EFFICACY OF FERAL PIG REMOVALS AT HAKALAU FOREST NATIONAL WILDLIFE REFUGE, HAWAI`I

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Abstract: We compiled and analyzed data from 1987 to 2004 on feral pig (*Sus scrofa*) population indices affected by control methods at Hakalau Forest National Wildlife Refuge, a tropical montane rainforest on the island of Hawai`i. These population data included annual sign surveys, the number of pigs removed from fenced management units, and age and reproductive status from necropsies. There was an even sex ratio (1 female:1.02 males) within the population and within age classes. Boars lived to 60 months while sows lived to 48 months. Pregnancy occurred throughout the annual cycle, but lactation peaked in April–June. Reproductive rates also increased with age, peaking at 2–4 years in sows. We reconstructed the standing population within a 2,024-ha closed unit to examine demographic processes. We estimated that annual removal of >41–43% of the population was necessary to affect a decline. Annual sign surveys showed a strong and sustained decline in pig activity after 1997 relative to unmanaged areas. When compared with staff or public hunting, snaring was the most efficient control method.

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Key words: activity index, control methods, eradication, feral pigs, Hawai`i, removals, *Sus scrofa*.

Feral pigs (*Sus scrofa*) modify native plant communities in continental and insular ecosystems through rooting and herbivory. In Hawai`i, feral pigs disperse alien plants (Diong 1982, Aplet et al. 1991, LaRosa 1992), inhibit native plant regeneration (Cooray and Mueller-Dombois 1981, Diong 1982), selectively browse and destroy native plants (Ralph and Maxwell 1984, Stone 1985), spread plant pathogens (Kliejunas and Ko 1976), accelerate soil erosion (Stone and Loope 1987), and alter nutrient cycling (Singer 1981, Vitousek 1986). Feral pigs in Hawai`i also create nutrient-rich wallows and troughs in tree fern trunks (*Cibotium* spp.) where alien mosquitoes (*Culex quinquefasciatus*) breed (Stone and Loope 1987). Mosquitoes are vectors for avian malaria (*Plasmodium relictum*), which has contributed to the decline of Hawaiian forest birds (Atkinson et al. 1995).

Removing feral pigs can have substantial benefits for the native Hawaiian avifauna by reducing the breeding habitats of malaria-carrying mosquitoes and increasing the recovery of native vegetation (Loope and Scowcroft 1985, Loope et al. 1991, Loh and Tunison 1999). Eradication of feral pigs in Hawai`i is difficult, particularly in the forest environments where they are the greatest threat to native biota. Feral pigs are cryptic, elusive, and have a high reproductive potential that allows populations to quickly rebound after reduction. Simple simulation models indicated that 30–40% semiannual removal would be required to maintain pigs at half their equilibrium density in Hawaiian forests (R. H. Barrett and C. P Stone. 1983. Hunting as a control method for wild pigs in Hawaii Volcanoes National Park, Hawaii Volcanoes National Park). Traditional means for this level of population control can be labor intensive and costly (Hone and Stone 1989).

The effectiveness of eradicating feral pigs in montane mesic forests by hunting with dogs was evaluated in Hawai`i Volcanoes National Park (HAVO), and the eradication rate was 20 worker-hours per pig (Katahira et al. 1993). Snares have been evaluated in remote rainforests

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on Maui. Although the terrain on Maui was more rugged than that on Hawai`i Island, the eradication rates were 7 hours per pig in a densely populated unit and 43 hours per pig in a more remote unit (Anderson and Stone 1993). Hakalau Forest National Wildlife Refuge (HFNWR) has been controlling and monitoring feral pigs since 1988 through public hunting, staff hunting, and snaring. Control methods vary substantially in their efficacy, but an analysis has never been done to assess their effectiveness and the effort required.

The objectives of this work were to: (1) summarize necropsy data on the age and sex composition and reproductive rates of feral pigs; (2) reconstruct population dynamics in a management unit based on the ages of removed pigs; (3) summarize surveys of feral pig activity; (4) relate the standing population within a management unit to activity surveys in a predictive model of feral pig density; (5) apply the predictive model to estimate densities of feral pigs in other management units; and (6) evaluate the efficacy of several control methods.

STUDY AREA

Hakalau National Wildlife Refuge (19°47´N, 155°18´W) is a tropical montane rainforest ranging in elevation from 750 to 2,000 m on the windward slope of Mauna Kea volcano on Hawai`i (Fig. 1). The refuge and associated management and monitoring activities were established in 1987 to protect endangered Hawaiian forest birds, but HFNWR also contains many rare and endangered plants and invertebrates. Although degraded by feral pigs and cattle for more than a century, large stands of old-growth `ōhi`a (*Metrosideros polymorpha*) and koa (*Acacia koa*) dominate the 15–30 m tall forest canopy. Understory shrubs and trees that may be sensitive to feral pigs include `ōlapa (*Cheirodendron trigynum*), `ōhelo (*Vaccinium calycinum*), pūkiawe (*Styphelia tameiamaeiae*), and tree ferns. Dense vegetation, high annual rainfall (approximately 250 cm), dissected terrain, and road access limited mostly to higher elevations make pig control efforts logistically challenging.

