Technical Report HCSU-004

EFFICACY OF FERAL PIG REMOVALS AT HAKALAU FOREST NATIONAL WILDLIFE REFUGE

Steven C. Hess[1], John J. Jeffrey[2], Donna L. Ball[2], and Lev Babich[3]

[1]USGS Pacific Island Ecosystems Research Center, P.O. Box 44, Hawaii National Park, HI 96718
[2]Hakalau Forest NWR, 32 Kinoole St. Suite 101, Hilo, Hawaii USA 96720
[3]Hawaii Cooperative Studies Unit (PACRC, UH Hilo), USGS Pacific Island Ecosystems Research Center, Kilauea Field Station, P.O. Box 44,Hawaii National Park, HI 96718

Hawai`i Cooperative Studies Unit
University of Hawai`i at Hilo
Pacific Aquaculture and Coastal Resources Center (PACRC)
200 W. Kawili St.
Hilo, Hawai`i 96720
808-933-0706

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[1]USGS Pacific Island Ecosystems Research Center, P.O. Box 44, Hawaii National Park, HI 96718
[2]Hakalau Forest NWR, 32 Kinoole St. Suite 101, Hilo, Hawaii USA 96720
[3]Hawaii Cooperative Studies Unit (PACRC, UH Hilo), USGS Pacific Island Ecosystems Research
Center, Kilauea Field Station, P.O. Box 44,Hawaii National Park, HI 96718

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Hawai`i Cooperative Studies Unit
University of Hawai`i at Hilo
Pacific Aquaculture and Coastal Resources Center (PACRC)
200 W. Kawili St.
Hilo, Hawai`i 96720
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Executive Summary

We compiled and analyzed data from 1987–2004 on feral pig (*Sus scrofa*) management and monitoring activities at Hakalau Forest National Wildlife Refuge, a tropical montane rainforest on the island of Hawai`i. These data included annual surveys of feral pig and cattle (*Bos taurus*) activity, the number of feral ungulates removed from closed management units, age and reproductive status from necropsies, and vegetation surveys repeated 4 times over a 16 year period. We found an essentially even sex ratio within the feral pig population and within age classes, although males lived to 60 months while females lived to only 48 months. The pregnancy rate was 23.5%, and lactation rate was 8.3%, regardless of season and age, but lactation peaked in April-June. Reproductive rates also increased with age, peaking at 2–4 years in females. We reconstructed the standing population within a closed unit to examine demographic processes. We estimated that annual removal in excess of approximately 41–43% would be necessary to affect a population decline. We examined annual feral pig activity surveys and found a strong and sustained decline in pig sign after 1997 relative to unmanaged areas. We related the standing population to feral pig activity surveys to build a predictive model of feral pig density, and then applied this model to other management units. We evaluated control methods and found snaring to be more efficient than staff or public hunting. Vegetation monitoring revealed a strong temporal increase in cover of native ferns, and marginally non-significant decreases in cover of bryophytes and exposed soil.

I) Introduction

Feral pigs (*Sus scrofa*) have tremendous impacts on native plant communities in both continental and insular ecosystems through rooting and herbivory. In Hawai`i, the actions of feral pigs are considered to disperse some alien plants (Diong 1982, Aplet *et al*. 1991, LaRosa 1992), inhibit regeneration of native plants (Cooray and Mueller-Dombois 1981, Diong 1982), selectively browse and destroy native plants (Ralph and Maxwell 1984, Stone 1985, Stone and Loope 1987), 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 have complex impacts far beyond plant communities. Feral pigs create nutrient-rich wallows and troughs in tree fern trunks (*Cibotium* spp.) where alien mosquitoes (*Culex quinquefasciatus*) breed (Stone and Loope 1987). These mosquitoes then vector avian malaria (*Plasmodium relictum*), which is often lethal to native Hawaiian forest birds and has been one of the most important factors in the decline of the Hawaiian avifauna (Atkinson *et al*. 1995).

The removal of feral pigs can have substantial benefits for the native Hawaiian avifauna, both by reducing the breeding habitats of malaria carrying mosquitoes, and through the recovery of native vegetation (Loope and Scowcroft 1985, Loope *et al*. 1991, Loh and Tunison 1999). Eradication of feral pigs in Hawai`i, however, is difficult, particularly in the forest environments where they pose the greatest threat to native biota. Feral pigs are cryptic, elusive, and also 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 (Barrett and Stone 1983). Traditional means to achieve this level of population control can be effort-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) on the island of Hawai`i, requiring 20 worker hours per pig (Katahira *et al*. 1993). The use of snares has also been evaluated in remote rainforests on the island of Maui. Although the terrain on Maui was considerably more rugged than the island of Hawai`i, the effort required only 7 hours per individual in a densely populated unit, while a more remote unit required 43 hours per individual (Anderson and Stone 1993). Although toxicants have not been developed and tested for feral pigs in Hawai`i, they were found to be highly cost effective in Australia (Hone and Stone 1989, Choquenot *et al*. 1990). Hakalau Forest National Wildlife Refuge (HFNWR) has been controlling and monitoring feral pigs since 1988 with a variety of removal methods including public hunting, staff hunting, and the use of snares. While these methods may vary substantially in their efficacy, a formal analysis never has been conducted to assess the effort and resulting effectiveness of these management actions.

II) Objectives

The objective of this research was to synthesize and analyze all of the existing feral pig removal data from HFNWR into a single report to the United States Fish & Wildlife Service (USFWS) in order to evaluate alternatives available to managers in controlling feral pigs. Feral ungulate removal was identified as a high priority in both the HFNWR Feral Ungulate Removal Plan and in the Hawai`i Forest Bird Recovery Plan (USFWS 2003). In this report, we extracted the most relevant and important findings that detail differences in management strategies and the effort required to control and eradicate feral pig populations. Specific objectives included:

1. Summarize the age, sex composition, and reproductive rates of feral pigs from necropsy data.
    a. Summarize the age distribution over time.
    b. Determine the overall sex ratio.
        i. Determine the sex ratio within age classes.
    c. Summarize pregnancy and lactation rates.
    d. Determine if seasonal patterns in reproduction exist.
    e. Construct a predictive model of age from the size of feral pigs.
2. Reconstruct population dynamics in one management unit over the course of removals based on the ages of removed pigs.
    a. Determine standing population and number of pigs removed over time.
    b. Use reconstructed population and removals to determine the proportion of the population removed annually.
    c. Determine population change over time.

    d. Relate the population change from year to year to the proportion of the population removed each year.
3. Summarize the feral ungulate activity surveys over time.
    a. Analyze factors influencing activity indices.
        i. Examine the effect of inter-observer variability
4. Relate the standing population in one unit to feral pig activity surveys to build a predictive model of feral pig density.
        i. Examine the effect of annual pre-survey precipitation.
5. Apply the predictive model to estimate the density of feral pigs in other management units over time.
6. Evaluate control effort.
    a. Compare control methodology.
7. Summarize vegetation monitoring.
    a. Analyze line-intercept data.

