

What does it take to eradicate a feral pig population?

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Abstract Control of feral pigs (*Sus scrofa*) has become a high priority for management of many island and mainland ecosystems, but few programmes have used population models to estimate the effect of harvest intensity on population size. We used data collected from 1991 to 1999 on density and sex/age structure of feral pigs on Santa Cruz Island, California, to develop a Leslie matrix model for estimation of the likelihood of eradication and number of years to eradication for different combinations of harvest rates and initial population size (N_0). The model included an estimated island-wide carrying capacity (K) of 3400, annual harvest rates of 0-95% for all sex and age classes, a management programme duration of ten years, and three levels of N_0 : 25% of K (low population), 75% (average population), and 150% (high population). The rate of reduction in population size depended on N_0 at low to moderate harvest rates (5%-65%) but not high harvest rates (>70%). Mortality from harvest shifted from compensatory to additive once harvest rates > 10%, but population size tended to stabilise, albeit at substantially reduced levels, for annual harvest rates < 70%. Harvest rates between 60% and 70% reduced the population to low enough numbers that pigs could be considered ecologically extinct, but there was no likelihood of eradication until 70-75% of the population per year was harvested. Once this threshold was crossed, the likelihood of eradication increased rapidly to 1 for all N_0 's. The median number of years to eradication when harvest rates > 70% ranged from ten (72% annual harvest rate) to 2.5 (95% harvest rate). The simulations suggest that N_0 will not add appreciable amounts of time to eradication programmes when harvest rates are high and that a strategy of intense harvest for five years will likely achieve eradication of many insular feral pig populations.

Keywords: Conservation, demography, invasive species, islands, feral animals, Leslie matrix, population management, population models, *Sus scrofa*

INTRODUCTION

The effects of non-native vertebrates on insular ecosystems have been recognised for decades (Atkinson 1989; Simberloff 1995; Mack *et al.* 2000). These include altered ecosystem processes (Fukami *et al.* 2006), destruction or degradation of vegetation communities (Coblentz 1978), altered trophic interactions (Fritts and Rodda 1998), and extinctions (Sax and Gaines 2008). Consequently, control or eradication of introduced species is widely regarded as being an integral step in conservation of island ecosystems (Myers *et al.* 2000; Veitch and Clout 2002; Courchamp *et al.* 2003).

Pigs (*Sus scrofa*) have been among the most devastating species introduced to island and mainland systems (IUCN 2005). They can cause long-term damage to crops (Geisser and Reyer 2004) and have been implicated in alterations to ecosystem, community, and species-level properties (Aplet *et al.* 1991; Cushman *et al.* 2004). Because of their impacts on natural and agricultural systems, control of pig populations has become increasingly common in many parts of the world (Choquenot *et al.* 1996; Bieber and Ruf 2005) and there has been an upsurge in efforts to eradicate them where possible, especially on islands (Lombardo and Faulkner 2000; Kessler 2002; Cruz *et al.* 2005).

Increased control and eradication efforts have resulted in sophisticated methods for programme planning, design, implementation, and monitoring (Morrison *et al.* 2007; Nogueira *et al.* 2007). Particular emphasis has been on methods for deciding when eradication has been achieved (Ramsey *et al.* 2009; Rout *et al.* 2009). Surprisingly, there has been less attention paid to the question of what harvest rates are necessary to achieve control or eradication. Determining what level of harvest can be economically sustained for a given period of time is crucial for determining if there are adequate resources for eradication, long-term control, or neither. First principles of population growth suggest that increasingly higher rates of harvest will likely lead to lower levels of abundance, greater probability of control or eradication, and shorter

programme duration. But these harvest rates are unknown, as is the approximate point where mortality from hunting ceases to be compensatory and becomes additive, how initial population size influences the likelihood of control or eradication, what levels of abundance can be expected to result from a given harvest rate, and how long an eradication programme will take to complete.

Feral pigs have had especially acute effects on California's Channel Islands, where they were introduced to the four largest islands in the 19th century (Knowlton *et al.* 2007). On Santa Cruz Island (SCI), the largest of the eight California islands, pigs were first recorded in 1852 (Schuyler 1988). Their long term effects have been increased erosion rates, alteration of native vegetation communities, damage or destruction of endemic plant populations, reduced abundance of some vertebrate species, and impacts to archaeological sites (NPS 2003). Pigs co-existed with feral sheep on SCI for at least 150 years, but there is little evidence of negative interactions between the two species (Klinger 2007). Historical accounts (Daily 1989, 1994), qualitative surveys conducted before sheep were eradicated in the 1980s (Baber 1982; Van Vuren 1994), and observations of island residents all indicate that the pigs were at times very abundant.

The Nature Conservancy (TNC) conducted a trial eradication of pigs in a fenced portion (2250 ha) of SCI from 1989 to 1991 to evaluate the feasibility of eradication throughout the island (Sterner and Barrett 1991). Despite the success of this trial (Sterner and Barrett 1991), TNC decided not to proceed with wide scale eradication at that time (Klinger 2007). Instead, data would be collected in a systematic monitoring programme to improve estimates of pig abundance (Sterner and Barrett 1991) and to model their population dynamics.

In this paper, we used a nine-year dataset from the SCI monitoring to develop a matrix population model of the influence of varying harvest rates on abundance of feral pigs for three different initial population sizes. Matrix

models are a common and powerful tool for analysing the relationship between the dynamics and vital rates of a population (Leslie 1945, 1946; Caswell 2001). To date, they have only been applied in a limited capacity to gain insight into population dynamics of pig populations (Neet 1995; Bieber and Ruf 2005), and none have been explicitly developed in the context of an eradication programme. Our goals were to use predictions from the models to help answer questions a manager might ask when designing a pig management programme: 1) what level of annual harvest is required to achieve eradication; 2) how long will it take to achieve eradication; and, 3) what is the effect of initial population size on the likelihood of achieving eradication?

MATERIALS AND METHODS

Santa Cruz Island

Santa Cruz Island (249 km²) is 40 km off the southern California coast. Although the highest point on the island is only 741 m, topography is very rugged. Two east-west trending mountain ranges flank a long central valley, with the interior and exterior flanks of each range cut by numerous small, deep drainages.

