical grouping designated an individual deer. The "capwire" package in R (R Core Team 2025) was used to analyse these data using a maximum likelihood based approach specifically designed for genomic data. As an urn (random sampling) model, it uses counts of detections within a single survey as a proxy for the number of times each identified deer was captured within that survey (Miller et al. 2005). Based on a likelihood ratio test, we used an equal catchability model (ECM) (Appendix S2).

To obtain a whole-of-forest population size from the fDNA survey, we calculated a deer density for the surveyed area (8.4 km^2) and then assumed that deer density was the same across the entire forest treatment area (14.2 km^2) (see Discussion).

fDNA-tDNA mark-recapture

To obtain tDNA samples, ground staff searched for 50 of the deer shot in the first three days of the trial. Of those, 49 were successfully relocated and a sample of ear tissue was collected. Each relocated deer was successfully genotyped, using the same methods as for fDNA (Appendix S2).

In addition to deer shot during the TAC trial, tDNA samples were also collected, and successfully genotyped, from 12 of the 24 deer shot on 14 March 2023 during the pre-trial buffer control operation. This enabled us to estimate the number of deer likely to have been removed from the population before TAC commenced and was accounted for in our pre-control population estimate.

The proportion of tDNA genotypes that matched fDNA genotypes was then determined. Using the fDNA genotypes as marks, and the tDNA genotypes as recaptures of those marks, we used the Chapman mark-recapture estimator (Chapman 1954) to estimate population size. This method has recently been shown to statistically outperform all other two-survey methods and reduces bias when sample sizes are small (Dettloff 2023). To assess the uncertainty of the estimate and generate confidence intervals, we applied non-parametric bootstrapping with 10 000 resamples using the R package "recapr" (Tyres 2021).

Analyses

To assess whether deer were more likely to be killed in some habitat types than in others, a use-availability design was employed. Habitat variables from the location of the kill sites were compared to an equivalent number (60) of random locations within the search area using logistic regression, which provided relative measures of habitat selection (Boyce et al. 2002). The habitat variables were extracted from the New Zealand Environmental Data Stack (McCarthy et al. 2021) and the New Zealand Land Cover Database v.5.0 (Manaaki Whenua–Landcare Research 2020) and processed in QGIS 3.28.2. There were four habitat types represented (indigenous forest, tall tussock grassland, sub-alpine shrubland, and landslide), but no kills occurred within landslide areas, so this category was merged with sub-alpine shrubland to prevent separation in the modelling. The logistic regression model (using a generalised linear model (GLM) with a binomial distribution and logit link) included a response variable representing location type (deer kill = 1, random point = 0) and explanatory variables describing the habitat at each location: aspect, elevation, slope, solar radiation, shortest distance to grassy areas, and vegetation type. The continuous variables (all but vegetation type) were scaled to a mean of zero and standard deviation of one. There were a relatively large number of variables compared to the number of observations, with an events-per-variable value of 8.6, which is below the recommended 10–15 for logistic regression (Heinze et al. 2018). For this reason, models were fitted using both standard maximum likelihood logistic regression (with function *glm* in R package "stats"; R Core Team 2025) and Firth penalised logistic regression (with function *logistf* in package "logistf"; Heinze et al. 2025), and the results compared. Model performance was checked graphically (R Core Team 2025). Habitat variables were considered to have a significant effect on kill probability if the 95% confidence interval of their coefficient did not intersect zero.

To assess how TAC kill rates varied with density, the number of deer present at the start of each sortie was calculated using what we considered our best point estimate of initial population size and then progressively subtracting the number of deer killed in each subsequent sortie. The percentage of the sortie-start populations killed per hour within each sortie was then calculated. We also compared the cost of control, in New Zealand dollars (NZ$ per deer), with density. A linear regression was fitted between each of these response variables using the *lm* function in the R package "stats" (R Core Team 2025), with deer density as the explanatory variable. Model validation was conducted by graphical assessment of independence, homogeneity of variance, and normality of residuals.

Other performance metrics were calculated for each sortie and overall, based on distance flown during aerial hunts (km), time flown (minutes) and area searched (km^2) within the survey area. Distance and time spent actively searching for and shooting deer were calculated from all tracklogs within 1 km of the treatment area. Effective area searched was calculated per flight by buffering the right-hand side (the camera side) of the tracklogs by 500 m, assuming a maximum effective detection distance of 500 m, and flattening these to a single layer. Spatial analyses of flight tracklogs to support calculations of catch per unit of effort were completed using QGIS 3.28.2.