III) Study Site

Hakalau National Wildlife Refuge (19°47´N, 155°18´W), is a tropical montane rain forest ranging from 750–2,000 m elevation on the windward slope of Mauna Kea volcano, island of Hawai`i (Figure 1). The refuge and associated management and monitoring activities were established in 1987 primarily for the protection of endangered Hawaiian forest birds, such as `Ākepa (*Loxops coccineus*), `Akiapōlāʻau (*Hemignathus munroi)*, Hawai`i Creeper (*Oreomystis mana*), and `Io (Hawaiian hawk; *Buteo solitarius*), as well as the endangered `ope`ape`a (Hawaiian hoary bat; *Lasiurus cinereus semotus*). There are also at least 4 endangered and 3 candidate endangered plant species, as well as 5 species of concern reported from HFNWR. Although degraded by herbivorous feral pigs and cattle grazing 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 more sensitive to the actions of feral pigs include `ōlapa (*Cheirodendron trigynum*), `ōhelo (*Vaccinium calycinum*), pūkiawe (*Styphelia tameiamaeiae*), and tree ferns (*Cibotium* spp.). Dense vegetation, high average annual rainfall (approximately 250 cm), dissected terrain, and limited road access, particularly to lower elevation areas, make feral pig control efforts logistically challenging.

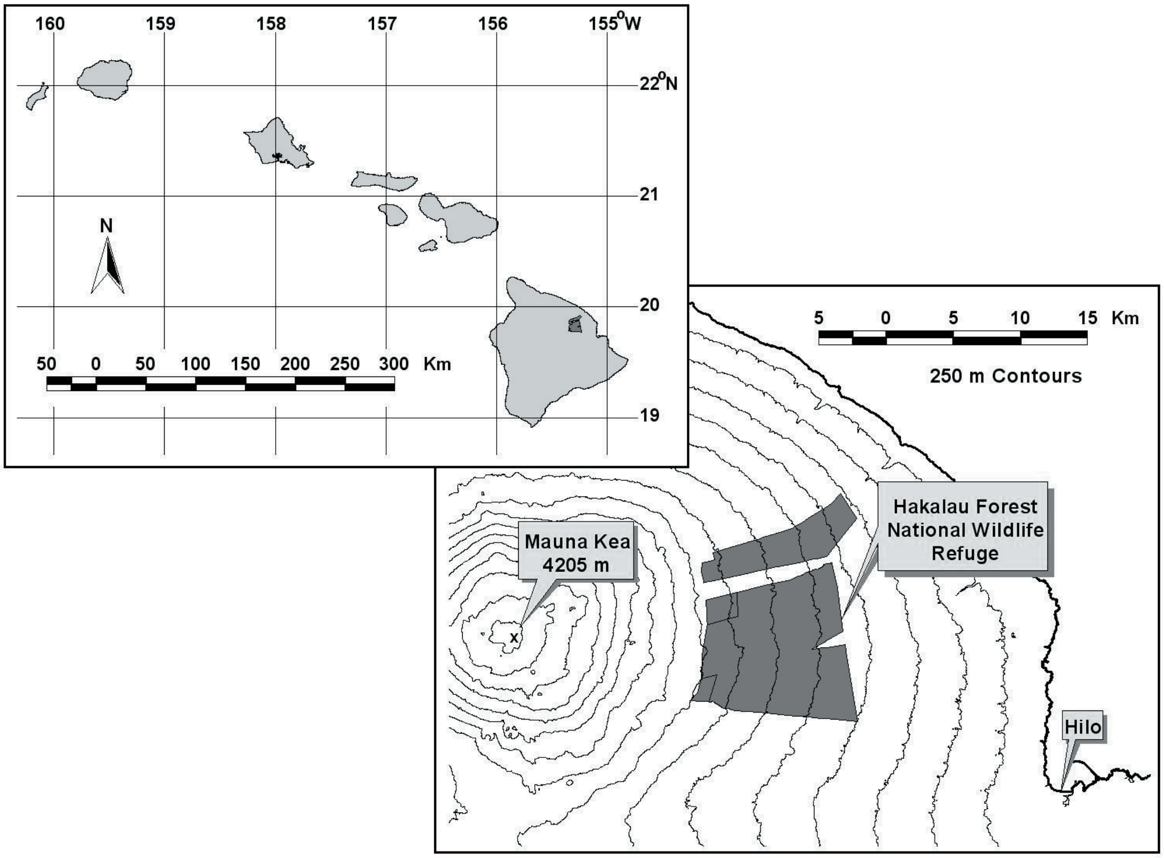

Figure 1.The Hawaiian Islands and Hakalau Forest National Wildlife Refuge on Hawai`i Island.

IV) General Methods

The existing data collected by HFNWR biologists included the effort in person-days used to remove feral pigs using 3 different techniques in 8 fenced units from 1988–2002, the corresponding pig activity index within these various management units, and vegetation monitoring. These data represented approximately 1,939 person-days of effort to remove 1,463 feral pigs (Table 1). Pig activity index also was measured at 29,881 plots in and outside these management units starting in 1987. These data were analyzed to determine the effectiveness of removal techniques in terms of labor and the desired management goal of reduction and ultimately population eradication within management units. Data also existed from the necropsies of 968 pigs from 1988–1999 which allowed the reconstruction of age and sex characteristics over periods of removal. These data were used to examine age structure and reproductive rates, to construct a population model of demographic processes during management removals, and to determine the population density in a management unit over time that could be related to activity indices. The overall goal of this approach was to relate each data set to the biological processes that occurred within management units based on the spatial coordinates ofc each attribute (Figure 2).