Climate on SCI is Mediterranean with warm, dry summers and cool, wet winters. Summer temperatures typically range from 27° to 35° C, while winter temperatures generally range from 5° to 15° C. Approximately 80% of the precipitation falls from November through April (L. Laughrin, UC Natural Reserve System, unpublished data). Inter-annual variation in precipitation is relatively high; the mean annual rainfall from 1903-1999 was 50.5 cm with SD \pm 23.4. The complex topography and soils on SCI have resulted in a diverse array of vegetation communities that are structurally similar to communities on the mainland (Brumbaugh 1980; Minnich 1980; Junak *et al.* 1995). The dominant vegetation communities include grasslands, chaparral, coastal scrub, woodland, and bishop pine (*Pinus muricata*) forest (Junak *et al.* 1995).

American Indians were the first human inhabitants on SCI, beginning approximately 9000 YBP (Glassow 1980). From the early 19th through latter 20th century SCI passed through a series of Spanish and American owners. The predominant land uses during this period were ranching and agriculture. Since the late 1970s, the island has been managed primarily as a conservation site by TNC and the National Park Service (NPS).

Human infrastructure on SCI is very limited; there are several small facilities in the central valley and the east and west ends of the island. A series of unpaved roads and trails provides access to 75% of the island; most of the northwestern 25% of SCI has no maintained roads or trails.

Pig abundance surveys and density estimation

Density estimates of feral pigs were derived from surveys conducted along 15 transects established on the western 90% of the island. The surveys were conducted during the wet season (late November through early March) each year from 1990 through 2000. The steep and irregular topography would have made cross-country transects impractical, therefore nine transects were established along existing roads and the other six on trails or abandoned roads. The 15 transects were selected randomly from a pool of 56 potential routes and varied in length from 2.9 to 20.4 km (Table 1). The order in which the surveys were conducted was randomised each year, including when repeat counts were conducted on the same transects in the same year. The surveys were conducted by a single observer on foot or in a vehicle. Observers on foot walked at a pace of 3-5 km/h; on surveys done from vehicles a single person would observe while another person drove the vehicle at a rate of 10-20 km/h. The data collected on the counts included the transect bearing, the distance and bearing to each group of pigs, the number in each group, and vegetation types where the groups were seen (Buckland *et al.* 2001).

The sighting distance and angle were used to derive the perpendicular distance of groups to the transect (Buckland

Table 1 The number of surveys per transect collected in each of ten seasons for estimation of feral pig density on Santa Cruz Island, California, 1990 – 2000. The counts were conducted from late November – early March each year (Season). Total is the number of transects surveyed (including repeat counts on the same transect), Length is the number of kilometres surveyed (including repeat counts on the same transect), Observed is the total number of pig groups sighted that season, and the Encounter rate is the mean number of groups observed per km (\pm SE).

Transect	Length (km)	Season									
		Wet 90/91	Wet 91/92	Wet 92/93	Wet 93/94	Wet 94/95	Wet 95/96	Wet 96/97	Wet 97/98	Wet 98/99	Wet 99/00
1	20.4	2	2	2	1		2	1		1	
2	15.0	2	2	2	2		1	2	1	1	1
3	14.7	2	2	2	2	1	1	2	1	1	1
4	18.4	2	2	2	2	1	2	1		1	
5	7.6	2	2	2	2	1	1	1	1	1	1
6	13.0	2	2	2	1		1	1			
7	9.3	2	2	2	2		1	1	1		
8	9.8	2	2	2	2		2	1	1	1	
9	12.1	2	3	3	2		1	1		1	
10	5.3	2	3	3	2		1	1		1	
11	3.4	2	3	3	1	1	2	1			1
12	2.6	2	3	2	2		1	1	1		1
13	4.3	2	2	2	2		1	2	1	1	
14	2.9	2	2	3	2	1	1	1	1		
15	6.1	2	2	3	2	1	1	1	1		1
Total		30	34	35	27	6	19	18	9	9	6
Length (total)		289.8	313.2	319.6	253.0	53.1	196.9	178.9	72.3	107.6	49.4
Observed		71	114	85	91	106	89	81	57	118	88
Encounter rate		0.24 \pm 0.01	0.36 \pm 0.01	0.27 \pm 0.01	0.36 \pm 0.02	1.99 \pm 0.24	0.45 \pm 0.03	0.45 \pm 0.02	0.79 \pm 0.05	1.1 \pm 0.09	1.66 \pm 0.12

et al. 2001). The distribution of the perpendicular distances were then used to model density with the programme DISTANCE (Buckland *et al.* 2001). Two key functions (uniform and half-normal) with cosine and polynomial expansion terms were used to generate and compare different models of density. We produced an initial set of models based on ungrouped perpendicular distances. If the fit of these models was inadequate (based on visual inspection of the observed and estimated distributions), we then grouped the data into intervals to improve model fit. The model with the lowest value for the corrected Akaike Information Criteria (AIC_c) was considered the one with the most support. When $\Delta AIC_c < 2$ then model selection was based on the visual fit of the model as well as χ^2 values for model fit.

Pig sex and age data

Data on pig population structure were collected during systematic hunts augmented with opportunistic kills. Hunting was conducted an average of 7-10 days per year in each of nine geographic zones in the western 90% of the island (Table 2). The hunts were conducted in all months of the year. From 1990 through 1994, all hunts were conducted with 1-6 Catahoula Leopard Stock Dogs working with hunter groups. From 1995-1998 a single Catahoula was used on the hunts. Hunter groups were comprised of trained volunteers, NPS staff, and members of two municipal southern California Special Weapons and Tactics (SWAT) teams. Hunter/dog teams would sweep individual drainages within a watershed and kill all pigs flushed out, regardless of size or coloration. Field necropsy was done on all kills to determine sex, age class (years), body condition (indexed by the thickness of rump fat), and reproductive status. Data collected for reproductively active females included the number of foetuses, the number of lactating teats, or the number of piglets accompanying her. Age was determined by patterns of tooth wear and eruption (Matschke 1967).