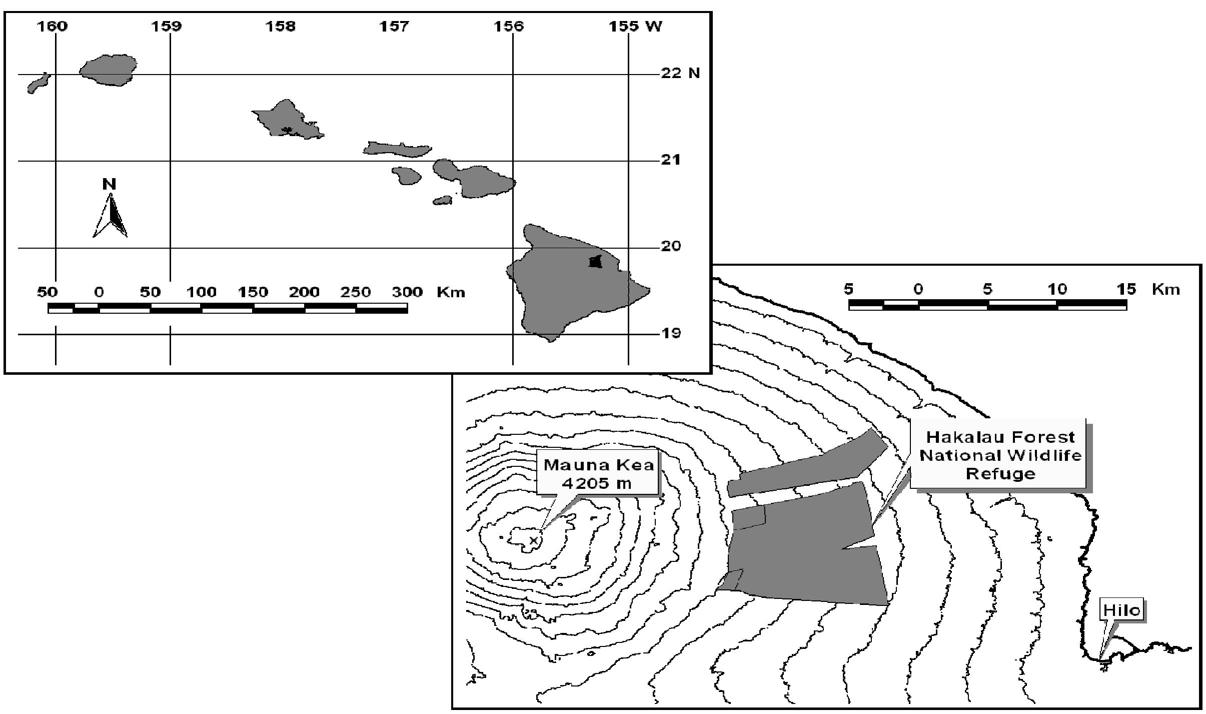

Fig. 1. The Hawaiian Islands and Hakalau Forest National Wildlife Refuge on Hawai`i.

METHODS

Data collected included the effort in person-days used to remove feral pigs using 3 different control techniques. Control efforts were carried out in 8 fenced units from 1988 to 2002, and pig activity was surveyed within 6 management units and an unmanaged area. Sex and reproductive status was determined from necropsies of 968 pigs done from 1988 to 1999. The ages of 636 pigs were estimated using tooth eruption and wear patterns (Matschke 1967).

Sex Ratio and Reproductive Status

We examined the sex ratio for 711 pigs of known sex. This analysis was restricted to 320 boars and 316 sows of known age to determine whether there was an age-related bias in sex ratio. The boars and sows within 6 age classes were evaluated for differences in sex ratios by age class with a χ^2 test. We examined potential reproductive rates and seasonality in reproduction of 327 sows by calculating the proportion of sows with corpora lutea (pregnancy scars), embryos, lactating teats, and the median and mean (and SE) number of corpora lutea, embryos, and lactating teats per sow. These data were aggregated across years to determine the proportion (and binomial SE) of pregnant and lactating sows by annual quarters to assess seasonality in reproduction. We also examined a subset of 304 aged sows to determine pregnancy, lactation, and corpora lutea by age class. Differences in reproductive rates between time periods and age classes were determined with χ^2 tests.

Population Reconstruction

We reconstructed the standing population of feral pigs from 1988 to 2004 in a 2,024-ha management unit from the number of pigs removed and their estimated ages. Dates of birth were back-calculated from necropsy and the estimated age of each animal according to Anderson and Stone (1994). The ages of 11 additional pigs were estimated by a regression equation using mass and sex as predictors (Hess et al. in press). Standing populations were estimated by calendar-year time steps to determine how many animals had been born into the population and not removed. Because ages were available for 634 of the 757 pigs (83.8%) removed, the number of pigs in the reconstructed population was corrected for the proportion of aged pigs in each age category based on the available data. We also assumed that the last 3 pigs found snared on 23 February 2004 were present since 2000, and that they were snared before 2004.

Using the total number of feral pigs removed (*R*) each year (*T*) from the unit and the reconstructed population (*N*), we calculated the proportion of the population removed as R_T/N_T and the change in population from year to year as N_{T+1}/N_T. The population change was regressed on the proportion removed to estimate the proportion of removal at which no change in standing population could be expected. We did not use data after 2000 because there were apparently <5 feral pigs remaining in the unit, resulting in proportion values of 0 or 1.

Activity Indices

Activity indices for feral pigs consisted of the presence of fresh or intermediate sign at 428 stations, each with 20 100-m^2 sample plots (Stone et al. 1991), compiled for 1987, 1990, and 1992–2004 (total = 29,881 plots). These data were joined to spatial coordinates and plotted annually using ArcView 3.2 (ESRI 1999). Stations were assigned to management units by UTM coordinates, and the proportion of 100-m^2 sample plots with fresh, intermediate, or both fresh and intermediate feral pig sign was calculated within each management unit.

We used a general linear model to examine the effect of inter-observer variability on feral pig activity indices after controlling for the effects of year and management unit. We designated the observer who had surveyed the most transects (JJJ) as the reference observer and all other observers were evaluated with respect to the reference observer. Observers who had surveyed <5 transects were grouped for analysis. We treated management units as a class variable and set the reference level to be unenclosed, unmanaged areas. We also treated year as a class variable, and the reference level was the first survey in 1987. We used observer, year, and management unit as predictors of the proportion of plots with either fresh or intermediate sign. We estimated least square means for all levels. Because there were many levels within each factor, significant factors contributing to variability in sign were evaluated as α = 0.05 ÷ the total number of levels within each factor. We did not use a repeated-measures design because plots were at different locations each year, additional transects and management units were added, and observers changed repeatedly in a nonrandom manner.

Indexing Pig Density

We used the known density from population reconstruction and activity indices to develop predictive models of feral pig indices. These analyses were restricted to the 2,024-ha unit after a pig-proof fence enclosed the population in 1992. The estimated standing population each year was divided by the area of the unit to determine pig density and these values were used as the response variable for regression analysis. We determined the proportion of plots with fresh, intermediate, and all sign for each calendar year. Arcsine-transformed proportions (Sokal and Rohlf 1981) were used as predictor variables in linear regression following the approach of Anderson and Stone (1994). Precipitation 30 days before activity surveys was an auxiliary predictor. Weather data were gathered from a National Climatic Data Center (Asheville, North Carolina, USA) automated climate station at Keanakolu Camp for 1986 through 2004. Models were constructed with all combinations of predictors except where the same predictors appeared more than once (e.g., fresh sign with all sign) both with and without intercepts (i.e., constant proportion indices) (Lancia et al. 1994). Interaction terms were not used because of insufficient data. Models were ranked with Akaike's Information Criterion corrected for small sample sizes (AIC_c) (Burnham and Anderson 1998). We determined 90 and 95% confidence intervals (CIs) from the estimated regression equations of the highest ranked models for the benefit of HFNWR managers.

