# Evaluation of feral pig control in Hawaiian protected areas using Bayesian catch-effort models

Mandy C. Barron[1*], Dean P. Anderson[1], John P. Parkes[1], Samuel M. 'Ohukani'ohi'a Gon III[2]

[1] Landcare Research, PO Box 40, Lincoln 7640, New Zealand
[2] The Nature Conservancy of Hawai'i, 923 Nu'uanu Avenue, Honolulu, HI 96817
[*] Corresponding author: barronm@landcareresearch.co.nz

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**Abstract:** In 2007 The Nature Conservancy (TNC) undertook an intensive ungulate control programme throughout three of its preserves on the Hawaiian islands of Maui and Moloka'i, with one aim being to reduce feral pig numbers to zero or near zero. The preserves were divided into manageable zones and over a 2 to 5 month period hunted from the ground with dogs in a series of up to four sweeps across the zones. More focussed hunting followed at sites with evidence of survivors. We used the data collected by the hunters to evaluate the efficacy of the control programme. The data comprised the number of pigs shot per zone per sweep and the hunters' effort and were used to fit a Weibull catch-effort model within a Bayesian framework. The fitted model provided posterior parameter estimates of the initial number of pigs resident in each zone and the relationship between hunting effort and the probability of detecting (and dispatching) a pig. The large shape parameter estimate indicated that the probability of detecting a pig increased substantially with cumulative hunting effort or experience in that zone. The control programme was successful in six out of eight of the control zones reducing pig numbers to zero or one per zone (equating to <1 pig per km$^2$) but was less successful in two zones where an estimated 9–14 pigs remained. However there were large credible intervals around some of the parameter estimates, suggesting an additional source of variation that was not captured by the current model. We suggest this was due to immigration of pigs back into the preserves. The quantified relationship between search effort and the probability of detecting a pig was used to make predictions on how much effort is required to detect all pigs, and can be used by TNC to interpret future monitoring data.

**Keywords:** catch per unit effort; detection; monitoring; pest control

## Introduction

Feral pigs (*Sus scrofa*) are a conservation problem in the Hawaiian islands (Nogueira-Filho et al. 2009) because they affect the survival and recruitment of native plants through consumption, rooting and trampling (Spatz & Mueller-Dombois 1975; Katahira 1980; Diong 1983), disperse exotic plant propagules (Huenneke & Vitousek 1990; Aplet et al. 1991), and accelerate soil erosion leading to increased sedimentation in waterways (Cuddihy & Stone 1993). They have also been implicated in the spread of avian malaria due to the creation of water pools when they eat the inner core of tree fern logs, which provides a breeding site for mosquito vectors (LaPointe 2000). To protect Hawaiian watershed forest ecosystems from browsing and disturbance by feral ungulates, The Nature Conservancy (TNC) launched an intensive ungulate control program throughout its preserves on the islands of Maui and Moloka'i in late 2007 (Case 2007). Feral pigs were the main ungulate species of concern and the objective was to reduce their numbers to zero or near-zero within the controlled zones of the preserves. Goats (*Capra hircus*) were also targeted although it was acknowledged by TNC that it would not be feasible to reduce their numbers to near-zero during this programme.

The professional wild animal management company Prohunt Ltd (now Native Range Inc. of Ventura, California) was contracted to cull all pigs across selected areas of TNC's preserves on the islands of Maui and Moloka'i. They used a method they developed in other ungulate island eradication programs, e.g. Santa Cruz Island (Parkes et al. 2010) of dividing the area into more-or-less isolated manageable zones and systematically covering these zones on foot with teams of hunters and dogs in a line formation. They aimed to kill each pig upon first encounter so no wary survivors were produced. Prohunt was not allowed to shoot pigs from a helicopter in Hawaii, although helicopters were used to transport the hunters and dogs to and from the hunting zones and to identify areas inhabited by pigs.