Population modelling

A two-step process was used to model the effect of different harvest rates on the pig population. First, a base model was developed to determine if parameter estimates derived from the kill and density data were biologically realistic. We knew from historic records that pigs had persisted on SCI for at least 150 years, but had pronounced fluctuations in density over this period. We reasoned that a

realistic model of the population would be highly variable over a 150 year period, but there would be no extinction events or abnormally high densities. Once we developed a biologically realistic base model, our second step would be the addition of annual harvest rates over a period of time representative of most pig eradication programmes.

Development and evaluation of the base model

Age-specific survival and fecundity rates for the base model were derived from the kill data. We developed a vertical life table (Skalski *et al.* 2005) for each sex in each calendar year from 1991 through 1998, as well as a table for data pooled across years. The number of pigs killed in each age class x for each sex (N_{xi} where $i = m$ for males, f for females) was multiplied by the age-specific kill rate then subtracted from the total number killed (N) to obtain an estimate of the number alive in each age class (N_{xi}). Because we could not count the number of newborn pigs (age $x = 0$), we estimated the initial population size for each sex N_{0i} as

$$N_{0i} = \left(\sum_{x=1}^n N_x \right) + \left[\left(\sum_{x=1}^n N_x \right) (M_i) \right]$$

where M_i was the mean per capita litter size (m_x) in that year. The proportion of each sex alive at the start of each age interval (l_{xi}) was derived from the N_{xi} , and the age-specific survival rates (s_{xi}) were calculated from the l_{xi} values. Age-specific fecundities (f_{xi}) were calculated from the estimates of m_x and s_{xi} . Pigs breed year round on SCI, therefore estimates of l_{xi} , s_{xi} , and f_{xi} were calculated as birth-flow values (Caswell 2001).

We used a generalised linear model (GLM) with a binomial error structure and logit link to analyse the degree to which l_x values varied among years

$$\text{logit } l_x = \beta_0 v_0 + u_{ix} v_{ix}$$

where v_0 is a constant, v_{ix} is the i th age class in the x th year, β_0 is an estimated parameter, and u_{ix} is an estimated parameter allowing l_x to vary randomly among years.

The estimates of s_{xi} and f_{xi} were used to parameterise a two-sex Leslie matrix model M (Skalski *et al.* 2005) with nine age classes. Both sexes were included in the model because males and females of all ages would be harvested in an eradication programme. We assumed that a small number of pigs was originally introduced to SCI, therefore we used an initial vector N of 25 animals as the starting population size. We incorporated demographic stochasticity into the model by deriving a standard deviation matrix S from the observed temporal variation in s_{xi} and f_{xi} . For each run of the model, values for s_{xi} and f_{xi} were drawn randomly from a lognormal distribution based on their age-specific mean and SD. Based on observations of pig behaviour during a population crash (see RESULTS), we selected contest density-dependence as the form most likely representative of that on the island.

Carrying capacity (K) was estimated directly by regression of the rate of population change (λ) against estimated abundance in the prior year (N_{t-1}). We used a simple exponential equation

$$\lambda = c * (\exp^{(b * N_{t-1})})$$

where C and b are estimated parameters for the intercept and slope, respectively. Carrying capacity was estimated as abundance where the regression line intersected $\lambda = 1$. Environmental stochasticity was incorporated into the model by: 1) randomly drawing estimates of K from a lognormal distribution with a coefficient of variation (CV) of 0.25; and 2) a catastrophic event every decade (approximately one generation). The estimate of the CV of K was based on variation in mast counts collected annually

Table 2 Effort and success rates for feral pig hunts on Santa Cruz Island, California. Days is the total number of days each year when hunts were conducted, Hunters is the mean number of hunters per hunt, Success is the number of hunts where at least one pig was killed, and Kills is the total number of pigs killed where data on sex and age class were collected ¹.

Year	Days	Hunters	Hunter-Days	Success	Success (%)	Kills
1990	9	1	9	8	88.9	16
1991	65	2.8	182.0	56	86.2	109
1992	73	2.4	175.2	71	97.3	276
1993	68	2.7	183.6	62	91.2	226
1994	85	2.2	187.0	85	100.0	390
1995	91	2.0	182.0	91	100.0	501
1996	78	2.3	179.4	78	100.0	394
1997	76	2.4	182.4	75	98.7	284
1998	45	3.9	175.5	42	93.3	227
Mean	65.6	2.6	180.9	568	95.1	2423

¹An additional 368 pigs were killed between 1990 and 1998, but these were on recreational or feral sheep hunts where no data were collected.