The cost-effectiveness (cost per kill) achieved in the TAC trial was compared to that achieved using dog-assisted ground-based hunting, which has long been used for deer control in forested areas of the Murchison Mountains. For this comparison, we used the TAC cost per kill achieved in the last successful (6th) sortie, when we estimate deer densities had been reduced to 1–2 deer per km^2. For ground-based hunting we used data from the 2008–2010 period (N. MacDonald (deceased), DOC, unpubl. data) when forest deer density was assessed at c. 1.2 deer per km^2 (Tanentzap et al. 2009) and ground-based hunters achieved a kill rate of 0.56 deer per day. We assumed an average TAC cost of $2500 per hour from the mean hourly full-service contract rate provided by the panel of four suppliers evaluated during the pre-trial procurement process. This contract rate included wet helicopter hire (including ferry time), shooter, firearm and ammunition, camera operator and equipment, and other supplementary expenses incurred by the operator. We used 2024 contractor rates for ground-based hunters ($800 per day) (GL, unpubl. data).

Results

Population size

Within the area searched (Fig. 1), transect coverage (a proxy for search effort for faecal pellets) was biased towards lower elevation and gentle slopes, with 95% of transect coverage on slopes < 50°, which comprised 82% of the treatment area (11.7 km^2). Only 5% transect coverage was achieved on slopes > 50° (2.6 km^2). The percentage of pellets found in each slope class was moderately positively correlated with the percentage of the slope class searched ($y = 0.62x + 0.048$; $R^2 = 0.41$), but with < 15% variation between the percentage searched and the percentage of available habitat in that slope class, indicating a relatively even distribution across slope classes searched.

From the 109 faecal samples collected (Fig. 1), 103 fDNA profiles were obtained, collectively representing 42 unique genotype groupings. Excluding genotype groupings with only tentative sex test results, at least 20 were estimated to be female and 18 estimated to be male. Assuming equal catchability (given the non-significant test for unequal catchability; Appendix S2), a combined-sex ECM capwire model produced a population size estimate of 49 deer (42–53, 95% CI) within the fDNA survey area that comprised c. 59% of the forest treatment area. Assuming densities were similar in the treatment area that was not surveyed, this extrapolates to an estimate of c. 83 (71–95, 95% CI) deer present in the treatment area when the fDNA survey was undertaken. However, 16.7% (2/12) of the tDNA genotypes obtained from 24 buffer control deer shot in March 2023 had tDNA profiles that matched an fDNA genotype grouping. This result indicated that 4.0 (2–6, 95% binomial CI) deer were likely to have been removed from the population before TAC commenced in June 2023. We therefore assumed that approximately 79 deer (68–92, 95% CI) were present at the start of the TAC trial in June.

The Chapman estimator produced a population size estimate of 92 deer (68–129, 95% CI) prior to TAC commencing.

TAC trial

A total of 10.65 hours were flown within the study area, with a total of 676 km flown. Search effort was similar across the treatment area, with 88–94% of the forested treatment area searched in each of the first seven sorties (Table 1). The whole treatment area was searched at least once, with 90% searched at least six times and just 1.2% searched less than three times.

Table 1. Summary of the Thermal Aerial Control (TAC) trial by sortie, showing hunting effort (minutes flown, distance flown, kilometres flown per km^2, and percentage of treatment area searched), hunting outcomes (kills, kills per hour and per kilometre flown, and percentage of remaining population removed) and cost per kill.

Sortie #	Date AM/PM	Minutes flown (min)	Mean ground speed (km h^{-1})	Distance flown (km)	Search effort (km km^{-2})	Area searched (%)	Deer killed	Kill rate (deer per h)	Kill rate (deer per km)	% of remaining deer killed	NZ$ per kill
1	07/06/2023 AM	105	46.3	81	6	90.0	21	12.0	0.26	27	$208
2	08/06/2023 AM	84	72.9	102	8	93.0	10	7.1	0.10	17	$350
3	08/06/2023 PM	88	71.6	105	8	94.0	3	2.1	0.03	6	$1222
4	09/06/2023 AM	96	61.9	99	7	94.0	7	4.4	0.07	16	$571
5	09/06/2023 PM	106	50.4	89	7	88.0	12	6.8	0.13	32	$368
6	27/06/2023 PM	100	64.8	108	9	89.0	7	4.2	0.06	27	$595
7	29/06/2023 AM	41	92.2	63	5	89.0	0	0.0	0.00	0	-
8	29/06/2023 PM	19	91.6	29	4	57.0	0	0.0	0.00	0	-
All	-	639	69.0	676	7	86.8	60	5.6	0.09	-	-

Average flight speeds ranged from 46 km h^{-1} in the first sortie to 92 km h^{-1} in the sixth, with an overall average of 69.0 km h^{-1} (Table 1). Mean height above ground level across all flights was 198 m (156–240, 95% CI).

Active hunting time in the first six sorties ranged from 80 to 110 minutes, but lasted just 41 and 19 minutes in the last two sorties (Table 1). The last two sorties were terminated early because no deer were detected. In total, 66 deer were detected and 60 deer (91%) were shot, 58 within the designated treatment area, and two more in forest within 200 m of that area (Fig. 2). The latter two deer are included as we assume their home ranges substantially overlapped the treatment area, given that the median distance between pairs of pellet groups with the same fDNA profiles was 776 metres. The last deer was killed after 9.28 hours of flying. A further 1.37 hours were flown with no deer killed or detected (Fig. 3).