Prior to the start of the programme it was thought that local eradication of pigs within some of the control zones was achievable because fences and natural barriers, such as cliffs, would prevent reinvasion of pigs from the surrounding areas. The intention was to use the pig hunting data to estimate the confidence that all the resident pigs had been removed as the hunting progressed, once pigs were no longer found on successive hunting events (Ramsey et al. 2009). However, monitoring of GPS-collared and ear-tagged pigs showed breaches of these barriers (Barron et al. 2009) showing the control zones were not truly isolated units. Thus the focus of this work shifted from auditing of eradication to auditing of sustained control to provide some basic information on the likely frequencies of intervention required given immigration and in situ recruitment if some pigs survived the control. In particular we sought to quantify the efficacy of control in terms of residual pig abundance. To estimate the initial number of pigs resident in each control zone and thus the number remaining, we fitted a catch-effort model using Bayesian techniques. The model also estimates the relationship between hunting effort and the probability of detecting a pig which can be used to make predictions about how much hunting effort is required to detect all of the pigs in a zone.

## Methods

### Hunting areas and data collection

Prohunt staff removed pigs across five zones in Waikamoi Preserve and adjacent East Maui Watershed area on the east of Maui Island between October 2007 and February 2008; in the Kapunakea Preserve on the west of Maui Island between February and March 2008; and across three zones on Moloka'i Island between March and July 2008 (Table 1, Fig. 1). Hunting was done by hunters on foot using trained dogs. Hunting consisted of a series of one to four systematic hunts called 'sweeps' covering the entire zone, followed by targeted forays called 'hot-spotting' to dispatch any known or suspected survivors. Successive sweeps were not used in Pelekunu Preserve on Moloka'i because of the steep terrain, rather hunting was concentrated in the accessible areas.

**Table 1.** Definition of the pig hunting zones targeted by Prohunt

| Hunting zone | Management unit | Island | Area (ha) | Perimeter unfenced (km) |
|---|---|---|---|---|
| Waikamoi 1a | Waikamoi Preserve | Maui (East) | 244 | 0.5 |
| Waikamoi 2 | Waikamoi Preserve | Maui (East) | 818 | 6.0 |
| Waikamoi 3 | Waikamoi Preserve | Maui (East) | 600 | 9.0 |
| Waikamoi 5 | Waikamoi Preserve | Maui (East) | 580 | 4.5 |
| Honomanu Makai | East Maui Watershed | Maui (East) | 346 | 7.4 |
| Kapunakea | Kapunakea Preserve | Maui (West) | 547 | 20.2 |
| Kamakou Remote | Kamakou Preserve | Moloka'i (East) | 404 | 5.8 |
| Upper Fenced South Slope | Moloka'i South Slope | Moloka'i (East) | 958 | 8.6 |
| Upper Pelekunu Valley | Pelekunu Preserve | Moloka'i (East) | 1386 | 13.8 |