Predicting Density in Other Units

The regression equation of the highest ranked model was used to predict density or the number of feral pigs in other management units and areas. We estimated densities in unenclosed areas and estimated population sizes within enclosed units with 90 and 95% predictive CIs based on the estimated regression equation, its variance, and the area of enclosed units.

Evaluating Removal Methods

We evaluated the efficiency of 3 methods of feral pig control—public hunting, staff hunting, and snaring—from 1989 to 2004. Data were based on the removal of 1,463 feral pigs with 1,939 person-days of effort, and analyzed as the number of pigs per person-day removed from management units within a calendar year. There were 44 cases with sufficient documentation for this analysis. There was public and staff hunting within the same units in 3 of 28 cases but, except in 1 case, snaring was exclusive of all other hunting. Before 1998, a small number of snares were deployed during staff hunting, but the effort expended for these methods was not recorded. Therefore, snaring before 1998 could not be evaluated. We used a general linear model to evaluate the effects of method, year, and management unit on the response variable pigs per person-day. Bonferroni adjustments were used for pairwise comparisons of the least squares means between control methods.

RESULTS

Sex Ratio and Reproductive Status

Capture and necropsy data from 711 feral pigs revealed 352 sows and 359 boars yielding an even female:male sex ratio of 1:1.02. Among 636 pigs of known age, there were no significant differences between sexes within 6 age classes (χ^2 = 5.1, df = 5, P > 0.40) (Fig. 2). The maximum age of boars was 60 months; the maximum age of sows was 48 months. Of the 352 sows captured, reproductive status was determined from necropsies for 327 animals (Table 1). Of the 327 sows, 77 (23.5%) were pregnant. The number of embryos per pregnancy ranged from 2 to 12. The mean number of embryos was 6.69 (± 0.22 SE); the median number of embryos was 7. Only 2 of 34 (5.9%) lactating sows were pregnant. Among 28 lactating sows, the average number of lactating

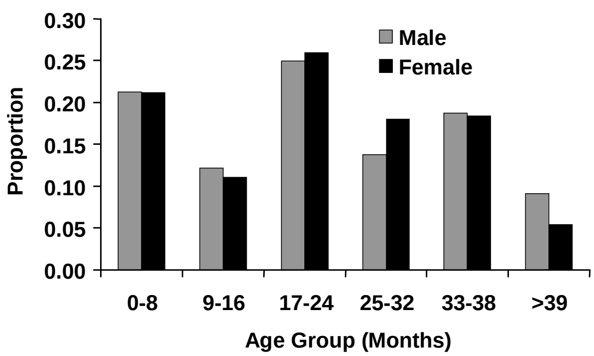

Fig. 2. Age distribution by sex of 636 known-age feral pigs from 1989 to 1999 at Hakalau Forest National Wildlife Refuge, Hawai`i.

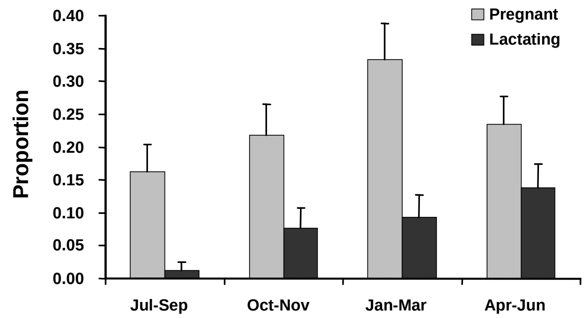

Fig. 3. Quarterly proportions (mean + binomial SE) of pregnant and lactating feral pig sows (*n* = 327) at Hakalau Forest National Wildlife Refuge, Hawai`i, 1988–1999.

Table 1. Proportion and binomial SE of 304 known-age feral sows by age class that were pregnant, lactating, or with corpora lutea at Hakalau Forest National Wildlife Refuge, Hawai`i, 1988–1999.

Age	Total	Pregnant			Lactating			Corpora lutea		
Yr	*n*	*n*	Proportion	SE	*n*	Proportion	SE	*n*	Proportion	SE
0–1	88	6	0.068	0.027	0	0.000	0.000	10	0.114	0.034
1–2	90	20	0.222	0.044	13	0.144	0.037	37	0.411	0.052
2–3	109	42	0.385	0.047	10	0.092	0.028	66	0.606	0.047
3–4	17	6	0.353	0.116	2	0.118	0.078	9	0.529	0.121

teats was 4.96 (± 0.42 SE); the median number of lactating teats was 5. In 124 sows, the mean number of corpora lutea was 8.51 (± 0.33 SE); the median number of corpora lutea was 8.

Although sows were pregnant in every month except November, which we attributed to low sample size (*n* = 14), there was marked seasonality in reproduction. The annual peak of pregnancy, although not significant, was January–March and the low was in July–September (χ^2 = 6.5, df = 3, *P* < 0.09) (Fig. 3). The number of lactating sows differed significantly among quarters, with a peak in April–June and a low in July–September (χ^2 = 9.2, df = 3, *P* < 0.03) (Fig. 3). No sows were lactating in January or August–September. There were marked differences in reproduction among age classes in 304 sows. The number of pregnant sows differed strongly among age classes (χ^2 = 27.9, df = 3, *P* < 0.001) (Table 1), and the number of lactating sows also differed among age classes (χ^2 = 12.9, df = 3, *P* < 0.005) (Table 1). Sows $\leq$1 year old showed no evidence of lactation. Pregnancy rates and the presence of corpora lutea were highest in sows 2–3 years old, but the proportion of lactating sows did not increase predictably with age. There was high variability in all measures of reproduction among 3–4 year old sows, reflecting the small sample size for this age class. Although the mean number of lactating teats and corpora lutea in 2- to 3-year-old and 3- to 4-year-old sows, respectively, were slightly lower than that in younger sows, median numbers of embryos, lactating teats, and corpora lutea increased with age (Table 2)

Population Reconstruction

The standing population of feral pigs in the 2,024-ha acre management unit was reconstructed from 634 (83.8%) aged pigs of the 757 pigs removed from the unit (Fig. 4). The increase in the reconstructed population from 1988 to 1992 reflected immigration during this period. In 1995, management efforts temporarily ceased for administrative reasons, but lower pig density after 1998 most likely increased the difficulty of removal. When year-to-year population change was plotted on the proportion of the population removed, the estimated point at which the population remained stable (population change = 1.00) occurred at an annual removal level of 43.2% (Fig. 5). There was a strong linear relationship (R^2 = 0.91, P < 0.001) between population change and proportion removed. Using only the data from the closed period, the relationship was still strong (R^2 = 0.80, P = 0.001), yielding a similar estimate of the point at which the population remained stable (41.3%).