Of the six deer detected but not shot (three each in the first two sorties), some may have been shot in subsequent sorties. However, the second to last deer detected (in the 6th sortie) escaped, so at least one detected deer remained after the trial.

The regression models relating habitat variables to deer kills produced similar coefficients when using standard maximum likelihood and Firth-penalised logistic regression. This suggested that the maximum likelihood model was not overfitting, so these results were used for interpretation. They showed that deer were significantly more likely to have been shot at locations with steeper slopes (range 24–57°) than at randomly selected locations (Fig. 4). None of the other habitat variables of kill sites differed significantly in relation to the randomly selected locations.

Hunting efficiency and efficacy

Kill efficiency (kills per detection) was high, with 91% (81–97%, 95% CI) of the 66 deer detections resulting in kills (60 in total). Kill efficiency did not decline over the trial, with three of the 34 deer detections in the first three sorties and three of the 32 in the next three sorties resulting in escapes.

Kill rate (kills per hour) was high (9.8 deer per hour) for the first two sorties and then much lower in the next two sorties (3.2 deer per hour), but higher again in sorties 5 and 6 (5.6 deer per hour), before reaching zero for the last two sorties (Table 1; Fig. 3). Linear regression indicated a significant positive relationship between kill rate and density (Fig. 5a; $t = 4.21$, $p = 0.006$), with a zero-kill rate predicted at a deer density of c. 1.0 deer per km^2.

Efficacy appeared to have been high. Using our pre-TAC (early June) fDNA mid-point estimate of population size in the treatment area (79 deer, 5.6 deer per km^2), killing 60 of those represents an efficacy of 76% in reducing deer to 1.3 deer per km^2. Again, assuming a pre-TAC population of 79, efficacy per sortie (represented by the percentage of the population killed per hour within each sortie; Fig. 5b) varied widely and was not significantly correlated with density ($t = -0.20$, $p = 0.85$).