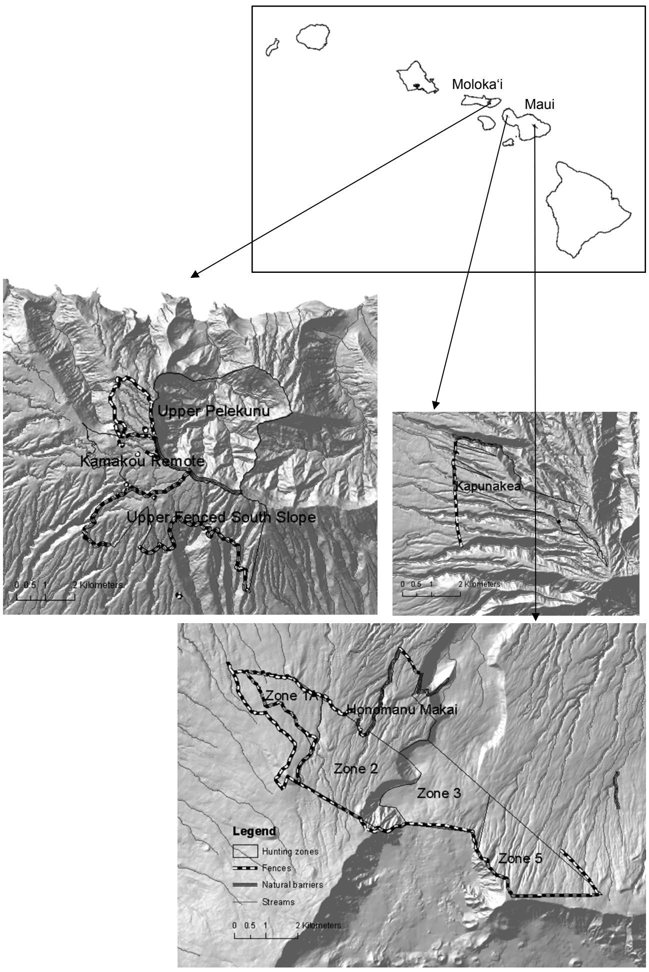


**Figure 1.** Location of pig hunting zones.

The hunters used a Garmin Astro 220 dog tracking system which logged the position every minute of both the hunter and the collared dog(s), giving a record of their paths ('tracks') as they hunted the zone. The locations of all dispatched (or seen) pigs were also recorded on the hunters' GPS unit. Hunting effort was quantified by dividing the total length of ground hunters' tracks in each zone by the zone area giving a measure of kilometres travelled per square kilometre ('track density').

### Analysis

The hunting effort and pig removals per sweep (Tables 2 & 3) were used to fit a catch-effort model using Bayesian methods (Ramsey et al. 2009). The analysis relates the probability of detecting and dispatching an individual pig to the amount of hunting effort expended. It was assumed that all pigs detected were subsequently captured as the hunters recorded no instances where a pig escaped capture once encountered (N. Macdonald pers. comm.) The analysis simultaneously estimates the initial population size in each of the hunting zones, which was subsequently used to estimate the proportional kill per zone. The catch-effort model was fitted to the first eight zones listed in Table 1; removals from upper Pelekunu Valley zone were omitted because this zone was not hunted in successive sweeps.

A key feature of the data was that for four of the eight zones the catch-per-unit-effort (CPUE) increased with cumulative hunting effort, which is contrary to the expectations of the standard exponential model that assumes CPUE declines as the population is progressively reduced (Seber 1982). To accommodate this we fitted a Weibull catch-effort model which allows the hazard rate or the instantaneous rate of a pig being detected to change with cumulative hunting effort rather than being constant as in the standard exponential model. The model assumes that the cumulative number of pigs captured in zone $i$ up to and including sweep $j$, $R_{i,j}$, was binomially distributed:

$$R_{i,j} \sim \text{Binomial}(\theta_{i,j}, N_i)$$

where $N_i$ is the initial population size in zone $i$ (number of trials) and $\theta_{i,j}$ is the probability of detecting a pig (probability of success) from the initial population in zone $i$ on sweep $j$.

For a given amount of (log-transformed) cumulative hunting effort $H$ in zone $i$ and up to and including sweep $j$, the probability of a pig being detected $\theta_{i,j}$ was modelled as:

$$\theta_{i,j} = 1 - \exp[-\{\rho_i H_{i,j}\}^{\kappa}] \ ;$$

where $\rho$ is a detection rate parameter and $\kappa$ is a shape parameter for the Weibull distribution. A value of $\kappa > 1$ generates a hazard rate that increases with cumulative effort, a value of $\kappa < 1$ generates a hazard rate that decreases with cumulative effort and if $\kappa = 1$ it collapses to the exponential model. The detection rate parameter $\rho$ was assumed to vary between zones, hence the index $i$ in the above equations representing a random zone effect. To fit the model, the above equation was linearised using a complementary log-log link function:

$$\log[-\log(1 - \theta_{i,j})] = \kappa[\log(\rho_i) + \log(H_{i,j})] \ .$$

Bayesian inference requires the specification of prior distributions or "priors" for the model parameters which are then updated by the data to provide posterior parameter distributions. Lognormal priors were used for detection rate parameters ($\rho_i$) and the shape parameter ($\kappa$): Normal(ln($\rho_i$) | 0,1); and Normal(ln($\kappa$) | 0,1) respectively. The priors for the initial number of pigs per zone ($N_i$) were weakly informative and drawn from a uniform distribution with a lower bound equal to the total number of pigs removed per zone, $R_{i,t}$, and the upper bound equal to this number plus fifteen:

$$N_i \sim \text{Uniform}(R_{i,t}, R_{i,t} + 15) \ .$$

Fifteen pigs being approximately half the maximum number of pigs removed from a zone.

We used Markov chain Monte Carlo (MCMC) techniques as implemented by the software winBUGS (version 1.4) and called via the R2WinBugs package in R (version 2.9.1) to obtain the posterior parameter distributions. Simulations were started from 3 chains and run for a burn-in period of 80000 iterations to obtain parameter convergence. Posterior parameter distributions were calculated from an additional 20000 iterations in which we sampled every fifth iteration (i.e. 12000 samples total). Parameter convergence was assessed using the Gelman–Rubin statistic (Gelman and Rubin 1992; Gelman et al. 2004) and inspection of sample histories using the coda package for R. Samples from the posterior parameter distributions of the most parsimonious model were used to infer the initial number of pigs resident in each zone and to explore how pig detection probabilities changed with increasing hunting effort.

## Results

### Hunting effort and numbers of pigs dispatched by Prohunt

In total, 54 pigs were captured (then collared or dispatched) from the East Maui zones, 17 from Kapunakea in West Maui, and 136 from the Moloka'i zones (Table 2).

Total hunting effort across all sweeps (excluding hotspotting) expressed as track density ranged from 6 km/km$^2$ in zone 5 up to 136 km/km$^2$ in zone 1a (Table 3). In upper Pelekunu Valley total effort was 29 km/km$^2$, which was the median total effort value across the zones.

**Table 2.** Number of pigs removed per zone.

| Zone | Sweep 1 | Sweep 2 | Sweep 3 | Sweep 4 | Hot spots | Other[a] | Total |
|---|---|---|---|---|---|---|---|
| Waikamoi 1a | 2 | 2 | 0 | 4 | 0 | - | 8 |
| Waikamoi 2 | 21 | 2 | 0 | 0 | 0 | - | 23 |
| Waikamoi 3 | 14 | 3 | - | - | 2 | - | 19 |
| Waikamoi 5 | 0 | - | - | - | 0 | - | 0 |
| Honomanu Makai | 4 | 0 | 0 | 0 | - | - | 4 |
| Kapunakea | 5 | 5 | - | - | 6 | 1 | 17 |
| Kamakou Remote | 22 | 2 | 5 | - | 0 | 2 | 31 |
| Upper Fenced South Slope | 2 | 3 | 10 | - | - | 1 | 16 |
| Upper Pelekunu Valley[b] | 89 | - | - | - | - | - | 89 |

[a] Captures or dispatches with no associated hunter track records, e.g. pigs caught in a trap.
[b] Pelekunu was not hunted in successive sweeps, rather as one big effort.