Table 2. Mean, SE, and median number of embryos, lactating teats, and corpora lutea among 304 known-age feral sows by age class at Hakalau Forest National Wildlife Refuge, Hawai`i, 1988–1999.

Age	Embryos				Lactating teats				Corpora lutea			
yr	*n*	Mean	SE	Median	*n*	Mean	SE	Median	*n*	Mean	SE	Median
0–1	6	5.33	0.92	4.5	0	0.00	0.00	0.0	10	7.70	1.71	6.5
1–2	20	6.60	0.30	6.0	13	4.85	0.56	4.0	37	7.78	0.51	7.0
2–3	42	6.95	0.32	7.0	10	4.50	0.79	4.5	66	8.82	0.44	8.0
3–4	6	7.00	0.52	7.5	2	7.50	0.50	7.5	9	8.78	1.01	10.0

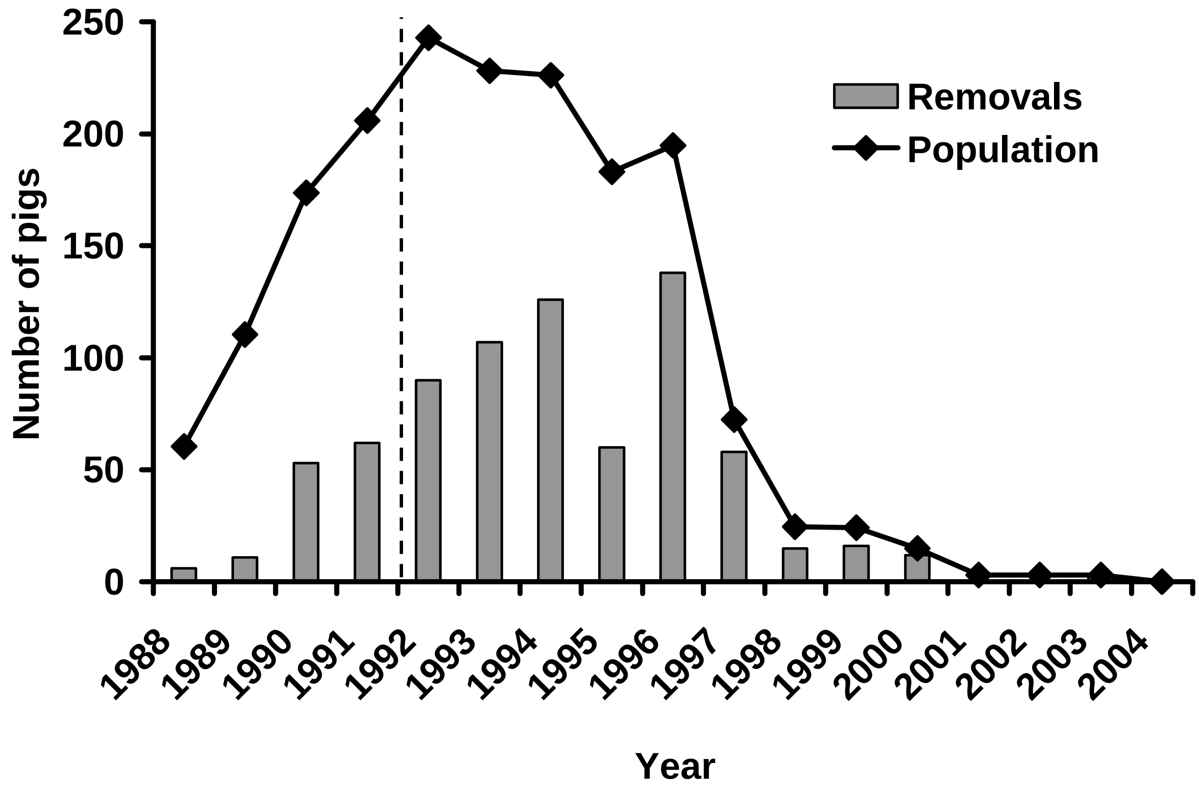

Fig. 4. Reconstructed population and the number of feral pigs removed by year from a 2,024-ha management unit at Hakalau Forest National Wildlife Refuge, Hawai`i, 1988–2004. The unit was enclosed in 1992 (vertical dashed line).

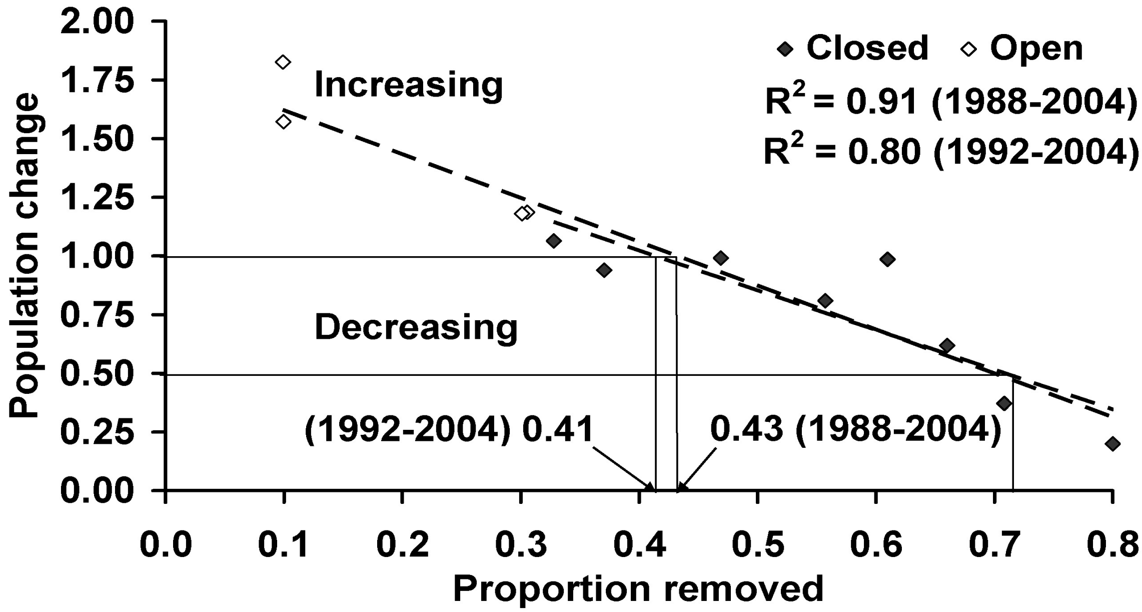

Fig. 5. Population change as a result of the proportion of feral pigs removed based on a population reconstruction from a 2,024-ha management unit at Hakalau Forest National Wildlife Refuge, Hawai`i, 1988–2004. The unit was enclosed in 1992.