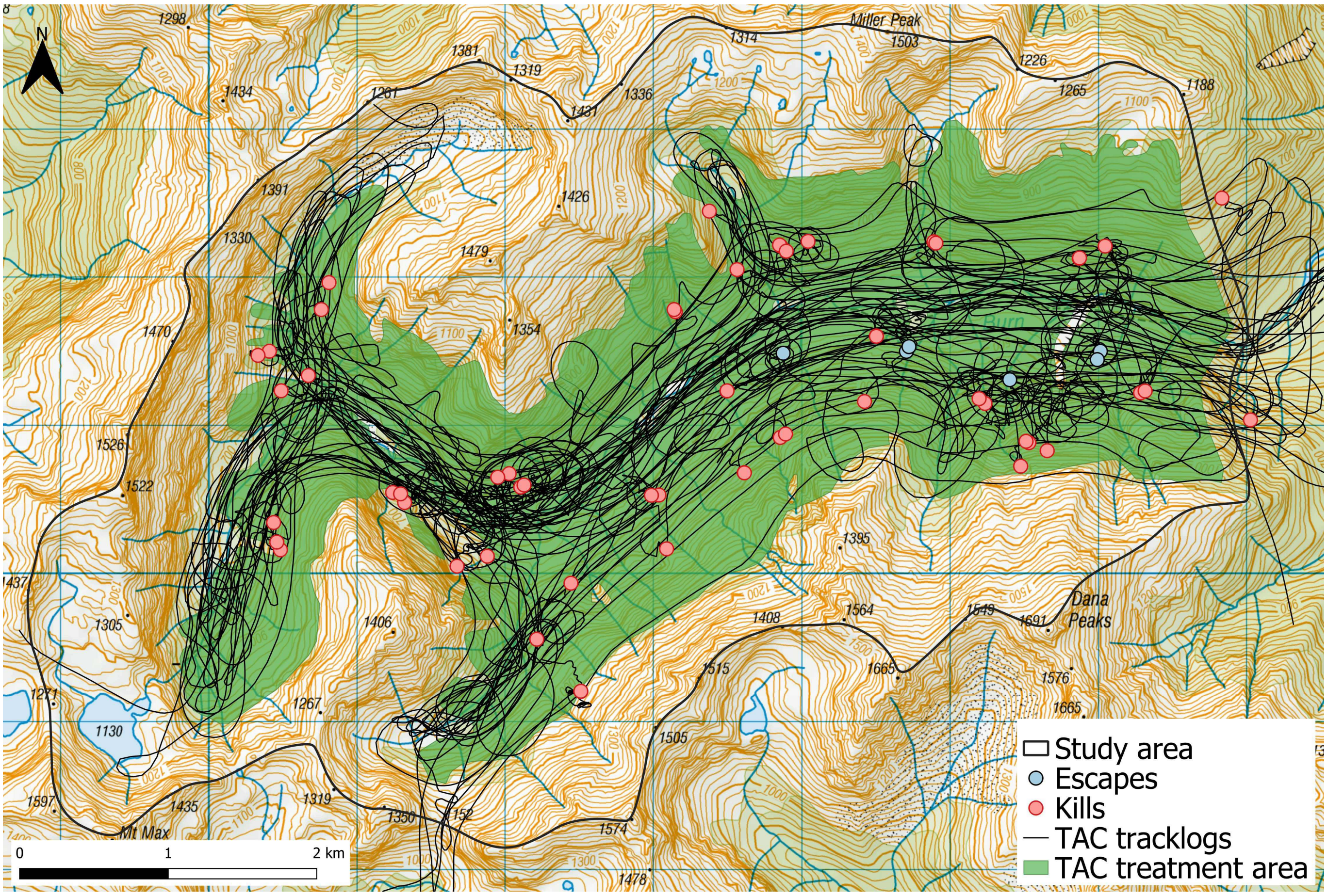

Figure 2. Map of the study area showing all Thermal Aerial Control (TAC) tracklogs from eight sorties (light black lines). The red circles show the locations of confirmed deer kills and blue circles where deer were detected but not shot (escapes). Basemap: NZ Topo50 Basemap (LINZ Data Service. https://data.linz.govt.nz; accessed 29 July 2025).

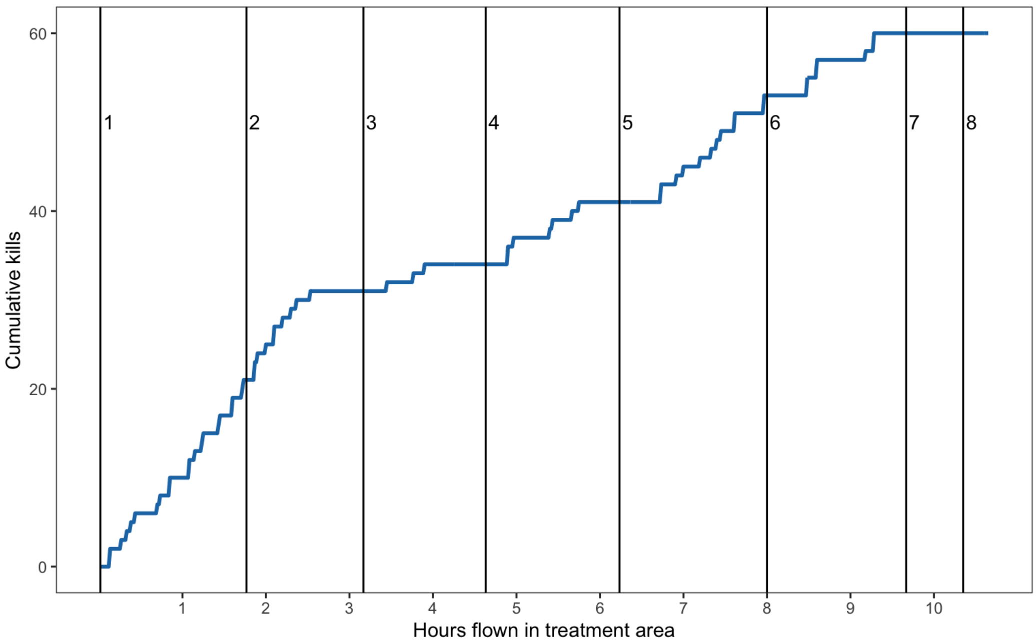

Figure 3. Cumulative deer kills through time flown within the treatment area. Vertical lines represent the start of each sortie flown.