**Table 3.** Hunting effort per zone (track lengths, unit = km/km$^2$)

| Zone | Sweep 1 | Sweep 2 | Sweep 3 | Sweep 4 | Hot spots | Total effort (over 4 sweeps) | Average effort per sweep |
|---|---|---|---|---|---|---|---|
| Waikamoi 1a | 37 | 21 | 43 | 34 | 8 | 136 | 34 |
| Waikamoi 2 | 18 | 12 | 10 | 11 | 3 | 52 | 13 |
| Waikamoi 3 | 17 | 10 | - | - | 2 | 27 | 14 |
| Waikamoi 5 | 6 | - | - | - | 3 | 6 | 6 |
| Honomanu Makai | 17 | 11 | 9 | 11 | - | 48 | 12 |
| Kapunakea | 11 | 9 | - | - | 6 | 20 | 10 |
| Kamakou Remote | 29 | 20 | 15 | - | 2 | 64 | 21 |
| Upper Fenced South Slope | 11 | 9 | 7 | - | - | 27 | 9 |
| Upper Pelekunu Valley | 29 | - | - | - | - | 29 | 29 |

**Catch-effort model**

Plots of sample histories and the Gelman-Rubin statistic (*R*=1.01) indicated model convergence. The posterior distributions for the initial pig abundance per zone were highly skewed (Fig. 2) so the modes (rather than means or medians) were used as point estimates for *N*. Based on these estimates, hunting efficacy ranged from relatively poor in the upper fenced South Slope at around 53% to greater than 95% for three of the Waikamoi zones and the Kamakou Remote zone (Table 4).

Density plots of the estimated initial number of pigs per zone (Fig. 2) revealed that the distributions for the Kapunakea and upper fenced South Slope zones were diffuse and skewed towards the upper prior estimates (total number removed plus fifteen). Re-running the simulation with a higher upper limit on the prior distribution of pigs per zone (total number removed plus twenty-five) resulted in the same modal posterior values for the all zones except for Kapunakea and upper fenced South Slope, which were higher at 27 and 40 respectively. This sensitivity to prior values and the resulting diffuse posterior distributions indicates a poor model fit and unreliable parameter estimates for these two zones. This could be indicative of a violation of the assumption that populations were closed and there was good evidence that pigs were immigrating into the upper fenced South Slope zone (Prohunt unpublished report).