Feral Pig Activity Indices

In a general linear model, inter-observer variability, year, and management unit were significant factors influencing the proportion of plots that had either fresh or intermediate feral pig sign ($P < 0.001$). The number of different observers who participated in activity surveys in 15 different years was 39; 20 observers surveyed more than 5 transects and were treated separately, and 19 observers were combined and treated as a single observer. Only 7 observers differed from the reference observer in their detection of sign ($P < 0.002$). Surveys in 9 years differed from the reference year (1987) ($P < 0.003$). There was an increase in sign from 1987 to 1990, but there were more sign in 1987 than in 1997–2004 (Fig. 6). Managed units had fewer sign than unmanaged areas ($P < 0.007$).

Indexing Pig Density

Models of pig sign were significantly and positively related to pig density, but precipitation alone was not a significant predictor. Models with all sign, fresh sign, and intermediate sign, but without intercepts, were essentially equivalent among the highest ranked by AIC_c (Table 3). The highest ranked model with an intercept ranked >2.6 AIC_c units lower than any of the 3 highest ranked models. Precipitation was not a factor among the 6 highest ranked models. Activity indices were variable at densities > 8/km^2 (Fig. 7). In every model, 1994 was a strong outlier because there was high pig density with a relatively low activity index. A small number of pigs remained after most had been removed by 2000, resulting in 4 points at low density. This caused the estimated regression intercepts to be negative in most cases. Because models without intercepts have rescaled R^2 values, models with and without intercepts could not be compared using this criterion.

Predicting Density in Other Units

When applied to other management units, the model derived from the 2,024-ha unit predicted highly variable densities of feral pigs primarily

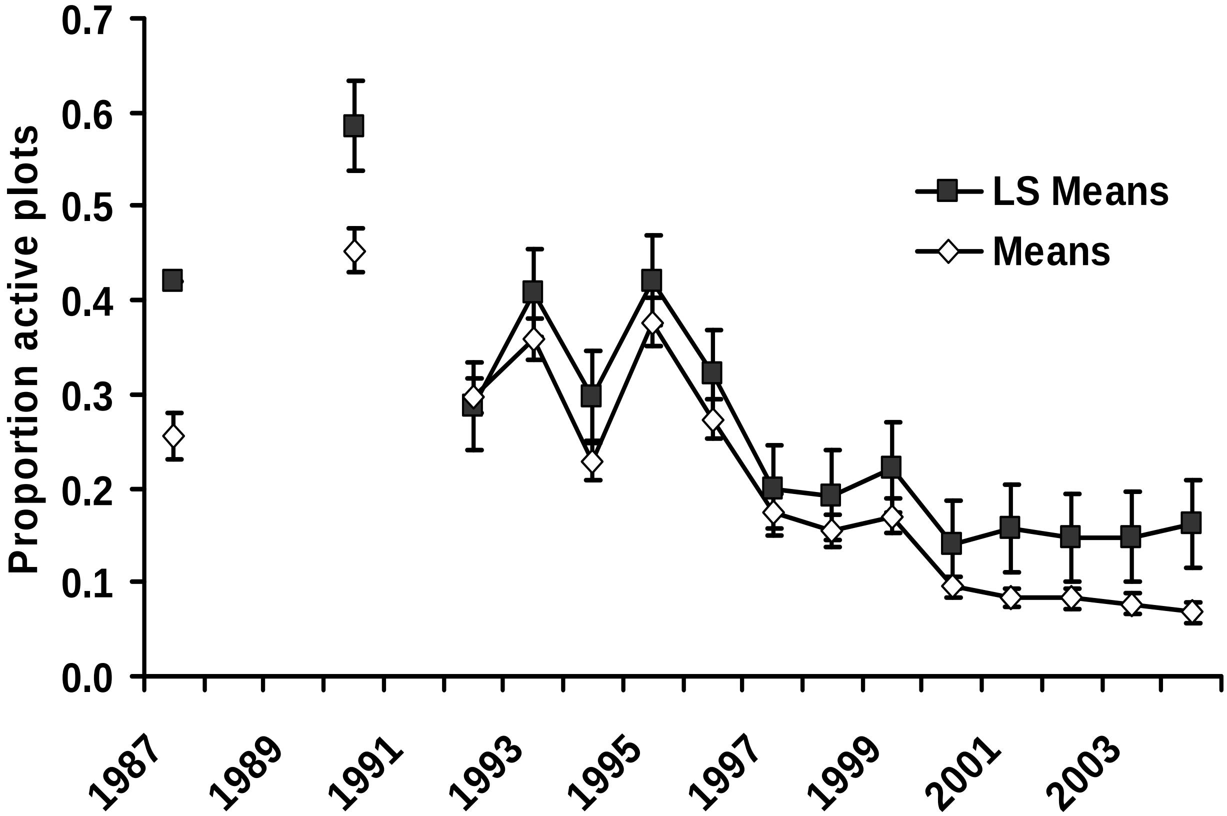

Fig. 6. Means and least square (LS) means of pig activity surveys across all management units at Hakalau Forest National Wildlife Refuge, Hawai`i, 1987–2004. Data represent the mean proportion of 100-m^2 sample plots with either fresh- or intermediate-age feral pig sign.

because of annual variability in pig sign within units, reflecting ingress in some cases (Fig. 8). The unmanaged area of Middle Maulau and Unit 3 had predicted densities of feral pigs that were ≥2.5 times greater than the Unit 2 maximum of 12.1 pigs/km^2. The density predicted in Unit 4 also exceeded the 2,024-ha unit maximum in 1993, but is unreliable because density was greater than the data used to derive the model. The predicted population of pigs in Units 1 and 4 terminated at 0 in 2002 and 2000, respectively. The predicted terminal population of Unit 3 was 118 ± 36 (90% prediction CI) in 2004, while Unit 6 contained 24 ± 20 pigs. Unit 7 had a variable but low predicted population ranging from 0 to 17 from 2000–2004.