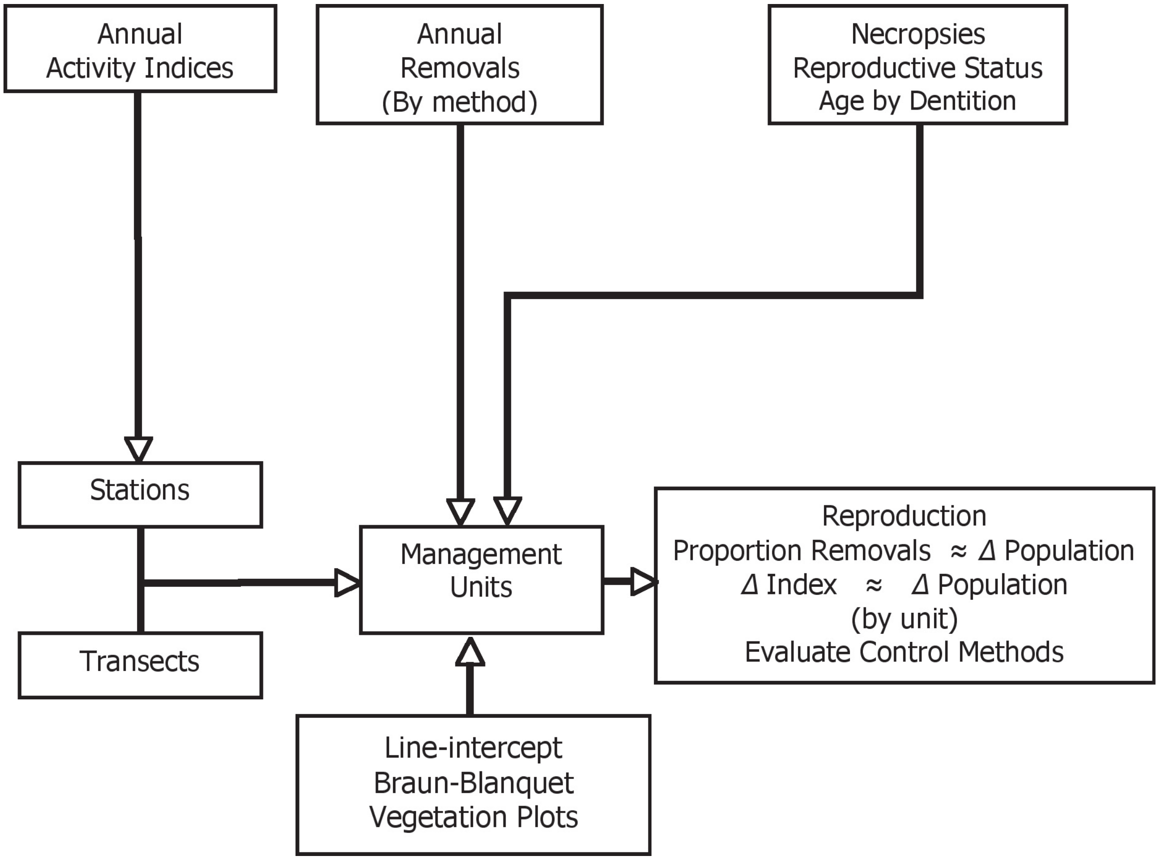

Figure 2. Schematic representation of linkages between data (activity indices, removals, necropsies, and vegetation plots), spatial locations (management units stations, and transects), and analyses at Hakalau Forest National Wildlife Refuge, island of Hawai`i.

Table 1. Management units and initiation dates of management activities to control feral pigs and feral cattle at Hakalau Forest National Wildlife Refuge, island of Hawai`i.

			Date of Initiation					
Name	Unit	Acres	Fence	Staff Hunt	Dog Hunt	Public Hunt	Snare	Aerial Hunt
Honohina Middle	1	494	Dec 1988	1989	–2000	--	2000–	--
Shipman Upper	2	4,953	Nov 1991	1989	–1999	--	1989[a]–	1990–2002
Honohina Lower	3	1,789	Jun 1993	1992	–1999	--	1992–1999[b]	--
Maulua Upper	4	1,877	Feb 1994	1998	–1999	1992-1997	--	--
Honohina Upper	5	1,006	Nov 1995	1996	–1999	--	--	--
Hakalau Middle	6	1,170	Feb 1997	1997	–1999	1997-2000	2001–	1996
Papaikou Middle	7	1,615	Feb 1997	2000	–1999	1997-1998	1998–	1996
Pua Akala	8	514	Oct 1996	2001	–1999	--	1998–	--

[a] Snares removed 23 June 1999 and redeployed 2 November 1999.

[b] 331 additional snares deployed in 1997.

Vegetation cover was repeatedly monitored on 6 plots and adjacent 50-m line-intercept transects to primarily determine change after the release of cattle grazing. Six permanent plots (Figure 3), 20 X 20 m in size, were begun in 1987 (Mueller-Dombois and Elenburg 1974; Stone *et al*. 1991). Braun-Blanquet cover-abundance value was recorded for each species. Braun-Blanquet cover estimates were made for each of 6 general strata categories (canopy, subcanopy, shrub 1, shrub 2, herb, and ground layer). Cover values for life forms (native ferns and woody plants, bryophytes, lichens, alien grasses and herbs, litter, exposed soil, and logs) were measured by line-intercept transects. Changes in line-intercept values were suitable for repeated measures ANOVA to determine response to feral pig management over time.

V) Analytical Methods

a. Demographic Structure and Vital Rates from Necropsy Data

To determine if control efforts may have caused systematic changes in age structure of the feral pig population over time, we constructed a histogram of annual median age and mean age (and SE) in months. We restricted this analysis to pigs taken from Unit 2 because this unit had the longest period of continuous data collection. Combining data from other units could confound trends because control efforts did not commence simultaneously, which could have affected pigs of different ages in a systematic manner. Ages were estimated by tooth eruption and wear patterns (Matschke 1967) for 623 feral pigs for years 1988–1999.

We examined the overall sex ratio for 711 pigs of known sex to determine if a bias existed in the population. We further restricted this analysis to 320 boars and 316 sows of known age to determine if age-related bias in sex ratio existed. The number of boars and sows within 6 age classes were compiled and evaluated for differences in sex ratio within age classes by a χ^2 test.

We used multiple regression to determine the relationship between age and body size in feral pigs to predict the age of feral pigs for cases where this data had not been collected. We further restricted analyses to 330 records with data on age (in months), sex, girth, and weight (in pounds). Sex was represented as 0 for female and 1 for male. Girth and weight were square root transformed to improve normality.