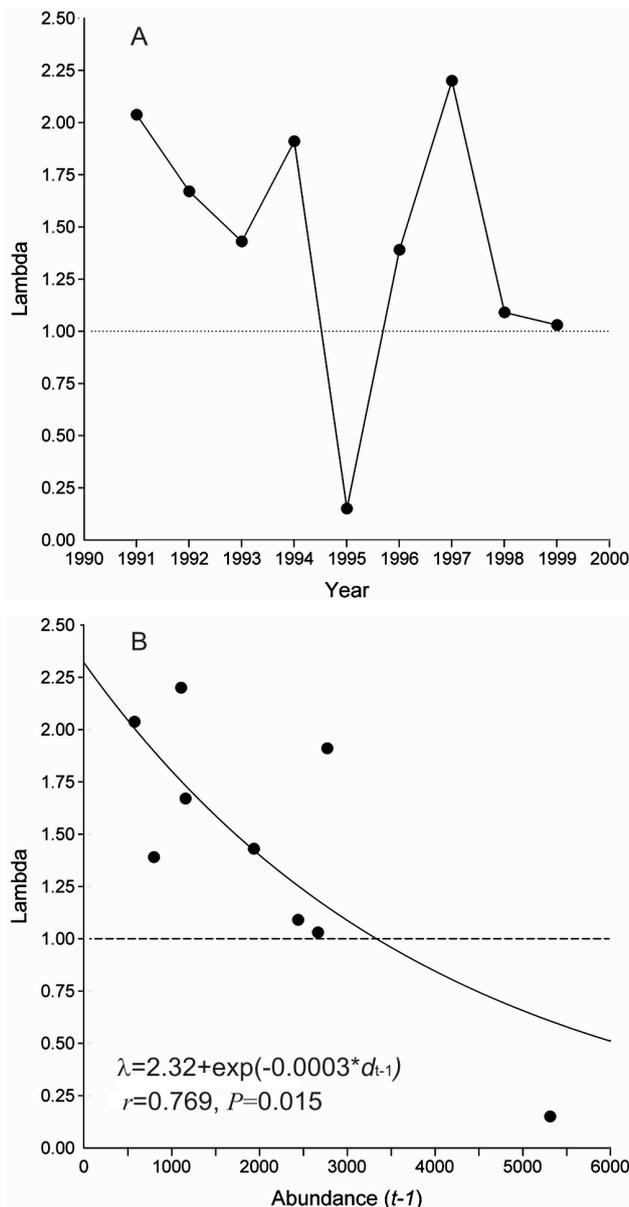


Fig. 1 (A) Variation in lambda (λ ; the rate of population change) for feral pigs over a 10-year period on Santa Cruz Island, California; and, (B) the relationship between lambda and abundance of feral pigs in the previous year (d_{t-1}).

from 1990 through 1999 (R. Klinger, unpublished data), and the catastrophes represented mast failures, years of extreme drought, or both.

We evaluated performance of the models in three ways. First, we conducted 10,000 simulations (Caswell 2001) based on estimates of s_{xi} and f_{xi} from each individual year (1991-98) and the model with years pooled ($N = 9$ models). We visually inspected the distribution of the mean population estimates in 5% percentile intervals for each model, and then compared the mean population estimates among them with standard least-squares ANOVA. Next, we used a jackknife procedure to derive estimates of s_{xi} and f_{xi} by sequentially removing each year from the pooled model. We then conducted 10,000 Monte Carlo simulations for each model with a missing year, as well as the model with years pooled. We compared mean population estimates among the models with ANOVA and visual inspection of the distribution of the model estimates in percentiles at 5% intervals. All of the simulations spanned a period of 150 years. Finally, we generated 10,000 bootstrap samples

Table 3 Estimated abundance (\pm SE) of feral pigs on Santa Cruz Island, California, from 1990 through 2000. The model for all seasons is Half-normal w/ cosine and is the base model and expansion term used to derive the density estimate; Type is whether the data were analyzed ungrouped or grouped into predefined intervals; and N is the total number of observations used to derive the estimates. Distance data were collected along transects annually from late November through early March (wet season).

Season	Abundance	Type	N
Wet 1990-91	579 \pm 97	Ungrouped	71
Wet 1991-92	1161 \pm 130	Ungrouped	114
Wet 1992-93	1940 \pm 300	Ungrouped	85
Wet 1993-94	2776 \pm 428	Grouped	91
Wet 1994-95	5315 \pm 984	Grouped	99
Wet 1995-96	801 \pm 108	Grouped	83
Wet 1996-97	1110 \pm 199	Grouped	78
Wet 1997-98	2444 \pm 454	Ungrouped	57
Wet 1998-99	2670 \pm 416	Ungrouped	112
Wet 1999-00	2753 \pm 387	Ungrouped	88

consisting of 150 random draws of abundance and its CV from the models generated in the previous steps. We then determined which percentile of the bootstrapped values the mean estimates of abundance and CV for each individual model fell.

Harvest Models

We incorporated annual harvest rates (h) from 5% to 95% at 5% intervals for models with three different starting levels of island-wide abundance (N_0): a low abundance model where $N_0 = 800$ (approximately 25% of K ; see RESULTS), a mean abundance model where $N_0 = 2400$ (75% of K), and a high abundance model where $N_0 = 5000$ (150% of K). Harvest effort was targeted equally among all sex and age classes for ten years. To simplify interpretation of the trajectories we set the environment as constant ($CV K = 0$) and eliminated catastrophes. We conducted 10,000 runs for each of the three models, then calculated the probability of eradication (Pr_e), the median time to eradication in years for $0 \leq Pr_e < 1$, the time to eradication for $Pr_e = 1$, and the mean percent reduction in abundance at each for the harvest rates in each model.

RESULTS

Abundance, population change, and carrying capacity

Abundance of feral pigs on SCI ranged from 579 (\pm 97 SE) in 1990/91 to 5315 (\pm 984 SE) in 1994/95 (Table 3). The coefficients of variation ranged from 11.1% to 18.9%. The population exhibited a “boom or bust” pattern, with a steady increase in abundance from 1990/91 through the wet season of 1994/95, followed by a severe crash the following year. The population recovered rapidly though, and continued to increase through the wet season of 1999/2000 (Fig. 1A). There was a significant negative relationship between lambda and N_{t-1} ($r = 0.769$, $F_{1,7} = 10.13$, $P = 0.015$). With the exception of the wet season 1994/95, lambda tended to decrease as island-wide abundance of the pigs approached 3000 (Fig. 1B). Abundance for lambda = 1 was 3400, which was used as the estimate of K .

Population structure and evaluation of the base model

Sex and age data were collected for a total of 2423 pigs. The sex ratio of the population was approximately 1:1 ($N = 1221$ females, $N = 1202$ males). Values for l_x between 1991 and 1998 are given in Table 4. Model-derived estimates from the GLM analysis indicated that variation in l_x was similar across years (Fig. 2).

Table 4 The estimated proportion of feral pigs surviving at the start of nine age classes (years) on Santa Cruz Island, California.