Evaluating Removal Methods

In the general linear model, control method ($P = 0.001$), but not year ($P < 0.081$) or management unit ($P > 0.55$), was a significant factor in the efficiency of control effort. When management unit was removed as a factor from the model, control method ($P < 0.001$) remained highly significant, and year ($P < 0.057$) was marginally non-significant. Year was retained as a factor in the final model to control least square means for some of the density imbalances between years. In pairwise comparisons, the least square mean for snaring was greater than staff hunting ($P < 0.039$) by 0.95 ± 0.35 (SE) pigs per person-day, and greater than public hunting ($P < 0.0004$) by 1.51 ± 0.33 (SE) pigs per person-day (Fig. 9). There was no significant difference, however, between staff hunting and public hunting ($P > 0.10$).

DISCUSSION

We determined several demographic measures and vital rates from necropsies of feral pigs removed from HFNWR. Importantly, these data

Table 3. Predictive models for estimating feral pig density derived from a reconstructed population at Hakalau Forest National Wildlife Refuge, 1992–2004. Indices of activity (fresh, intermediate, or all sign) were arcsine transformed. Precipitation (precip) represents rainfall (mm) 1 month before surveys at Keanakolu Cabin, Hawai`i.

n	K	AIC	AIC*c*	Δ AIC*c*	Var S	*P* value	Model
13	1	22.50	24.87	0.00	2.290	< 0.001	20.7 * all sign
13	1	23.17	25.53	0.67	2.350	< 0.001	26.4 * intermediate sign
13	1	23.46	25.83	0.96	2.376	< 0.001	34.6 * fresh sign
13	2	23.30	28.50	3.63	2.283	< 0.001	- 1.1 + 23.4 * all sign
13	2	23.79	28.99	4.13	2.328	< 0.001	- 1.2 + 30.3 * intermediate sign
13	2	24.22	29.42	4.55	2.366	< 0.001	16.2 * fresh sign + 14.2 * intermediate sign
13	2	24.47	29.67	4.81	2.389	< 0.001	20.5 * all sign + 0.01 * precip
13	2	24.96	30.16	5.30	2.435	< 0.001	25.7 * intermediate sign + 0.02 * precip
13	2	25.21	30.41	5.54	2.457	< 0.001	- 0.5 + 36.6 * fresh sign
13	3	22.44	31.11	6.25	2.146	< 0.001	- 2.71 + 31.9 * intermediate sign + 0.1 * precip
13	3	23.87	32.53	7.67	2.267	< 0.001	- 2.0 + 24.0 * all sign + 0.1 * precip
13	3	25.06	33.73	8.87	2.374	< 0.001	- 1.1 + 13.7 * fresh sign + 19.7 * intermediate sign
13	3	25.46	34.13	9.26	2.482	< 0.001	34.6 * fresh sign - 0.002 * precip
13	3	26.19	34.85	9.99	2.478	< 0.001	15.3 * fresh sign + 14.7 * intermediate sign + 0.08 * precip
13	3	27.09	35.75	10.89	2.566	< 0.001	- 0.8 + 36.7 * fresh sign + 0.02 * precip
13	4	24.42	37.42	12.56	2.261	< 0.001	- 2.8 - 2.4 * fresh sign + 33.9 * intermediate sign + 0.1 * precip
13	1	47.65	50.01	25.14	6.023	0.056	0.2 * precip
13	2	45.33	50.53	25.67	5.330	1.000	4.7 - 0.0 * precip

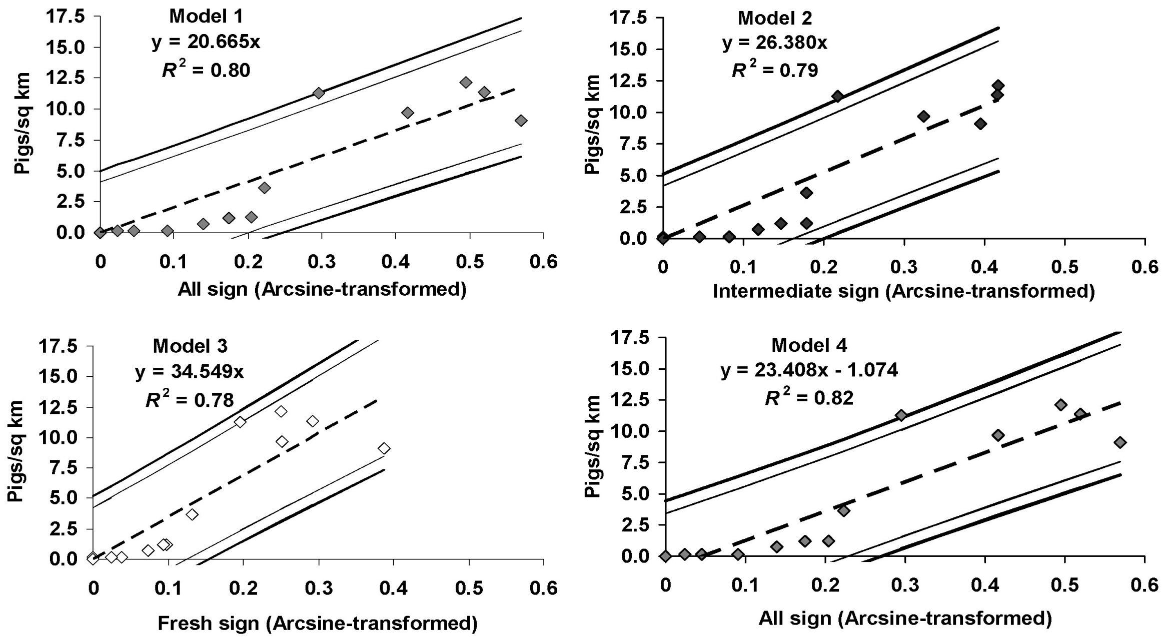

Fig. 7. Highest ranked predictive models for estimating feral pig density derived from a reconstructed population and pig sign at Hakalau Forest National Wildlife Refuge, Hawai`i, 1992–2004. Dashed lines represent models, solid light lines represent 90% prediction confidence intervals (CIs), and solid bold lines represent 95% prediction CIs.

represented only the removed feral pigs; data from the pigs remaining after removal efforts may have differed in subtle respects. For example, we might expect pigs with cumulative exposure to hunting experiences to be older than the pigs that were removed. Food preferences or behavioral differences between sexes could also result in differential tooth wear and bias age data. The longevity and even overall sex ratio we found at HFNWR were similar to that of feral pigs in Kipahulu Valley, Maui, except Kipahulu pigs exhibited age-specific variation in sex ratio (Diong 1982).