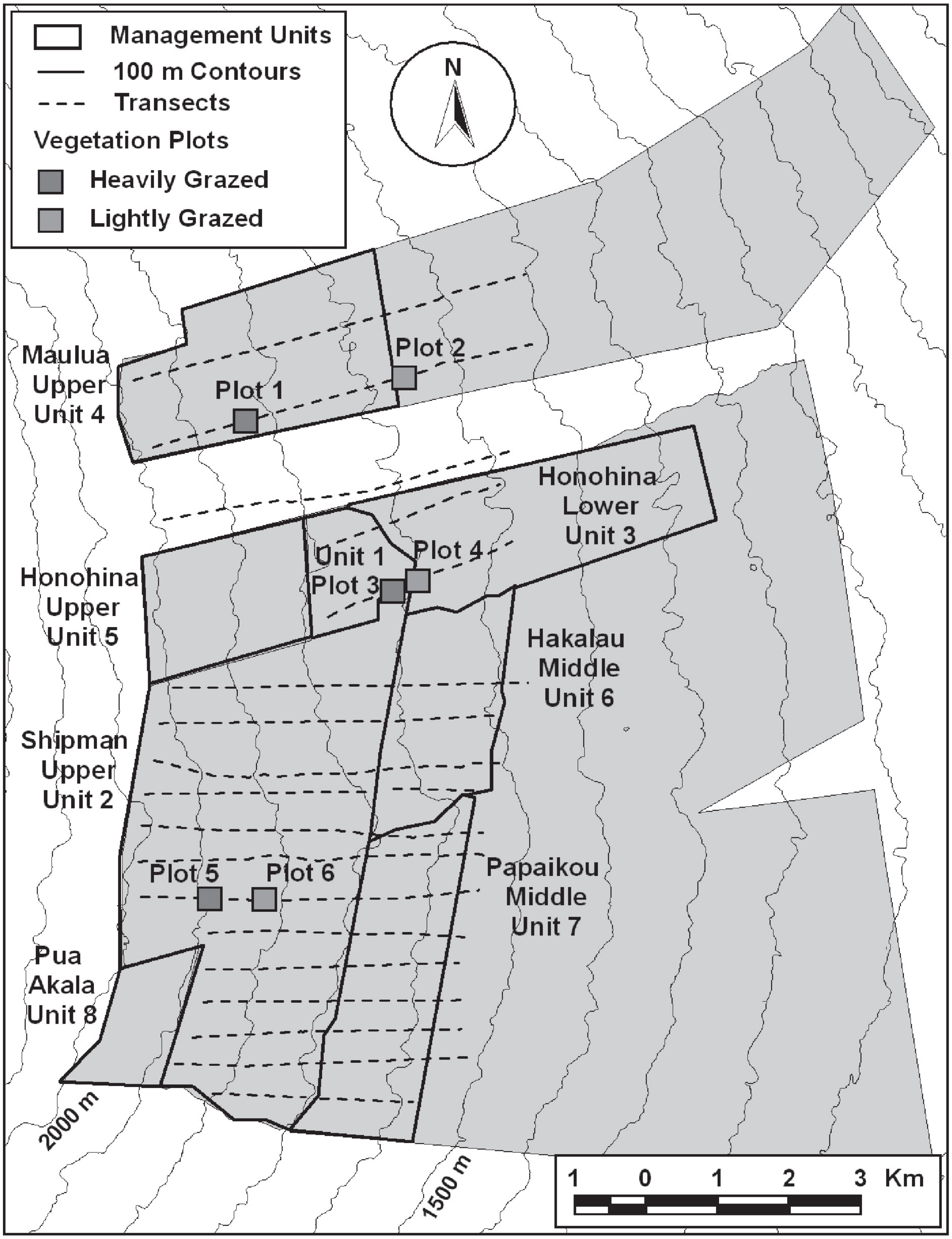

Figure 3. Management units, transects, and vegetation plots at Hakalau Forest National Wildlife Refuge, island of Hawai`i.

We examined the reproductive status of 327 sows with information on presence and number of corpora lutea (pregnancy scars), embryos, and lactating teats to determine potential reproductive rates and seasonality in reproduction. We calculated the proportion of sows with corpora lutea, embryos, lactating teats, and the median and mean (and SE) number of corpora lutea, embryos, and lactating teats per sow. We aggregated these data across years and determined the proportion (and binomial SE) of pregnant and lactating sows by annual quarters to examine seasonality in reproduction. We also examined a subset of 304 sows with data on age and reproductive status 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.

b. Population Reconstruction

We reconstructed the standing population of feral pigs in a 5,000 acre management unit (Unit 2) from the number of removals (Appendix I) and their estimated ages for the period of 1988–2004. The ages of 623 pigs were estimated using tooth eruption and wear patterns (Matschke 1967). Dates of birth were back calculated from the dates of necropsy and estimated age of each animal according to Anderson and Stone (1994). The ages of 11 additional pigs were estimated by the regression equation of mass and sex as described in the previous section. Standing populations were estimated at annual time steps by calendar year using estimated birth dates to determine how many animals had been born into the population and not removed, such that:

The number of pigs alive in the last year of removals $= Y_0$
Pigs alive 1 year prior to last removal $= \left[Y_{-1} + \left(Y_0 \geq 1\right)\right]$
Pigs alive 2 years prior to last removal $= \left[Y_{-2} + \left(Y_{-1} \geq 1\right) + \left(Y_0 \geq 2\right)\right]$
Pigs alive 3 years prior to last removal $= \left[Y_{-3} + \left(Y_{-2} \geq 1\right) + \left(Y_{-1} \geq 2\right) + \left(Y_0 \geq 3\right)\right]$
Pigs alive 4 years prior to last removal $= \left[Y_{-4} + \left(Y_{-3} \geq 1\right) + \left(Y_{-2} \geq 2\right) + \left(Y_{-1} \geq 3\right) + \left(Y_0 \geq 4\right)\right]$

Because age estimates were available for only 634 of the 757 pigs (83.75%) removed from Unit 2, 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 in Unit 2 since year 2000, and that they were snared sometime before year 2004.

Using the total number of feral pigs removed (R) each year (T) from the unit, and the reconstructed population (Y), we calculated the proportion of the population removed as: ${}^{R_T}\!/_{Y_T}$. We then determined the change in population from year to year as: ${}^{Y_{T+1}}\!/_{Y_T}$. 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 (i.e., the point of stability). We did not use data from after year 2000 because there were apparently <5 feral pigs remaining in the unit resulting in proportion values of 0 or 1.

c. Feral Ungulate Activity Indices

Activity indices for feral pigs, consisting of the presence of fresh or intermediate sign (Stone *et al*. 1991) at 428 stations, each with 20 sample plots, were complied for years 1987, 1990, 1992–2004 (Appendix II). These data were joined to their spatial coordinates and plotted by year using ArcView 3.2 Geographic Information System (ESRI 1999). Stations were assigned to management units by UTM coordinate locations. The proportion of sample plots with fresh, intermediate, and both fresh and intermediate feral pig sign (hereafter all sign) was calculated for each survey 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 completed the most transects (JJJ) as the reference observer (i.e., all other observers were evaluated with respect to the reference observer). Observers who had completed < 5 transects were grouped as a single observer for analysis. We treated management units as a class variable and set the reference level to be unmanaged areas outside of units. We also treated year as a class variable with the reference level designated as the first survey in 1987. We used observer, year, and management unit as predictors of the proportion of plots per stations with either fresh sign or intermediate sign. We estimated least square means for all levels. Statistical significance was evaluated as $\alpha = 0.05/$ the total number of levels within each factor. We did not use a repeated measures design because stations were at different locations each year, transects and management units were augmented to surveys over time, and observers changed in non-random manner.