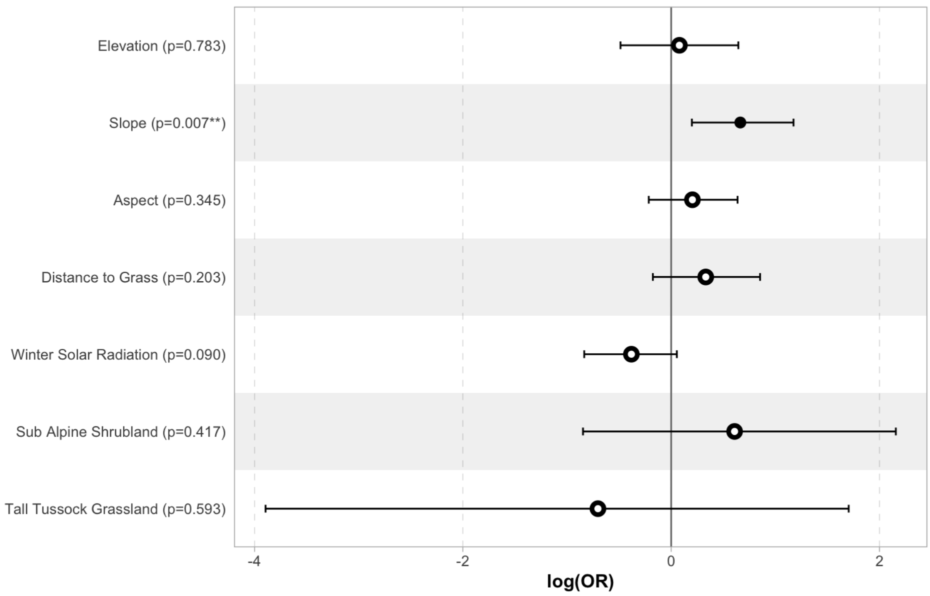

Figure 4. Coefficients of the (maximum likelihood) logistic regressions comparing habitat variables at 60 deer kill locations and 60 randomly selected locations. The vegetation coefficients are relative to the reference vegetation category of indigenous forest, which is not shown. Significant terms with a p-value below 0.05 are shown as filled circles and non-significant terms as open circles.

Cost effectiveness

The total hunting-time cost of the TAC trial was $26,582 ($18.70 per ha, $444 per deer). The total cost to kill 60 deer was $23,166 ($16.30 per ha, $386 per deer), with a further $3,416 spent with no additional deer killed. Given the wide variation in kill rates between sorties, costs per kill also varied widely. Our linear regression model identified no significant effect of deer density on the sortie-specific cost per kill (Fig. 5c; $t = -0.78$, $p = 0.48$). However, we note that the operational hunting-time cost per deer for the first five deer killed averaged $208 compared to $595 for the last seven.

Using kill rates achieved by ground-based hunting in the Murchison Mountains in 2008–2010 (when deer densities were c.1.2 deer per km^2) and 2024 ground-hunter costs, we estimate a cost per kill of $1,428 per ground-shot deer.

Discussion

This trial provides the first quantitative analysis of the efficiency, efficacy, and cost-effectiveness of TAC in a remote, heavily forested and mountainous landscape. To our knowledge, it also documents the first Australasian use of DNA-based mark-recapture methods to estimate deer density. As such, it provides managers with two new tools for managing and measuring deer densities.

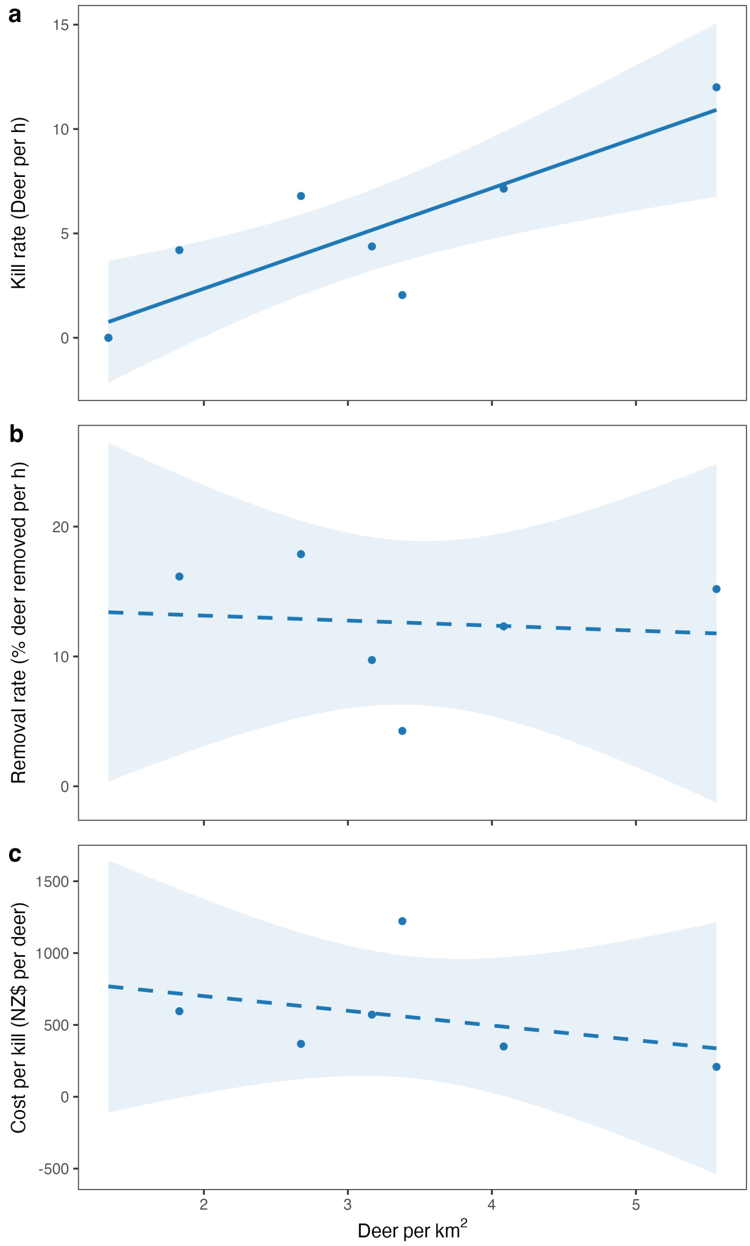

Figure 5. Relationship between deer density (deer per km^2) and (a) kill rate (deer per h), (b) removal rate (% deer removed per h) and (c) cost per kill (NZ$ per deer). Linear regressions were significant for (a) ($t = 4.21$, $p = 0.006$), but not for (b) ($t = -0.20$, $p = 0.85$), and (c) ($t = -0.78$, $p = 0.48$). Data points represent the mean value per sortie. Lines show linear regressions with regression significance indicated by line type (solid line if $p \leq 0.05$; dashed line if $p > 0.05$) and 95% confidence intervals by shaded areas.