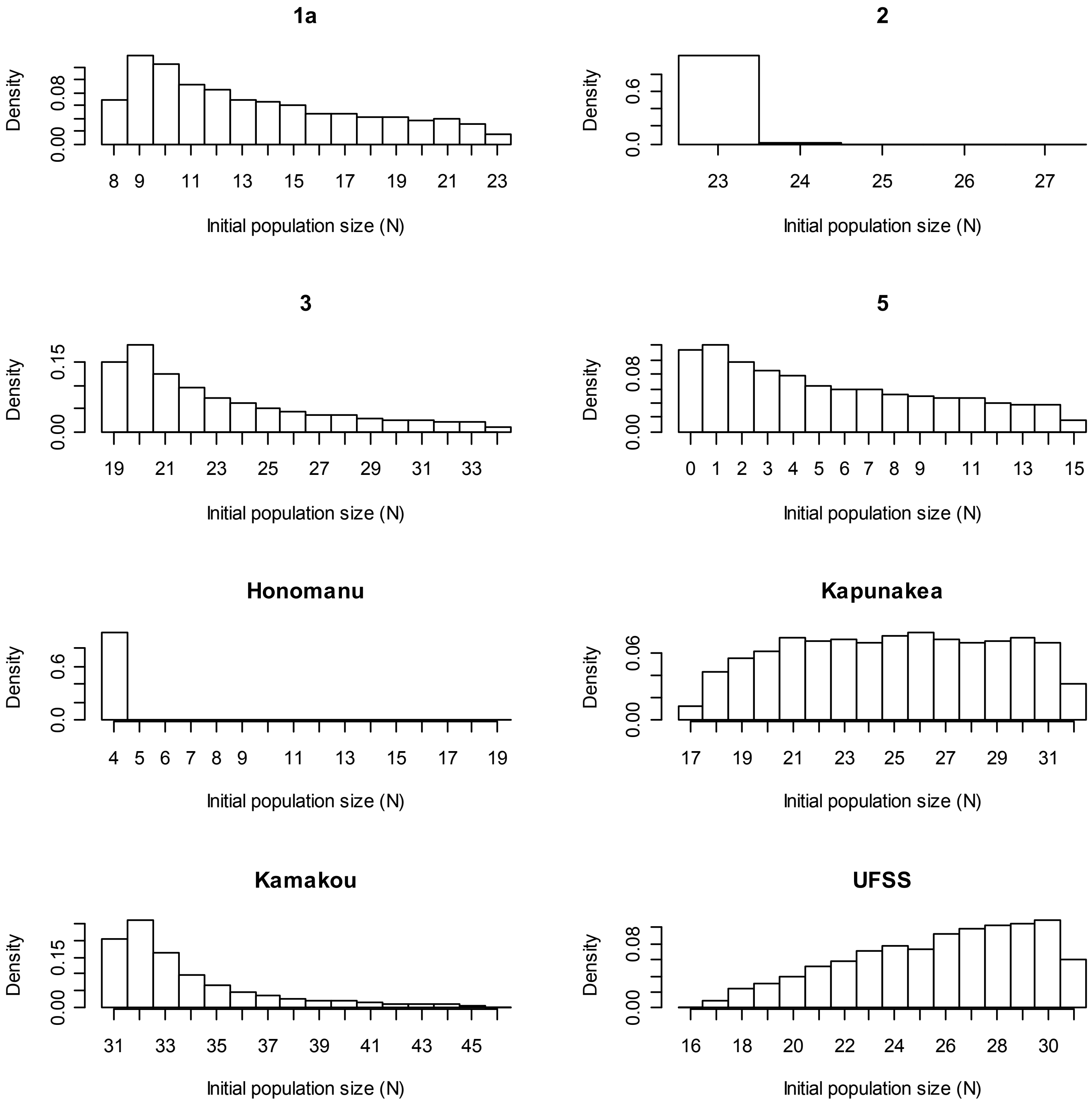


**Figure 2.** Posterior distributions of the initial population size parameter for each zone (*N*).

**Table 4.** Estimates of initial population size in each hunting zone before control and the estimated proportion of pigs removed and residual densities, with credible intervals in brackets.

| Population size | Estimated initial no. of pigs (95% CI) | No. pigs removed by Prohunt | Proportion pigs removed by Prohunt (95% CI) | Estimated residual density (pigs per km$^2$) |
|---|---|---|---|---|
| Waikamoi 1a | 9 (8–21) | 8 | 0.89 (0.38–1.00) | 0.41 |
| Waikamoi 2 | 23 (23–23) | 23 | 1.00 (1.00–1.00) | 0.00 |
| Waikamoi 3 | 20 (19–32) | 19 | 0.95 (0.59–1.00) | 0.17 |
| Waikamoi 5 | 1 (0–14) | 0 | NA * | 0.17 |
| Honomanu Makai | 4 (4–4) | 4 | 1.00 (1.00–1.00) | 0.00 |
| Kapunakea | 26 (18–31) | 17 | 0.65 (0.55–0.94) | 1.65 |
| Kamakou Remote | 32 (31–41) | 31 | 0.97 (0.76–1.00) | 0.25 |
| Upper Fenced S. Slope | 30 (19–31) | 16 | 0.53 (0.52–0.84) | 1.46 |