d. Indexing Pig Density

We used the known density of feral pigs from the population reconstruction, and feral pig activity indices to develop predictive models of feral pig indices. These analyses were restricted to the 5,000 acre (20.02 km^2) unit after a pig-proof fence enclosed the population in 1992. We divided the estimated standing population at each time step by the area of the unit to determine pig density and used these values as the response variable for regression analysis. We determined the proportion of stations with fresh pig sign, intermediate sign, and the proportion of stations with all sign for each calendar year. We transformed proportions to arcsine values (Sokal and Rohlf 1981), and used these as predictor variables in linear regression following the approach of Anderson and Stone (1994). We also used precipitation 30 days prior to activity surveys as an auxiliary predictor. Data was from a National Climatic Data Center (Asheville, NC) automated climate station at Keanakolu Camp for the time period 1986–2004. We constructed models 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 considered. Models were ranked with Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 1998). We determined both 90 and 95% confidence intervals for estimated regression equations of the highest ranked models.

e. Predicting Density in Other Units

We applied the regression equation of the highest ranked model to predict the density or number of feral pigs in each of the other management units and other areas where activity indices were measured. We estimated densities in open areas and estimated population sizes within enclosed units with both 90 and 95% predictive confidence intervals based on the estimated regression equation, its variance, and the area of each unit.

f. Evaluating Removal Methods

We evaluated the efficiency of 3 methods of feral pig control from 1989–2004; public hunting, staff hunting, and snaring. Data represented the number of pigs per person day removed from management units within calendar years. There were a total of 44 cases where effort and removals were sufficiently documented for this analysis. Public and staff hunting occurred within the same units in 3 of 28 cases, but snaring was exclusive of all other hunting, except in 1 of the 44 cases. Prior to 1998, a small number of snares were deployed during staff hunting, but the effort expended in each of these methods was not recorded. Therefore, snaring prior to 1998 could not be evaluated, and the amount of effort spent in staff hunting was likely over-represented in the data. Moreover, high-effort snaring began in 1998 after staff and public hunting reduced pig densities in most management units, which may have reduced the estimated of efficiency of this method in comparison to hunting methods. We used a general linear model to evaluate the effects of method, year, and management unit on the response variable pigs per person day, and Bonferroni adjusted pairwise comparisons to examine differences between the least square mean of each control method.

g. Vegetation Change

Six plots and 6 50-m line-intercept transects were monitored from 1987–2003. Three plots occurred in locations that were formerly heavily grazed by cattle, and 3 were in lightly grazed locations (Table 2). The original plots 1 & 2 used in 1987 were never subsequently relocated; therefore new plots at the same location were established in 1991 and followed through the study. The design consisted of 2 plots and line-intersect transects arrayed on 3 of the feral ungulate survey transects such that one plot and line-intercept transect were located within a formerly heavily grazed area, and the other was located in a formerly lightly grazed area. We restricted analyses to only line-intercept data for this report. The data within each life form category were amenable to analysis with a balanced repeated measures design; however, there were insufficient replicate surveys for multivariate hypotheses tests, therefore, only within-subject univariate effects could be tested. Repeated measures ANOVA consisted of the response variable of cover measured over 4 time periods. Cover values were square root transformed for analyses. Predictors consisted of the 3 transects, each with 2 levels of grazing intensity.

Table 2. Summary of locations and years in which vegetation surveys were conducted at Hakalau Forest National Wildlife Refuge, island of Hawai`i, 1987-2003.

Plot	Grazing Intensity	Unit	Transect	Station	1987	1991	1992	1996	1997	2002	2003
1	Heavy	4	13	4	X[a]	X		X			X
2	Light	NA	13	16	X[a]	X		X			X
3	Heavy	1	10	6	X		X		X		X
4	Light	3	10	8	X		X		X		X
5	Heavy	2	5	6	X	X		X		X	
6	Light	2	5	10	X	X		X		X	

[a] Subsequent vegetation surveys were not conducted at exact locations of original plots and line-intercept transects.

VI) Results

a. Demographic Structure and Vital Rates from Necropsy Data

Age structure of the population varied over the period of 1988–1999 in an apparently non-systematic manner (Figure 4). The oldest mean and median aged feral pigs were removed from Unit 2 in 1990, while both the median and average age of feral pigs was ≤ 18 months in 1988, 1991, 1995, 1996, and 1999. The difference between maximum and minimum median ages across all years was 19 months, while the greatest difference in mean ages across years was 17.4 months.

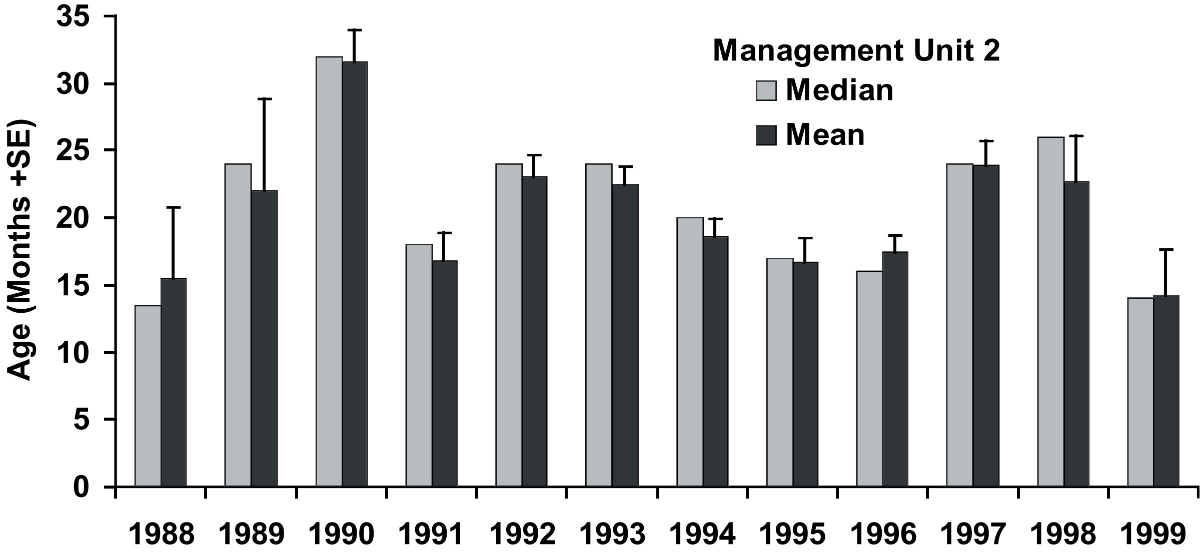

Figure 4. Median and mean (+ SE) ages of 623 feral pigs removed from Unit 2 of Hakalau Forest National Wildlife Refuge, island of Hawai`i, 1988–1999.