Although sows were pregnant year round at HFNWR, pregnancy was lowest during July–September and highest during January–March. Lactation followed this same general pattern with a lag such that the peak in lactation occurred in April–June. These data suggest a delay compared to Diong's (1982) November–March farrowing season in Kipahulu Valley, Maui. Given these results, August–November is when management is most likely to be effective at HFNWR if perinatal mortality has already reduced the number of young pigs. Ideally, enclosure of new management units and removal of pigs should not commence during the annual peak period of farrowing. Pregnancy and lactation also varied with age. Although no sows <1 year old were lactating at the time of necropsy, we found a small number that were pregnant and others that had pregnancy scars, indicating that young sows may occasionally bear litters. Giffin (1978) reported successful breeding by sows at 10 months old. Although 2–3 years was the prime age for pregnancy, the pattern for lactation was not as clear, apparently peaking at 1–2 years old. The number of embryos per pregnancy (range 2–12; median = 7), and the median number of lactating teats (5) demonstrated a high reproductive potential. Therefore, when new management units are enclosed, removals should commence immediately and all available resources should be committed without interruption to the unit.

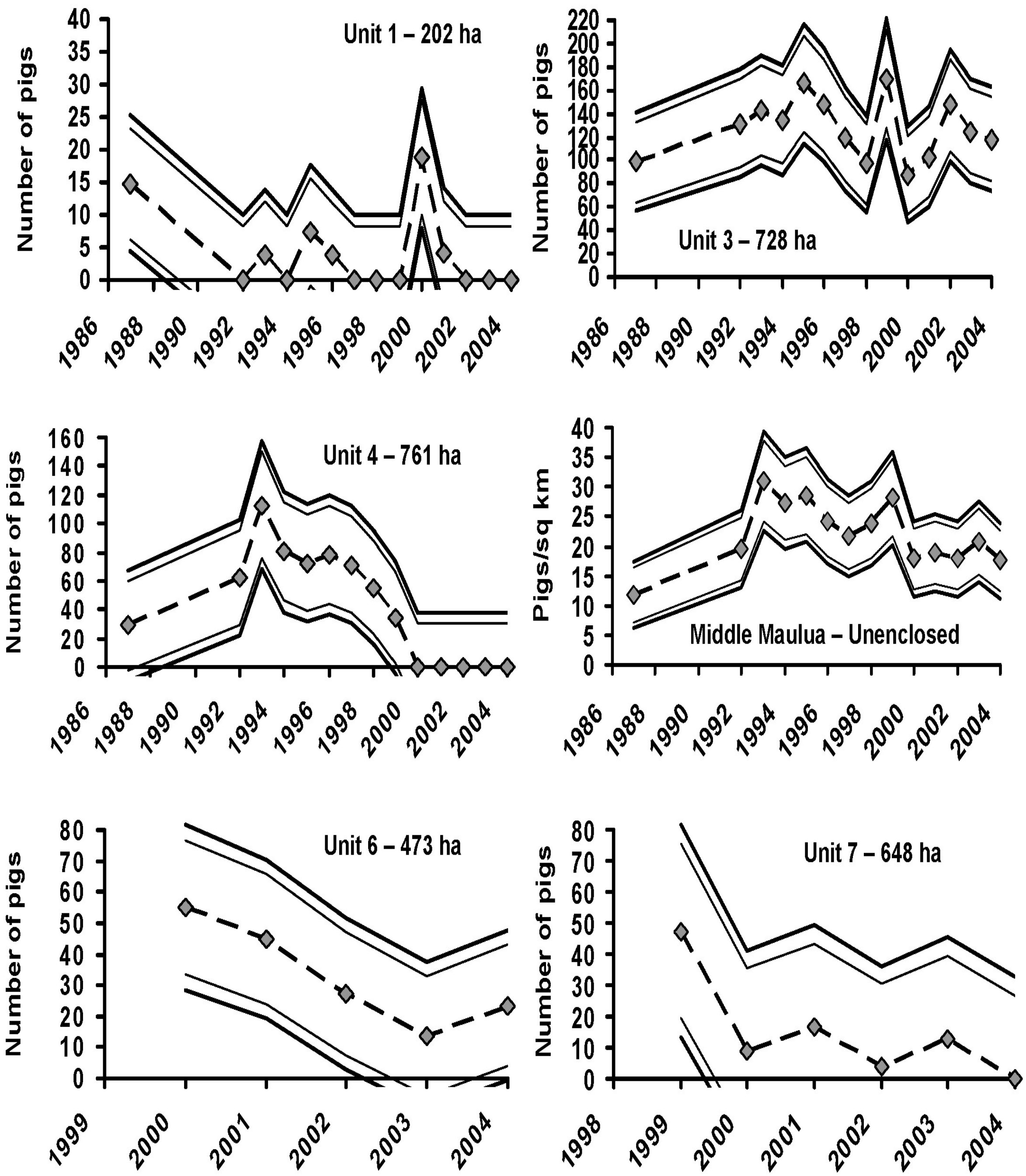

Fig. 8. Predicted feral pig abundance in 5 closed management units and an unmanaged, unenclosed area based on a model of all pig sign at Hakalau Forest National Wildlife Refuge, Hawai`i, 1987–2004. Dashed lines represent model predictions, solid light lines represent 90% prediction confidence intervals (CIs), and solid bold lines represent 95% prediction CIs. Predictive model was based on a reconstructed population from a 2,024-ha unit (Unit 2).

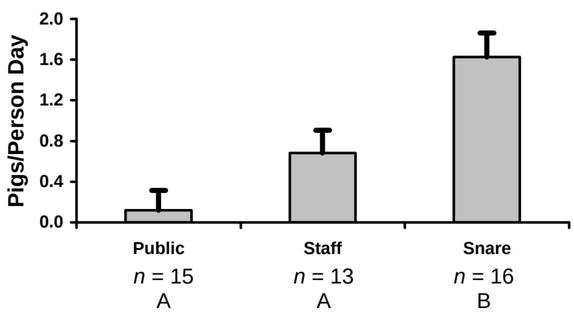

Fig. 9. Least square means (+ SE) of the efficiency of 3 feral pig control methods at Hakalau Forest National Wildlife Refuge, Hawai`i, 1989–2004. Means with same subscripts were not different (Bonferroni grouping, $\alpha = 0.05$).