* Cannot divide by zero

The estimate for the shape parameter κ was very high at around 4.3 indicating a large increase in hunting/detection ability with cumulative hunting effort. The detection rate parameter $\rho$ varied between the zones even within Waikamoi preserve (Table 5). We used the parameter estimates to predict how pig detection probabilities change as a function of search effort in the 1a and 2 zones both in the Waikamoi Preserve in East Maui. These two areas have a low and high rate parameter ($\rho$) estimate respectively, and consequently conclusions drawn from further monitoring will have very different implications. A high rate parameter results in the detection probability increasing relatively quickly and approaching 1 (where all pigs would be detected) much quicker than when the rate parameter is low (Fig. 3a, 3b). In the Waikamoi 2 zone, the detection probability exceeds 0.95 after approximately 20 km/km$^2$ units of hunting effort (≈ 3 $\log_e$(km/km$^2$)) with the 95% credible intervals converging upon the median as cumulative hunting effort increases. In the Waikamoi 1a zone, the detection probability would only exceed 0.6 after approximately 148 km/km$^2$ units of hunting effort (≈ 5 $\log_e$(km/km$^2$)) and the 95% credible intervals remain very wide.

**Table 5.** Detection rate ($\rho$) and shape ($\kappa$) parameter estimates from the Weibull catch-effort model (model 2).

| Model parameters | Median | 2.5% credible interval | 97.5% credible interval |
|---|---|---|---|
| $\kappa$ | 4.3 | 2.603 | 6.095 |
| $\rho$ – Waikamoi zone 1a | 0.194 | 0.150 | 0.241 |
| $\rho$ – Waikamoi zone 2 | 0.429 | 0.374 | 0.513 |
| $\rho$ – Waikamoi zone 3 | 0.342 | 0.279 | 0.400 |
| $\rho$ – Waikamoi zone 5 | 0.214 | 0.024 | 0.410 |
| $\rho$ – Honomanu Makai | 0.518 | 0.216 | 1.367 |
| $\rho$ – Kapunakea | 0.304 | 0.256 | 0.356 |
| $\rho$ – Kamakou Remote | 0.300 | 0.256 | 0.336 |
| $\rho$ – upper fenced South Slope | 0.269 | 0.223 | 0.313 |

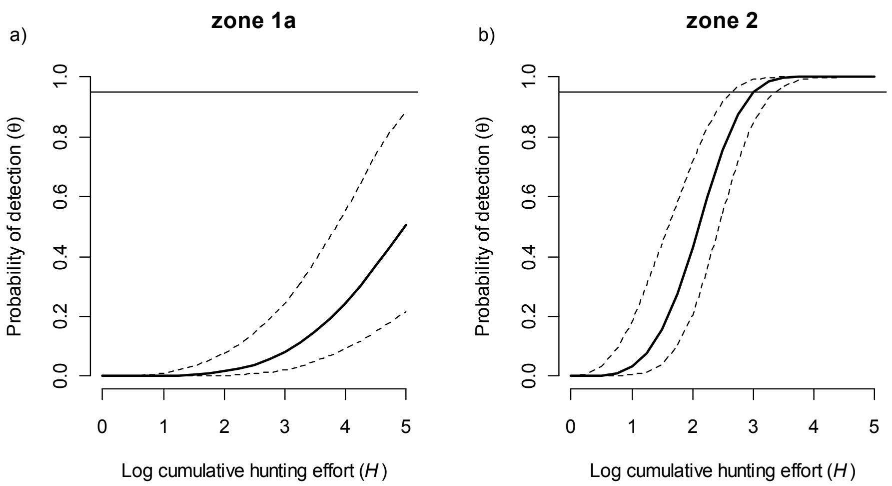


**Figure 3.** Pig detection probabilities ($\theta$) in zones with relatively low (a) and high (b) rate parameters ($\rho$). Median values are shown with bold line and 95% credible intervals are dashed lines. A horizontal line at 0.95 detection probability is included for visual reference.

## Discussion

There was a positive relationship between hunting effort and the probability of detecting a pig and this relationship varied with hunting zone. This enabled the estimation of initial population sizes for most of the control zones and provided an informative measure of success for the control program, which varied from very good (including local eradication in two zones) to poor. The wide 95% credible intervals about the parameter estimates in some zones, however, indicate substantial uncertainty that is not accounted for in the model. This uncertainty combined with low baseline detection rates for some of the zones results in the situation illustrated in Fig. 3a, where even with substantial hunting effort (log($H$)=5 equivalent to 10 sweeps of a zone) the predicted probability of detecting a pig is still low with wide credible intervals.