Capture and necropsy data from 711 feral pigs revealed 352 sows and 359 boars, yielding an essentially even population 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 = 5.06, df = 5, *P* > 0.40; Figure 5), although the maximum age of boars was 60 months while the maximum age of sows was 48 months.

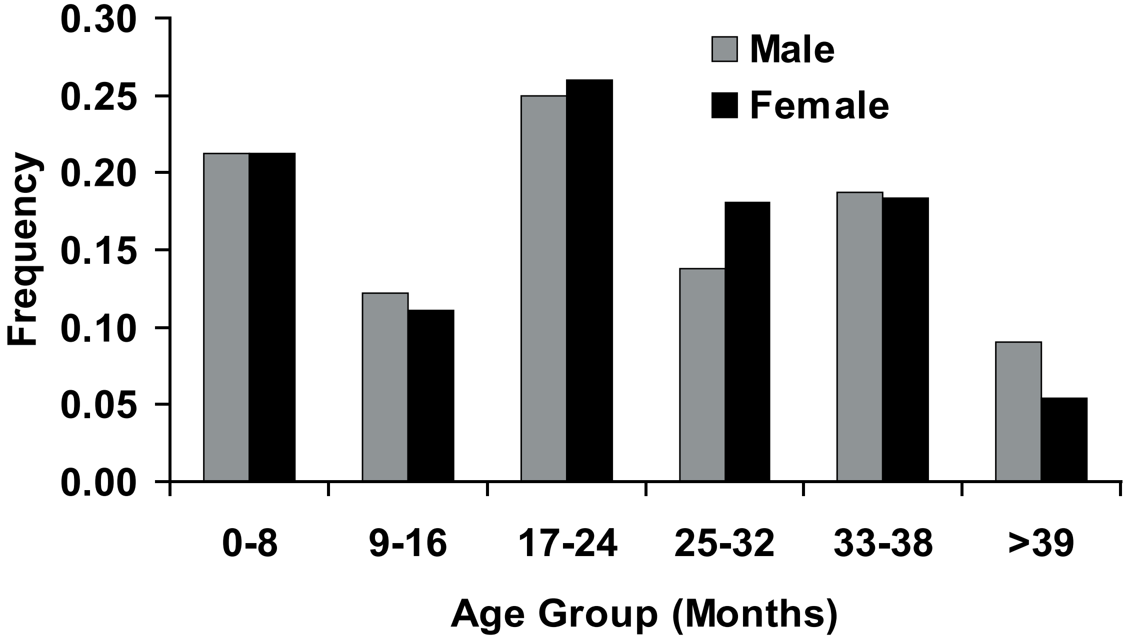

Figure 5. Age distribution of 636 known age feral pigs by sex from 1989–1999 at Hakalau Forest National Wildlife Refuge, island of Hawai`i.

Girth and weight (square root transformed) of feral pigs were highly correlated ($P < 0.001$; $R^2 = 61.5$), and therefore redundant variables for multiple regression. Moreover, because more observations were missing values for girth than for weight, we chose to use weight as the predictor variable for body size. Transformed weight ($P < 0.001$), and sex ($P < 0.001$) were both highly significant variables in predicting the age of feral pigs (Figure 6). The final model had an adjusted $R^2 = 51.9$, and took the form:

$$\text{Age} = (4.66 \text{ X} \sqrt{\text{Weight}}) - (4.46 * \text{Sex}) - 17.9$$

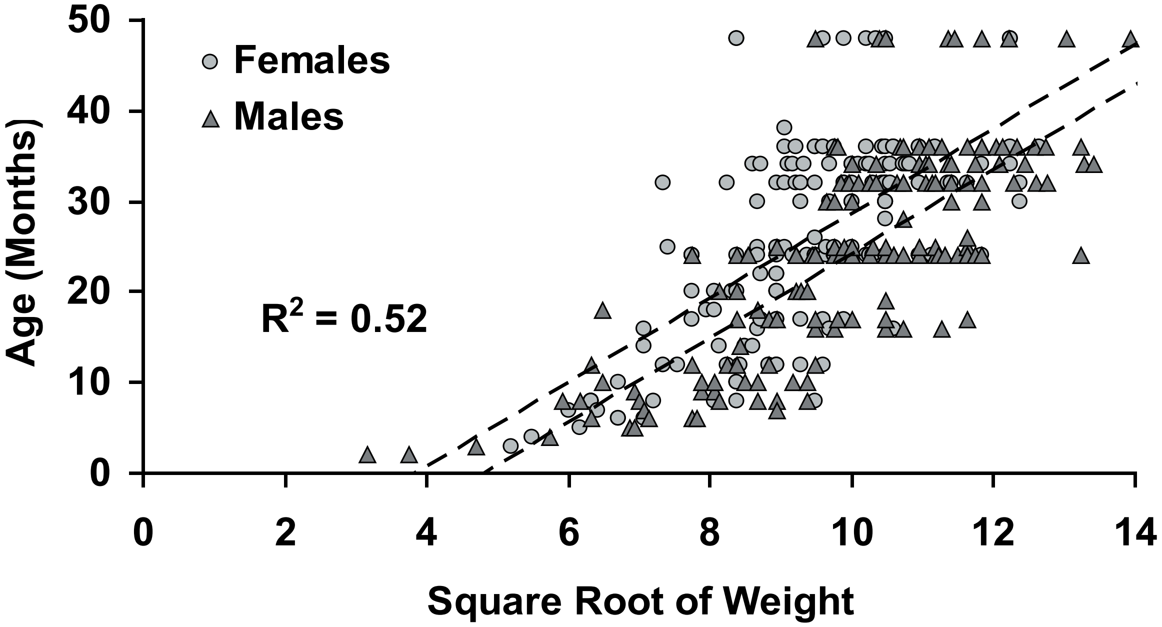

Figure 6. Relationship between weight (square root transformed), sex and age of feral pigs removed from Hakalau Forest National Wildlife Refuge, island of Hawai`i, 1988–1999.