DNA-based mark-recapture

The lack of accurate, affordable and real time tools for estimating the population size and density of forest-dwelling deer has long been a major constraint on the ability of managers to quickly and accurately assess the impact of management actions, both globally (Wäber & Dolman 2015) and in New Zealand (Forsyth et al. 2022).

The application of DNA-based mark-recapture methods in this study demonstrates how managers and researchers can credibly estimate actual animal densities in forested areas where alternative methods are typically prohibitively difficult and expensive to deploy (e.g. satellite collars), or imprecise (faecal pellet counts) (Forsyth et al. 2022). We chose a single-survey fDNA method primarily because the single-survey approach is logistically simpler, more affordable, and less likely to be adversely affected by poor weather than a dual survey approach. One limitation of the capwire method is that it may not be appropriate for rare, wide-ranging species (Lonsinger et al. 2019) or large populations (*n* > 100; Miller et al. 2005). However, Miller et al. (2005) demonstrated that for small populations of 49–100 animals, with 2.0–2.5 observations per individual, their model provided estimates within 10–15% of the true population. As we collected 2.3 fDNA samples per genotype, and our sample size was within the optimal range, we consider the population was adequately sampled to generate reliable model outputs.

The main sampling limitation in this survey was our failure to sample the full extent of forest habitat. Our subsequent extrapolation from the fDNA survey area to the whole forest could therefore be biased if deer densities were markedly different in unsurveyed higher elevation forest areas. However, the median distance between all pairings of faecal samples was 776 m, suggesting deer in the treatment area had home ranges that extended into the survey area and were therefore available for detection. Additionally, the majority of the 41% of unsurveyed forest was in steeper valley side and upland areas, which are less preferred forest habitat types for deer (Stewart & Harrison 1987). Historical faecal count surveys in the Snag Burn (Fraser & Nugent 2003) showed markedly reduced faecal pellet abundance in these areas (zero in slopes > 50°, which constitute 18% of the treatment area; Nugent & Sweetapple 1989). Thus, we consider that these potential biases are much more likely to have resulted in over- rather than under-estimation of overall population size.

Our supplementary two-survey fDNA-tDNA estimate of 92 deer was encompassed by the 95% CI for the single-survey fDNA estimate. However, the 5-month period between fDNA marking and tDNA recapture encompassed a change in seasons (summer to winter) with the rutting season in between. Red deer can migrate between separate summer and winter ranges (e.g. Luccarini et al. 2006), and males often move to rutting ranges separate from their summer or winter ranges (e.g. Jarnemo 2008). Any emigration would have reduced the number of marked individuals available to be recaptured during the TAC trial, while immigration would conversely have increased the number of unmarked individuals available to be shot. Both would result in overestimation of population size by the 2-survey fDNA-tDNA estimate. Thus, while the fDNA-tDNA estimate provides broad support for the single-survey fDNA estimate, it is more susceptible to positive bias and should therefore be interpreted with greater caution. The implicit assumption is that deer numbers remained unchanged between the fDNA survey and the TAC trial, with any emigration likely to be offset to some degree by immigration. This is supported by the apparent lack of deer emigration into the alpine zone from the surrounding forest, as the second and third buffer control sorties (approximately four weeks apart) detected no deer. Nonetheless, the matching of two tDNA genotypes from deer killed in the initial buffer control operation indicated at least some deer had large home ranges. Previous studies indicate that red deer tend to retreat from alpine areas in late summer and autumn (Zweifel-Schielly et al. 2009; Forsyth et al. 2010b; Zhang et al. 2013). Our early and apparently successful removal of most deer from the alpine zone seems likely to have minimised immigration into the treatment area between the fDNA survey and commencement of TAC.

Together, the evidence from model performance, sampling coverage, deer spatial occupancy, and the independent fDNA-tDNA estimate suggests that the pre-TAC population estimate of 79 deer provides a robust and credible representation of deer abundance within the treatment area at the commencement of TAC operations.

High TAC efficacy

The TAC trial demonstrated conclusively that high grade thermal imaging provided helicopter-based hunters with the ability to detect and kill a high proportion of deer in mostly full-canopied beech forest habitat. Two factors contributed to the high efficacy: an increased ability to detect deer and an increased ability to kill the deer detected.