The catch-effort model assumed that the population was closed over the duration of the study and the only change in numbers was due to removals by hunting. While reproduction was not included in our model and could be a cause of uncertainty, the effect is likely to be small due to the short timescale of the operation. A likely source of important uncertainty is the immigration of small numbers of pigs into the control zones. We tried to incorporate immigration into a catch-effort model by making the immigration rate a function of the unfenced perimeter of the preserve. Unfortunately this model did not converge, possibly because it involved fitting two more coefficients to an already sparse data set. Another possibility is that unfenced perimeter length was not a good predictor of the potential immigration rate. In the case of the upper fenced South Slope zone there was evidence that goats and therefore probably also pigs (S. McKnight pers. comm.) were getting through holes in the southern boundary fence, so that a fenced boundary didn't necessarily prevent immigration. Also, the immigration rate may be more influenced by the source population size so that zones adjacent to favourable pig habitat and/or where pigs have not been recently controlled are more susceptible to immigration than zones without these characteristics. Reliable estimates of population pressure outside the preserve boundaries were not available in this case but could greatly inform the model if immigration is indeed the source of uncertainty.

Another key assumption of the catch-effort model was that the detection was equal for each individual pig within a sweep. There was some concern following the hunt in Waikamoi Preserve that there was a bias towards catching females because only four adult males were caught out of the 54 pigs caught in total (Barron et al. 2009). This could be a result of females being more likely to be found in social groups and thus easier to detect compared with males, which do not tend to associate with other pigs. This sex bias, however, was not apparent in the other areas hunted and since most pigs (73%) captured were singletons (Barron et al. 2009) we presume that the assumption of equal detectability has been adequately met. The high proportion of apparently solitary individuals in a normally social species was thought to be due to previous control efforts (including snaring and recreational hunting) causing sparse and highly dispersed populations (N. Macdonald pers. comm.).

The large shape parameter ($\kappa > 4$) for the Weibull distribution indicates that pig detection rates increased substantially with cumulative hunting effort. This could be due to hunters using the experience gained from their first sweeps of the zone to improve their chances of detecting a pig on subsequent sweeps for example by noting the location of pig sign or pig trails. Similarly observations from the air whilst transporting hunters by helicopter to and from the hunting zone or on flights to identify areas of high pig use could improve subsequent detection rates on the ground. This additional search effort from a helicopter was not included in the estimation of hunting effort because it was difficult to quantify incidental searching and the hunters still had to traverse the zones on foot to make the kill. Analysis of detection rates of different types of hunting for the Santa Cruz Island pig eradication showed that, overall, detection per unit of search effort was similar for aerial hunting and ground hunting (Ramsey et al. 2009), although aerial hunting appeared to be more successful in open grassland and herbaceous habitats compared with forested habitats where ground hunting with dogs was more favourable (Parkes et al. 2010). Habitat complexity may also provide an explanation for the differences in the baseline detection rates ($\rho$) found between zones, although descriptors of habitat complexity were not available to test this theory.

For TNC this analysis provides some confidence that their ungulate control program did reduce pig abundance to zero or near-zero in most of the control zones. The original intention to use the estimated probabilities of pig detection for a given search effort (i.e. the surveillance sensitivity) to validate local eradication was void since one of the requirements for eradication, that of preventing reinvasion, was clearly not met. However the surveillance sensitivity can be used to interpret future monitoring data providing similar methods are used and search effort is concurrently measured. The Bayesian framework also means that the model parameters can be updated as new monitoring data come to hand with the posteriors from this analysis forming the priors for a new analysis. Estimation of the population rates of recovery within the preserves using this framework will enable TNC to make informed decisions on how often and how intensively to control to maintain pigs at near-zero densities and achieve their conservation goals.

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