Of the 352 sows captured, 327 had information on reproductive status from necropsy (Table 3). Of the 327 sows of known reproductive status, 77 were pregnant, representing 23.5% of the population. The number of embryos per pregnancy ranged from 2–12. The mean number of embryos was 6.69 (± 0.224 SE), and the median number of embryos was 7. Only 2 of 34 lactating sows were pregnant. Among 28 lactating sows, the average number of lactating teats was 4.96 (± 0.419 SE), and the median number of lactating teats was 5. In 124 sows, the mean number of corpora lutea was 8.51 (± 0.326 SE), while the median number of corpora lutea per sow was 8.

Although sows were pregnant in every month except November, which we attributed to an artifact of low sample size, there appeared to be marked seasonality in reproduction (Table 4). There was a non-significant difference in the number of pregnant sows between annual quarters, with a peak in January–March and annual low in July–September ($\chi^2 = 6.49$, df = 3, $P < 0.0901$; Figure 7). The number of lactating sows differed significantly between quarters, with a peak in April–June, and an annual low in July–September ($\chi^2 = 9.19$, df = 3, $P < 0.027$; Figure 7). No lactating sows occurred in August–September, or in January.

Table 3. Reproductive status of 327 female feral pigs from 1989–1999 at Hakalau Forest National Wildlife Refuge, island of Hawai`i.

	N	Percent of Total	Average Number	Standard Deviation	SE Mean	Median Number	Minimum	Maximum
Corpora Lutea	124	37.9	8.508	3.633	0.326	8	1	24
Embryos	77	23.5	6.688	1.969	0.224	7	2	12
Lactating Teats	27	8.3	4.963	2.175	0.419	5	1	9

There were marked differences in reproduction among age classes in 304 sows of known-age and known reproductive status. The number of pregnant sows differed strongly between age classes ($\chi^2 = 27.92$, df = 3, $P < 0.001$; Table 5), and the number of lactating sows also differed significantly between age classes ($\chi^2 = 12.91$, df = 3, $P < 0.005$; Table 6). Sows $\leq$ 1 year old showed no evidence of lactation. Pregnancy rates and the presence of corpora lutea were highest in pigs 2–3 years of age, but the proportion of lactating sows did not increase predictably with age. There was high variability in all measure of reproduction among 3–4 year old sows, reflecting the small sample size for this age class. Although the mean number of lactating teats in sows aged 2–3 years and corpora lutea among sows 3–4 years of age were slightly lower than younger age classes, median numbers of embryos, lactating teats, and corpora lutea all increased with age (Table 6).

Table 4. Monthly reproductive status of 327 female feral pigs from 1989–1999 at Hakalau Forest National Wildlife Refuge, island of Hawai`i.

Month	Overall	Corpora Lutea			Pregnant			Lactating		
	N	*N*	Proportion	SE	*N*	Proportion	SE	*N*	Proportion	SE
Jan	21	4	0.190	0.086	8	0.381	0.106	0	0.000	0.000
Feb	30	10	0.333	0.086	10	0.333	0.086	3	0.100	0.055
Mar	24	11	0.458	0.102	7	0.292	0.093	4	0.167	0.076
Apr	23	11	0.478	0.104	7	0.304	0.096	4	0.174	0.079
May	29	14	0.483	0.093	7	0.241	0.079	2	0.069	0.047
Jun	42	13	0.310	0.071	8	0.190	0.061	7	0.167	0.058
Jul	32	10	0.313	0.082	3	0.094	0.052	1	0.031	0.031
Aug	19	11	0.579	0.113	5	0.263	0.101	0	0.000	0.000
Sep	29	9	0.310	0.086	5	0.172	0.070	0	0.000	0.000
Oct	22	9	0.409	0.105	4	0.182	0.082	2	0.091	0.061
Nov	14	3	0.214	0.110	0	0.000	0.000	1	0.071	0.069
Dec	42	19	0.452	0.077	13	0.310	0.071	3	0.071	0.040
Overall	327	124	0.379	0.027	77	0.235	0.023	27	0.083	0.015

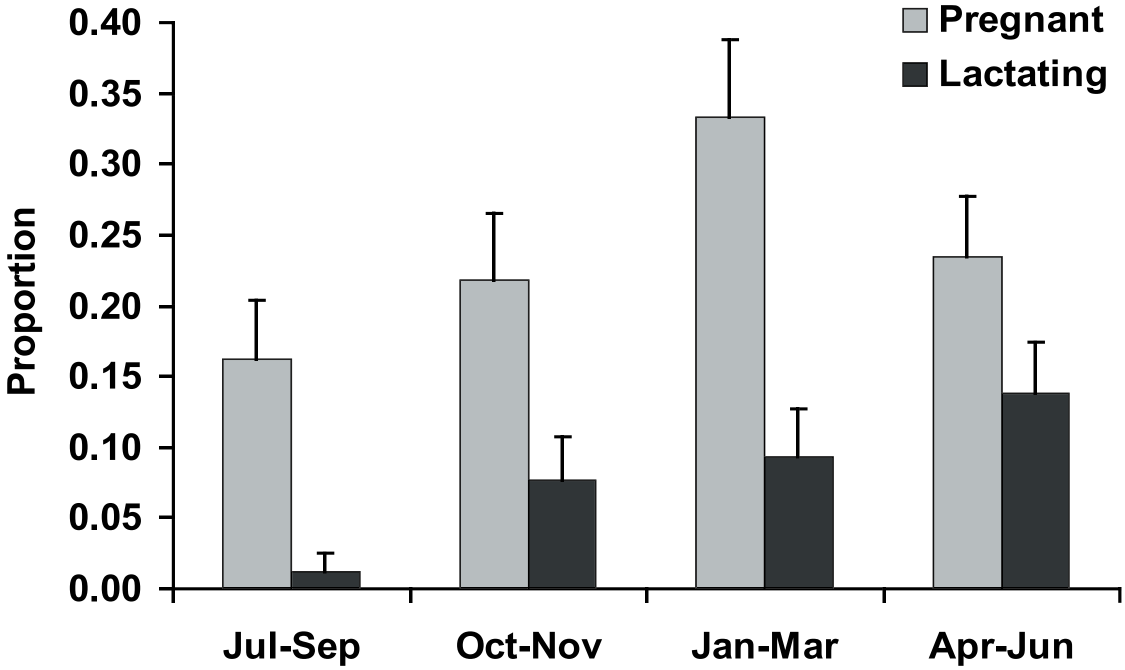

Figure 7. Quarterly rates of pregnancy and lactation among 327 feral pigs at Hakalau Forest National Wildlife Refuge, island of Hawai`i, 1988–1999.