Age Class	1991	1992	1993	1994	1995	1996	1997	1998	Years Pooled
1	0.553	0.427	0.394	0.537	0.490	0.575	0.430	0.522	0.489
2	0.381	0.320	0.270	0.396	0.375	0.429	0.326	0.359	0.357
3	0.279	0.192	0.155	0.219	0.247	0.315	0.230	0.223	0.231
4	0.195	0.068	0.044	0.067	0.074	0.109	0.070	0.101	0.072
5	0.106	0.039	0.019	0.032	0.028	0.039	0.024	0.041	0.031
6	0.053	0.014	0.003	0.007	0.004	0.007	0.006	0.005	0.008
7	0.004	0.009	0.000	0.001	0.001	0.000	0.005	0.002	0.002
8	0.000	0.002	0.000	0.000	0.000	0.000	0.002	0.000	0.000

There were no simulated model runs where the population went naturally to extinction. The mean minimum estimate of abundance from the models based on individual years was 805 ± 23 SE and from jackknifed models 847 ± 8 SE. Mean maximum abundance from models based on individual years was 6257 ± 64 SE and from jackknifed models 6314 ± 63 SE. The range in percentile abundance among years for both individual and jackknifed models was 17.6%, with 90% of the mean estimates of annual abundance falling between 1200 and 5900 (Table 5). Although the relative range among the simulated estimates tended to be $< 20\%$, the greatest differences were in the 5th percentile. All mean abundance and CV abundance estimates from the individual models fell within the 32nd and 71st bootstrap percentiles. There was no significant difference in mean estimates of simulated feral pig abundances for models based on simulations

Table 5 Estimated percentiles of abundance from two groups of models simulating feral pig abundance on Santa Cruz Island, California. Individual models were simulations run separately for each year, as well as an additional one with years pooled. Jackknifed models were run with one year removed from each simulation. Each simulation consisted of 10,000 runs over a 150-year period.

Individual Models	Percentile				
	5th	25th	50th	75th	95th
1991	1641	2648	3088	3855	5018
1992	1643	2596	3061	3945	5230
1993	1583	2278	2869	3912	5892
1994	1621	2371	3089	3793	5460
1995	1640	2503	3378	4038	5023
1996	1501	2554	3145	3808	5214
1997	1466	2526	3117	3752	5052
1998	1200	2262	2907	3693	5699
Pooled	1252	2618	3424	4027	5337
Mean	1505	2484	3120	3869	5325
Range	443	386	555	345	874
Range (%)	29.4	15.5	17.8	8.9	16.4
Jackknifed Models	Percentile				
	5th	25th	50th	75th	95th
No 91	1293	2363	2980	3773	5687
No 92	1226	2065	2867	3501	5648
No 93	1518	2073	2603	3897	5683
No 94	1577	2255	3046	3790	5446
No 95	1333	2029	2850	3440	5404
No 96	1411	2372	2965	3672	5537
No 97	1383	2070	2824	3822	5671
No 98	1402	2225	3027	3604	5637
Pooled	1388	2429	3054	3799	5123
Mean	1392	2209	2913	3700	5537
Range	351	401	451	457	565
Range (%)	25.2	18.2	15.5	12.4	10.2

from individual years ($F_{8,1350} = 1.433, P = 0.178$) or the jackknifed models ($F_{8,1350} = 0.641, P = 0.744$).

Because there was little evidence of systematic differences among the models, we selected the base model to be the one with demographic rates derived from the years pooled together. The mean and CV of the simulated abundance estimates from the pooled model were well within the range of bootstrapped estimates, and deriving estimates of s_{x_i} and f_{x_i} from kill data collected across years was likely the most appropriate approach for integrating the observed temporal variability in vital rates into the simulations. The mean minimum and maximum abundance from 10,000 simulated 150-year time series of the base model were $669 (\pm 107$ SE) and $5645 (\pm 636$ SE), respectively. The mean value of λ was 1.118 ± 0.128 SE. The population did not reach zero in any of the simulations for the base model.

Harvest Models

The effects of increasing harvest rates (h) on pig abundance for the three initial levels of abundance are shown in Fig. 3. At low initial abundance ($N_0 = 800$) $h > 45\%$ was required to reduce abundance below N_0 , and $h > 60\%$ was required to prevent the population from becoming stable. Levels of abundance for $45\% < h \leq 60\%$ were 40-80% below $N_0 = 800$. Harvest rates $\geq 20\%$ initiated declines when $N_0 = 2400$, but $h > 45\%$ was required to keep the population from stabilising. Levels of abundance for $45\% < h \leq 60\%$ were 10-87% below $N_0 = 2400$. Severe declines in pig abundance were independent of harvest when $N_0 =$

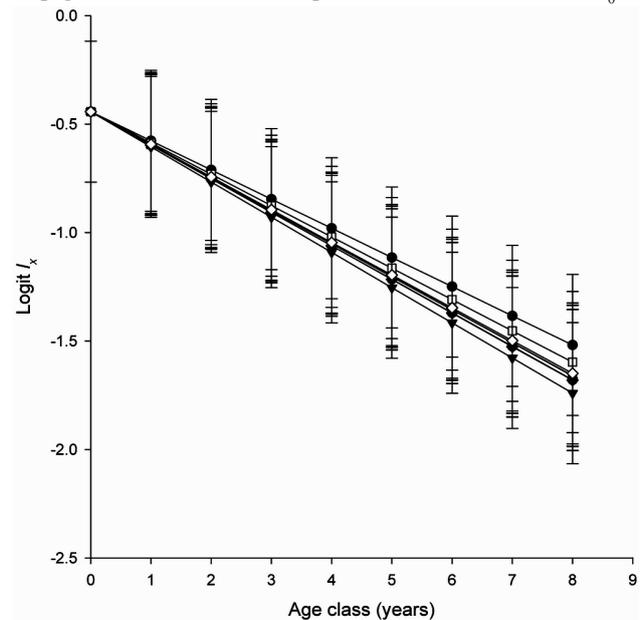


Fig. 2 Estimated variation in the proportions of feral pigs surviving at the beginning of eight age classes (l_x on a logit scale) from 1991-1998 on Santa Cruz Island, California. Year was modelled as a random effect, with each line representing the l_x distribution in any given year.