Using the extrapolated 95% CI of the fDNA density estimate, 67–92 deer were present. If each of the six escapees were detected only once, this suggests that 73–98% of the deer present were detected. That compares with the detection probability of just 19% estimated for radio-collared female sika deer (*Cervus nippon*) in the conventional aerial control of deer in beech forest in the central North Island (Latham et al. 2018). It is unlikely that the difference is due to much higher and/or denser canopy cover in those beech forests as many vegetation plots had low tree basal area (Husheer & Tanentzap 2024). It also seems unlikely that the smaller sika deer body size could result in a > 50% reduction in detection probability. In Australia, at low deer density sites, detections of single deer without thermal assistance were 42% fewer than those detected with thermal viewers (Gentle et al. 2026) and on Wild Duck Island TAC took approximately 28 minutes to detect and remove the last deer after 7.6 h of conventional aerial shooting had failed to detect it (Amos et al. 2026). Together, these findings support practitioner views that thermal sensors greatly enhance deer detection at low densities in forested habitats.

The high detection rate could reflect disproportionately high detectability in those forest habitats preferred by deer. However, deer kill sites were not biased towards warmer parts of the landscape or non-forested areas considered to be preferred habitat (Fig. 4). As already noted, the only significant positive predictor of where deer were killed was slope. We therefore hypothesise that deer on steeper slopes are more easily detected in steeper terrain simply because camera penetration angles are more oblique, as suggested by Latham et al. (2018). The zero-detection rate at the final density suggests a non-linear relationship between effort and detection, perhaps because the surviving deer occupied heavily forested low-slope habitats during the trial period.

Our other consideration was the proportion of deer detections that are killed, which was 91% in this study. Maximising this is important in maximising efficiency, but it is also important in minimising learnt aversion arising from non-lethal encounters (Proudman et al. 2020; Griesberger et al. 2022). The high kill to detection rates in the 5th and 6th sorties provided no indication that any learnt aversion was occurring. By way of comparison, operations targeting forest-dwelling deer with TAC in Australia have achieved high kill to detection rates of 84% for fallow deer (*D. dama*) (Cox et al. 2023) and 96–100% for Rusa deer (*Rusa unicolor*) (Pulsford et al. 2022). This is higher than conventional aerial control targeting female sika deer in North Island beech forest, where 63%, 73%, and 83% of the deer detected were killed during winter, spring, and summer respectively, with the probability increasing with the proportion of open (non-forested) habitat (Latham et al. 2018). Similarly, Hampton et al. (2021) reported that approximately 75% of fallow deer detected during conventional aerial control operations in Australian woodlands were successfully shot.

Overall, our results indicate that TAC can provide much more effective control of forest dwelling deer populations than conventional aerial control. However, with estimated residual densities of 1.34 deer per km^2 remaining, 65% forest cover does still provide some protection for deer.

It is important to consider applied operational factors that can affect efficacy such as TAC crew equipment, technical expertise, aerial hunting experience, and strategies (especially in relation to ambient temperature). These strategies need to account for weather conditions, temperature, time of day, and sortie duration to optimise deer detection probabilities and minimise risk of escapees developing helicopter aversion behaviours. Other factors that are likely to affect efficacy are the thermal characteristics of the target species and the extent to which vegetation cover and height, slope (or lack thereof), and landform can prevent thermal detection. Social behaviour (e.g. herding), body mass, and pelage are also likely to affect detection rates. However, ambient temperature aside, the most important factor overall is likely to be the height and completeness of the forest canopy. We expect deer detectability by TAC to be lowest in tall flatland warm-climate forests with a complete unbroken canopy.

Cost effectiveness of TAC

A specific target for this trial was to identify how much TAC effort was required to reduce deer to c. 1 deer per km^2. Overall, it cost c. $16.30 per ha of TAC hunting time to reach this approximate density. While the reduction cost may seem high, it is comparable to the estimated total cost of goat (*Capra hircus*) ground control knockdown operations to low (but not actually known) densities (c. $20 per ha; GL, unpubl. data).

Contrary to expectations based on Bengsen et al. (2022), percentage removal rates did not follow a curvilinear decline with decreasing population size, and costs did not increase exponentially. Removal rates appeared to occur in four sequential phases: high, low, medium, zero. That differs from the expected exponential increase in the cost per deer kill as density is progressively reduced (Nugent & Choquenot 2004), as was observed during the eradication of red deer from Secretary Island (MacDonald et al. 2019). Sorties 3 and 4, which comprised much of the low phase, were conducted in thermal conditions considered by the operator to be sub-optimal, with high contrast between the forest floor and canopy (J. Munn, Trap and Trigger Limited, pers. comm.). As it seems inevitable that it will take more time to find a deer as deer density is reduced, we hypothesise that either the TAC operators got better at finding deer and/or that better thermal conditions for detecting deer prevailed in sorties 5 and 6.