These data represent the largest reported sample of reproductive rates for feral pigs in Hawai`i, and are more precise than previously available estimates. Diong (1982) found 21.9% of mature sows were pregnant and 29.3% were lactating. We did not restrict our estimates of pregnancy and lactation to mature individuals because this determination was not made during necropsy. However, when we considered only the 216 sows >1 year old, the pregnancy rate at HFNWR was 31.5% and the lactation rate was 16.9%. Because of strong seasonality in lactation, seasonally unbalanced samples can result in biased estimates of overall reproductive rates. The larger sample from HFNWR varied from 75 to 94 sows per 3-month period, and correcting for seasonal differences in sample size resulted in <0.3% discrepancy in quarterly estimates of reproductive rates.

We reconstructed the annual standing population of pigs within a 2,024-ha management unit and examined several population processes including density, annual change in population, the proportion of the population removed each year, and the point at which the population remained stable. These data provided a rare opportunity for understanding demography during removals and was the basis for indexing surveys of feral pig sign. An important limitation of the data was that the total numbers of removals were reported by calendar year while necropsies were reported by exact date. We were unable to reconcile a small number of cases at time scales <1 year where pigs were removed but no necropsy was performed. Therefore, all removals were analyzed by calendar year.

Although removal of feral pigs commenced in 1988, enclosure of the 2,024-ha unit was not completed until 1992. Therefore, the population could not be reliably estimated from 1988 to 1991. The apparent population increase during this period was probably a result of pigs moving into the area despite an increasing number of annual removals. For the period after the area was enclosed, the population could be reliably reconstructed, the number of removals increased, and the reconstructed population declined except in 1 year. In 1995, management efforts were temporarily halted for several months for administrative reasons. Although this action delayed the ultimate eradication of all pigs from the unit, it is instructive to note that the population apparently increased by 6.5% from 1995 to 1996 despite the removal of 60 pigs (32.8% of the population in 1995).

We used information on the standing population and annual number of removals to determine the proportion of the population removed and the subsequent year's population change. Derived analyses such as these may technically violate regression methods because the same data appear in both dependent and independent variables. Nonetheless, this analysis is helpful and there are no other ways to examine these processes. The analysis showed that >41–43% of the population must be removed each year to cause a decline. Using the same regression equation, 70–71% of the population must be removed to reduce the population by 50% in each successive year. This agrees with Barrett and Stone's (1983) finding that 30–40% removal on a semiannual basis is required to maintain pigs at 50% their equilibrium density. Reducing densities in unenclosed areas is not as effective at achieving this goal as removals from enclosed areas.

Annual surveys of feral pig sign showed variability among years, management units, and observers. Observers were not rotated or randomized among units each year, which limited inferences about the causes of substantial year-to-year variability in sign from 1987 to 1997, when feral pigs were abundant. This period was followed by significantly lower sign and less year-to-year variability from 1997 to

2004. Intense rainfall immediately preceding surveys may have eliminated tracks, eroded signs of digging, and washed away scat. Heavy rainfall combined with higher temperatures can promote ground-level plant regrowth and faster scat decomposition, further obscuring signs of pig activity (Hone and Martin 1998).

Indexing pig density had mixed results because of high variability in sign when densities were high. Top-ranked models without intercepts supported a useful constant proportion index (Lancia 1994). Models including all sign were as good as models with only fresh or intermediate sign. While the data may have a nonlinear pattern, nonlinear models were not warranted because some data did not match appropriate levels of pig density. We found little sign during a year with high pig density, much sign in a year with intermediate density, and virtually no sign in several years with low densities. We did not examine stomach content data for potential shifts in diet that could have caused variability in sign. Precipitation was not a factor in top-ranked models because 1994 was the only year in which high pig density corresponded with heavy rainfall, which may have washed away sign. Nonetheless, future surveys should avoid periods during or soon after heavy rains.

Analysis of inter-observer variability did not support the hypothesis that observer bias in 1994 underestimated pig activity. None of the 1994 observers had significant negative coefficients relative to the reference observer. Nonetheless, observers should be trained to better recognize pig scat, tracks, and browse. It is not necessary, however, to distinguish fresh from intermediate sign during surveys. This simplifies field procedures and avoids problems with classifying sign.

The predictive model of pig density is unique and important in that the 2,024-ha unit was larger, had higher densities of feral pigs, had a long-term data set, and had higher levels of sign than that reported by Anderson and Stone (1994). The highest density of feral pigs, 6.53 pigs/km^2, reported by Anderson and Stone (1994) was at the Puhimau study area, whereas 12.12 pigs/km^2 inhabited the 2,024-ha unit of HFNWR in 1992. New techniques such as the seedling ratio method (Sweetapple and Nugent 2004) or the Passive Tracking Index (Engeman et al. 2003) have not been as widely used in Hawai`i as the method developed by Anderson and Stone (1994). Adapting any new index method in setting management goals requires calibration with reliable estimates of pig abundance.

When applied to other management units, the predictive model of pig density showed Units 1 and 3 were pig free for several years, as was Unit 7 in 2004. The model also predicted a small terminal population remaining in Unit 6. The predictive model most likely did not accurately estimate densities for Unit 3 and the unmanaged area of Middle Maulua because sign values exceeded the range of the model, but it did confirm high densities of feral pigs in these areas.

Comparing the efficiency of control methods was difficult because: (1) the effort expended in deploying snares was not recorded separately from staff hunting effort before 1998; (2) multiple methods were used in units within a year; and (3) densities had decreased in most units by the time high-effort snaring commenced in 1998. Least square means of the general linear model controlled for some imbalances among years by providing estimates of efficiency as if all methods had been conducted together. Although there was no significant difference in efficiency between public and staff hunting, snaring was significantly more efficient than hunting methods. The eradication rate at HFNWR using staff hunting with dogs (11.8 worker-hours per pig) was at least as efficient as the reported rate at HAVO (20 worker-hours per pig) (Katahira et al. 1993), and snaring at HFNWR (4.9 worker-hours per pig) was at least as efficient as that of a densely populated unit on Maui (7 worker-hours per pig) (Anderson and Stone 1993).

There are several considerations from our study that can help managers eradicate feral pigs from protected areas. By applying the index model to sign surveys of units where management will be initiated, pig populations can be estimated and removal objectives can be set to reduce densities by desired goals in subsequent years. The model's value may be greater for use across multiple years than in a single year because of the inherent year-to-year variability in sign, particularly at high pig densities. Using estimated removal rates, managers can also estimate the effort required to achieve these goals with different techniques, and determine whether enough hunting effort or snares have been deployed to reduce feral pig populations by set objectives.

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