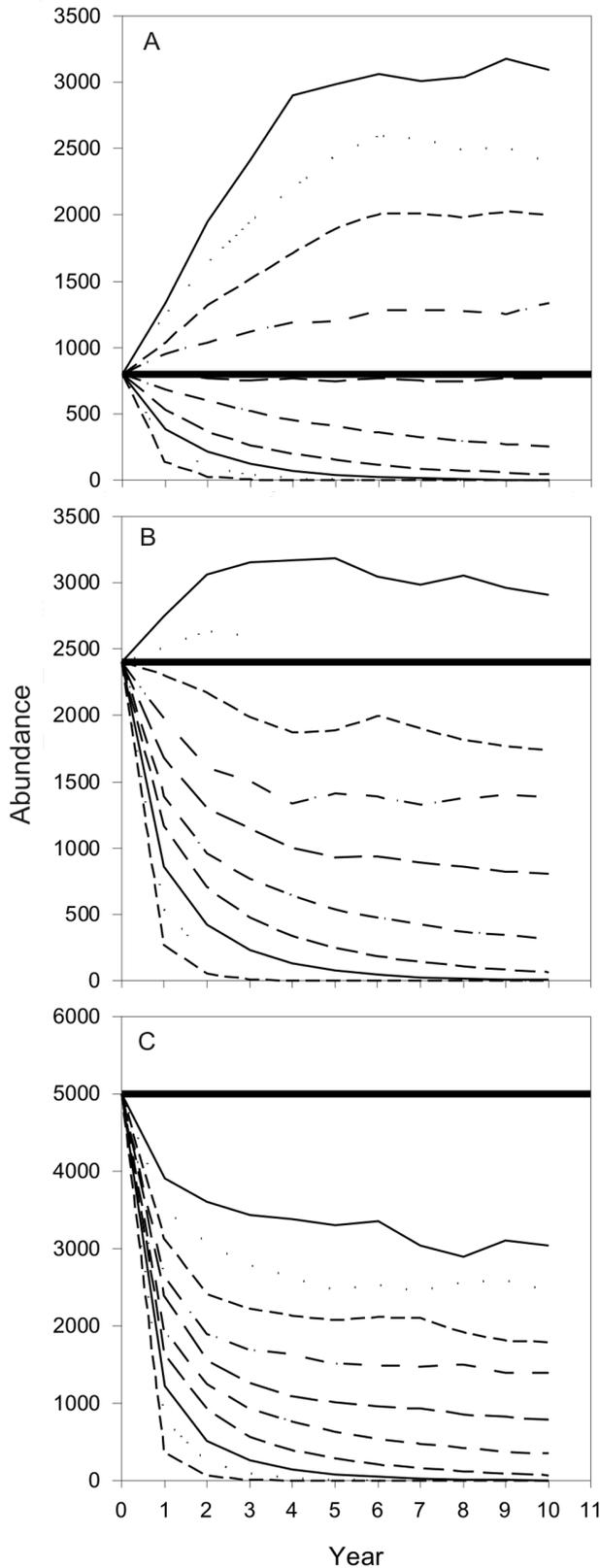


Fig. 3 Results of simulated harvest rates on a feral pig population on Santa Cruz Island, California, over a 10-year period. There were three starting levels of abundance (heavy black horizontal limit lines); $N_0 = 800$ (A), $N_0 = 2400$ (B), and $N_0 = 5000$ (C). Harvest rates range sequentially from 0 (solid line) to 90% in 10% increments.

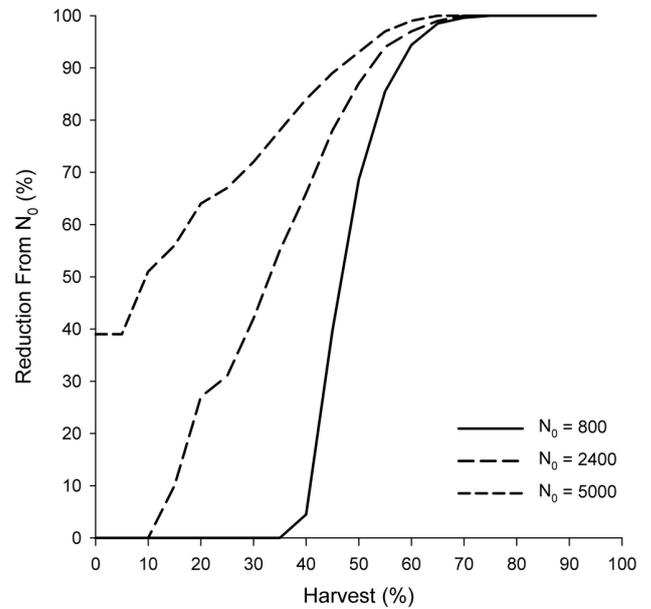


Fig. 4 Simulated rate of reduction at different harvest rates for a feral pig population on Santa Cruz Island, California. Simulations ($N = 10,000$) were run for three levels of initial abundance (N_0).

5000. Modest harvest rates of 10-35% during the decline phase when $N_0 = 5000$ reduced abundance to stable levels; levels of abundance for $10\% < h \leq 35\%$ were 26-68% below K . The population at $N_0 = 5000$ continued to decline when $h > 35\%$ (Fig. 3). The initial size of the population had a strong influence on proportional reduction relative to N_0 at low to moderate harvest rates (5%-50%), but the influence decreased as harvest rates approached 70% (Fig. 4). By year 10 of the simulations, the 95% confidence intervals for all three initial population sizes overlapped that of the unharvested population when $h < 10\%$.

There was no probability of eradication until $h > 70\%$ (Fig. 5). The probability of eradication (Pr_e) was < 1 for $70\% < h < 80\%$ (Fig. 5), but as h approached 80% Pr_e rapidly increased. For $h = 70\%$ values of Pr_e ranged from 0.02 to 0.09, but when $h > 75\%$ values of Pr_e ranged from 0.97 to 0.98. $Pr_e = 1$ when $h > 80\%$. There was

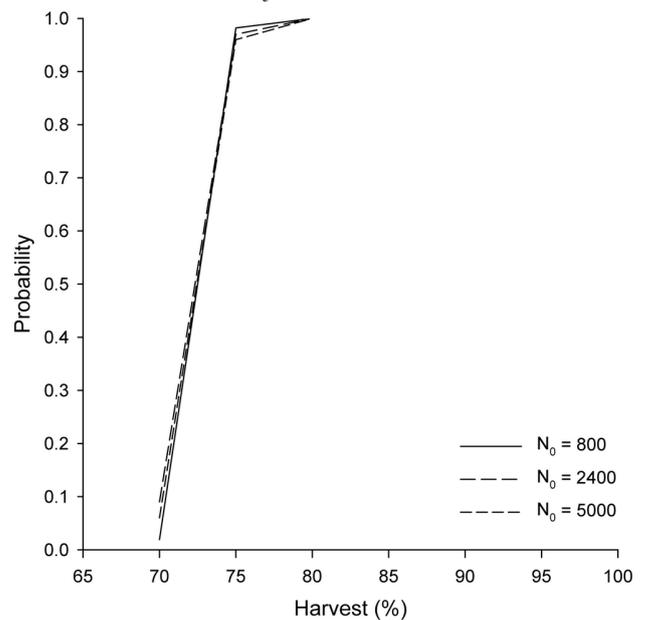


Fig. 5 Simulated probability of eradication at different annual harvest rates for a feral pig population on Santa Cruz Island, California. Simulations ($N = 10,000$) were run for three levels of initial abundance (N_0).