The cost per kill for TAC in the final successful sortie was almost one-third of that estimated for ground control at comparable deer densities in the wider Murchison Mountains area during 2008–2010 ($595 vs. $1428). Similarly, the cost per kill at comparable densities on Secretary Island in 2009 equates to > $4000 per deer using 2024 costs (MacDonald et al. 2019). We therefore consider that TAC has the potential to at least halve deer control costs in habitats similar to or more open than the Snag Burn. Subsequent maintenance control using TAC is likely to cost even less. For example, assuming an annual rate of increase of 35% (Forsyth et al. 2010b), and a mean removal cost of $595 per deer, maintaining the estimated post-TAC population size will require killing six or seven deer annually (at a cost of $3–4 per ha) provided there is no net immigration or learnt aversion.

Importantly, the desired density reductions were achieved over just five days of TAC. The logistical and administrative complexities of managing ground hunters in a remote location over the several multi-day sorties typically required to achieve similar outcomes is likely to result in substantially greater project administration costs than those required for TAC.

Achievement of control objectives

The relatively high deer density observed at the start of this trial is consistent with qualitative assessments by DOC staff indicating a marked increase in deer abundance in the wider Murchison Mountains over the past decade. Those apparent increases are considered likely to have resulted from insufficient conventional control since about 2000, possibly coupled with increased immigration from adjacent PCL. Whatever the cause, the almost five-fold increase in deer density suggested by our results highlights how quickly historical gains can be lost.

The reduction in our pre- and post-TAC deer density estimates from 5.5 deer per km^2 to 1.3 deer per km^2 is therefore, in our opinion, a major operational success. As already noted, this matches historical estimates (for the whole Murchison Mountains area) of c. 1.2 deer per km^2 in 2008, which represented a 92% decline over the preceding 40 years of ground-based and aerial deer control (Tanentzap et al. 2009). In this trial, a similar reduction was achieved in under 11 hours of TAC. Achievement of that target density is expected (if maintained) to result in improved regeneration of deer-preferred plant species, as has been documented in New Zealand forests elsewhere (Nugent et al. 1997; Husheer 2007), and in the Murchison Mountains in the mid-2000s when deer densities were at historic lows (Tanentzap et al. 2009).

The fDNA mark-recapture method combined with the capwire modelling of population size produced a range of estimates that we are confident included the actual population size given the number of deer subsequently killed. In fact, we believe the mean estimate of population size is likely to be an overestimate given the zero-detection rate in the last hour of TAC hunting, and the likelihood that deer densities in the areas not covered in the fDNA survey were lower than average. Nonetheless, there are several ways our fDNA approach could be improved. Ideally, the TAC trial should have been undertaken immediately after the fDNA survey to minimise emigration/immigration risks, and the fDNA survey could be designed to initially sample all parts of the treatment area within the first few days (with fill-in coverage on subsequent days as far as possible). New genomic approaches based on Single Nucleotide Polymorphisms (Solari et al. 2025) offer a pathway to more reliable identification and matching of genotypes, with the technology already being widely used in agriculture in New Zealand (Costilla et al. 2025).

In summary, this is (to our knowledge) the first study globally to directly estimate the efficacy of TAC in reducing the density of over-abundant deer in heavily forested habitat. Efficacy was very high, with a probable reduction of > 76% achieved in < 11 hours of aerial hunting time. It performed better than conventional aerial control in the detection of deer in forest and in killing more of the deer detected. Further, it was substantially cheaper than ground hunting, with the latter requiring much longer timeframes and consequently higher administrative costs to achieve similar target densities. The authors consider this validates the inclusion of TAC into the forest deer control toolbox, although we advise caution in expecting comparable results in all forest situations.

Importantly, the residual deer density achieved appears low enough (if maintained) to allow improved regeneration of preferred native plant species. We estimate that maintaining the current density would require $3–4 per ha per year in aerial (TAC) hunting time. Although further trials are required to assess TAC efficacy in other, more dense, forest types, beech-dominated forest types broadly like those in the Snag Burn comprise > 50% of New Zealand's native forests, suggesting the findings are widely applicable. We suggest that the priority for further testing and development of TAC in New Zealand should be the measurement of TAC efficacy and cost-effectiveness in conifer-broadleaved forests on gently sloping terrain, where multi-tiered forest structures and dense, uniform canopies may substantially reduce efficacy.

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Additional information and declarations

Conflicts of interest: The authors declare no conflicts of interest.

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Ethics: This research utilised data collected from ongoing deer control operations undertaken by the Department of Conservation, which do not require animal ethics approval. No other permits were necessary.

Data and code availability: In addition to the online Supplementary Material describing our methods in more detail, the data, code, and supplementary reports used in this paper may be available by contacting the corresponding author.

Author contributions: GAL designed the study, JSA and TB-C undertook DNA analysis, AD and GAL analysed the data, GAL and GN wrote the manuscript with input from AD and JSA.

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Supplementary Material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Thermal aerial control trial methods

Appendix S2. Estimation of population size using DNA-based mark-recapture - methods and analysis.

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