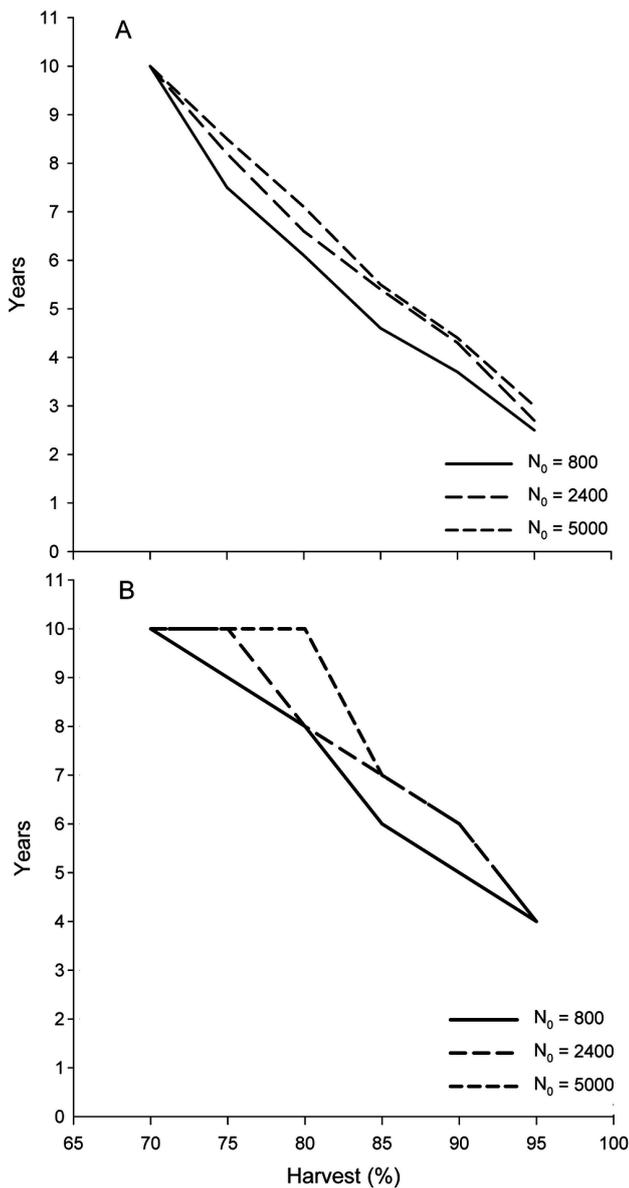


Fig. 6 Simulated time to eradication at different annual harvest rates for feral pigs on Santa Cruz Island, California. Simulations ($N = 10000$) were run for three levels of initial abundance (N_0). Panel (A) is based on the median number of years when probability of eradication (Pr_e) < 1 . Panel (B) is based on the number of years when $Pr_e = 1$.

no relationship between N_0 and Pr_e (Fig. 5), but N_0 did influence the number of years to eradication (Fig. 6). The median number of years to eradication ranged from ten (72% annual harvest rate) to 2.5 (95% annual harvest rate). There was a linear decrease in median years to eradication for all three levels of abundance (Fig. 6). Median years to eradication for programmes initiated when $N_0 = 800$ was predicted to be between 3 and 9 months less than those begun when $N_0 = 2500$. Programmes initiated when $N_0 = 800$ were predicted to be between 6 and 12 months shorter in duration than those begun when $N_0 = 5000$. Eradication programmes that began when $N_0 = 2500$ were predicted to be completed 1-6 months sooner than those initiated when $N_0 = 5000$ (Fig. 6).

Time to eradication when $Pr_e = 1$ decreased linearly with increasing rates of annual harvest for $N_0 = 800$. Time to eradication also decreased linearly when $h > 75\%$ for $N_0 = 2400$, while the pattern of decrease for $N_0 = 5000$ exhibited a more stepwise pattern (Fig. 6). Eradication programmes that were initiated when $N_0 = 800$ were generally a year shorter in duration than those that began when $N_0 = 2400$

for $70\% < h < 95\%$, and 1-2 years shorter than those that began when $N_0 = 5000$ for $70\% < h < 95\%$ (Fig. 6). Time to eradication when $Pr_e = 1$ for $N_0 = 2400$ and $N_0 = 5000$ were the same at all harvest rates except $h = 80\%$, which was the threshold value for $N_0 = 5000$ (Fig. 6).

DISCUSSION

Simulations of the effect of varying harvest rates on abundance of feral pigs modelled when a population was likely to be controlled and when it was likely to be eradicated. For example, attempts to manage pig populations with annual harvest rates below 10%, which are likely typical of sport hunting, will have little or no detectable effect on abundance (Barrett *et al.* 1988; Waithman *et al.* 1999). Harvest rates in the range of 15% to 50% will reduce and maintain numbers below that of a population that is not hunted, but abundance may still be greater than desirable relative to conservation goals. For instance, in models with moderate and high levels of initial abundance ($N_0 = 2400$ and $N_0 = 5000$), annual harvest rates below 45% resulted in population size in excess of 1000 individuals even after 10 years of hunting. When actual numbers of pigs were above this level on SCI, they continued to have undesirable ecosystem and species-specific effects, including widespread rooting and impacts to two species of rare endemic plants (Klinger *et al.* 2002; Klinger 2007). So, while pig numbers can be controlled with annual harvest rates between 15% and 50%, their reduced abundance may still be above that required to meet conservation objectives.

Mortality from hunting was largely compensatory at low annual harvest rates (5%), but became additive as rates increased beyond 10%. However, the importance of the additive mortality depended on harvest rates and the abundance of the population when hunting commenced. At low abundance, the rate of growth was high enough that, despite mortality being additive, control was unlikely if the annual harvest rate was between 5% and 40%. When initial population size was low, and annual harvest rates were between 45% and 65%, control became more likely. When initial population size was relatively high, but still below carrying capacity, control was likely when annual harvest rates exceeded 20%. This likely reflected the additive effects of harvest and the influence of negative density-dependence. Not surprisingly, when abundance exceeded carrying capacity strong negative density-dependence resulted in rapid population declines. Initiating harvest as the population declined pushed it to lower abundance than from density-dependent processes alone. When annual harvest rates were between 10% and 60%, the population still stabilised, albeit at progressively lower abundance. There was little likelihood of eradication unless annual harvest rates exceeded 75% per year. However, when harvest rates exceeded 75% then additive mortality had a very significant influence on the population and the likelihood of achieving eradication became independent of the initial level of abundance.

Although there was little possibility of eradication until annual harvest rates were greater than 75%, harvest rates between 60% and 70% reduced the population sufficiently for the pigs to be considered ecologically extinct. This condition would likely be acceptable if the goal of the management programme was control rather than eradication and there were financial resources available to sustain hunting. In this case, the effects of pigs as a transformer species would be eliminated and there would be far less likelihood of impact to high value species, such as rare endemic plants (Klinger *et al.* 2002). However, maintaining low numbers as a long term conservation strategy could be very risky. Animal removal programmes are controversial, so sustaining institutional support and financial resources for long-term control may be unrealistic when faced with

strong public opposition (Sagoff 2005; Perry and Perry 2008). Moreover, the expenditure of resources would be much greater to reduce and then maintain a population at low levels rather than implement a relatively short term but intense eradication programme (Cruz *et al.* 2005, 2007). These possibilities could result in situations that would be considered “a conservation nightmare”; that is, the cessation of control and the subsequent return of the population to previous levels of abundance (Campbell and Donlan 2005).

While the predicted ranges in abundance among the models tended to be relatively consistent, the results should still be interpreted with caution. Estimates of fecundity and survival derived from vertical life tables can be biased if data are collected from a single sample of a population when growth rates are not constant (Caughley 1977). Rates of change in the pig population were clearly not constant during the study, but our estimates of sex and age structure were collected across multiple years. This likely reduced error in the estimates, but some degree of bias is still possible (Caughley 1977; Skalski *et al.* 2005).

Comparison of the simulations with actual eradication programmes suggests that the estimates for time to eradication are realistic, though in some cases they may be somewhat conservative. For example, more than 18,000 feral pigs were removed from Santiago Island (Galapagos Islands; 584 km²) over a 30-year period, but the first phase of this project was largely a low-intensity effort with little evidence of substantial control (Cruz *et al.* 2005). When rates of removal were increased in 1995, the remaining few hundred pigs were eradicated within six years (Cruz *et al.* 2005). A similar pattern was reported from Santa Catalina in the Channel Islands (194 km²), where more than 12,000 pigs were removed from 1990–2003 (Garcelon *et al.* 2005). For the first seven years, the focus on Santa Catalina was control, but when it became an eradication programme in 1996, 2679 pigs were removed within seven years (Schuyler *et al.* 2002, Garcelon *et al.* 2005). Eradication of 200 pigs from a 57 km² fenced area at Pinnacles National Monument in central California, USA, was completed in 2.5 years (McCaan and Garcelon 2007), and 1206 pigs were eradicated from Santa Rosa Island (Channel Islands, California, USA; 215 km²) in three years (Lombardo and Faulkner 2000). Eradication of 143 pigs from Annadel State Park (20 km²) in central California was accomplished in under three years (Barrett *et al.* 1988).

Other cases suggest that eradication times can be substantially reduced from those predicted by the models. One factor is the size of the eradication area; eradication in very small areas with low pig density can be accomplished in a year or less (Kessler 2002). More important factors, though, may be a combination of resource allocation, technology, and hunting techniques, especially in larger areas. When eradication of feral pigs was undertaken on SCI, NPS and TNC invested considerable funds in fencing, helicopters, large numbers of hunters and dogs, Judas animals, strategically and tactically integrated hunting techniques, GIS and GPS technologies, and systematic monitoring (Morrison *et al.* 2007). These factors, as well as the commitment by NPS and TNC to eradicate and not control the population, resulted in the removal of 5036 pigs in 15 months, approximately 5–10 years less than anticipated (NPS 2003; Parkes *et al.* 2010).

The results of the simulations are likely applicable to many insular systems, but they may be less applicable to mainland systems where pigs have more predators and competitors (Barrett 1978). Competition between pigs and other vertebrates is rarely reported, and when it does exist it may alter patterns of distribution rather than reduce abundance (Ilse and Hellgren 1995). Predation could lead to significantly different estimates of vital rates though, especially survival (Woodall 1983, Okarma *et al.* 1995).

Moreover, dispersal from areas where pigs are not being controlled is likely to act as a “rescue effect” for sink populations where control efforts are underway (Barrett *et al.* 1988). Indeed, in many areas, eradication may not be a feasible option unless expensive measures are taken to prevent recolonisation (Hone *et al.* 1980; Barrett *et al.* 1988; Garcelon *et al.* 2005; McCaan and Garcelon 2007). In situations where such measures (eg. fencing) cannot be used, there may be few options other than control. At that point, a key decision will be what long term harvest rates can be sustained to prevent pigs from becoming too abundant (Cowled *et al.* 2006).

MANAGEMENT IMPLICATIONS

Our models suggest that, in general, a strategy of intense harvest for five years will likely eradicate many insular feral pig populations. When options are limited to some form of control, development of population models would be a substantial aid in justifying target harvest rates and developing monitoring programmes to evaluate if conservation goals are being met. But even when institutions are willing to commit fully to eradication, investing in the collection of several years of data to develop models projecting the likelihood of eradication for different harvest scenarios would help with planning and design.

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