Table 5. Proportion (and binomial SE) of 304 known-age feral pig sows by age class that were pregnant, lactating, or with corpora lutea at Hakalau Forest National Wildlife Refuge, island of Hawai`i, 1988–1999.

Age	Total	Pregnant			Lactating			Corpora Lutea		
Years	*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

Table 6. Mean (and SE) and median number of embryos, lactating teats, and corpora lutea among 304 known-age feral pig sows by age class at Hakalau Forest National Wildlife Refuge, island of Hawai`i, 1988–1999.

Age	Embryos				Lactating Teats				Corpora Lutea			
Years	*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	10	7.70	1.71	6.5
1–2	20	6.60	0.30	6	13	4.85	0.56	4	37	7.78	0.51	7
2–3	42	6.95	0.32	7	10	4.50	0.79	4.5	66	8.82	0.44	8
3–4	6	7.00	0.52	7.5	2	7.50	0.50	7.5	9	8.78	1.01	10

b. Population Reconstruction

The standing population of feral pigs in the 5,000 acre management unit (Unit 2) was reconstructed from 634 (83.75%) aged pigs of the 757 pigs removed from the unit (Figure 8). An apparent sharp increase in the reconstructed population from 1988–1992 reflects the fact that the unit was not enclosed until 1992, and was therefore open to immigration during this interval. The proportion of pigs removed from the population increased from 1994–2000, with the exception of 1995 and 1998. In 1995, management efforts were temporarily ceased due to administrative reasons, but in 1998, lower pig density may have increased the difficulty of removal. When the year-to-year population change was plotted on the proportion of the population that was removed, the estimated point at which the population remained stable (population change = 1.00) occurred at an annual removal level of 43.2% (Figure 9). A strong linear relationship (R^2 = 91.3; $P < 0.001$) between population change and the proportion removed indicated high correspondence. Using only the data from the closed period, the relationship was still strong (R^2 = 79.8; $P = 0.001$), and the estimate of the point of stability was similar (41.3%).

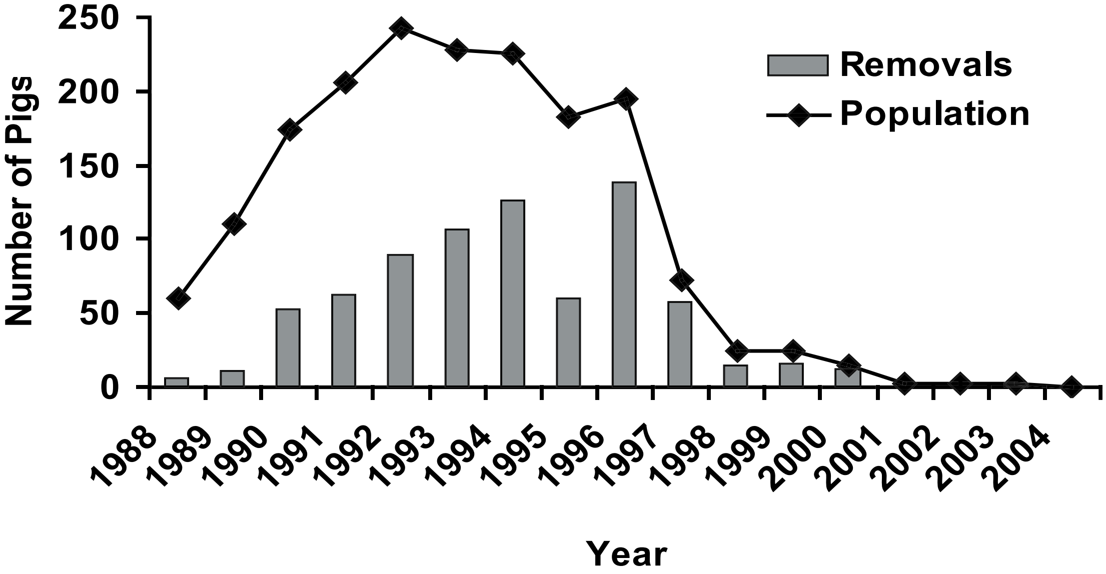

Figure 8. Reconstructed population and the number of feral pigs removed by year from a 5,000 acre management unit at Hakalau Forest National Wildlife Refuge, island of Hawai`i, 1988–2004.

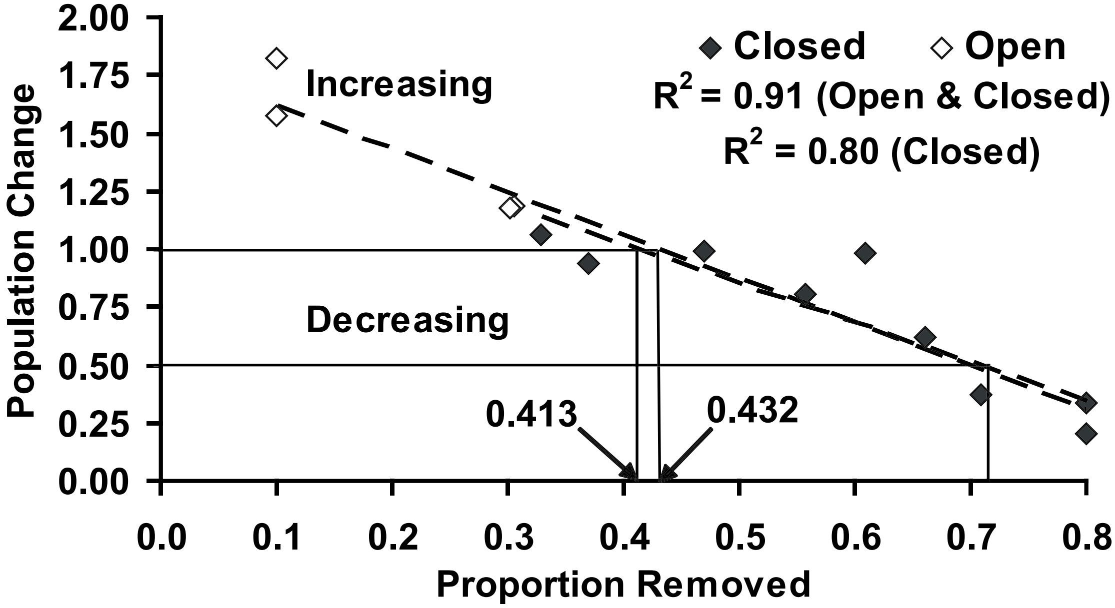

Figure 9. Population change and the proportion of feral pigs removed based on a population reconstruction from a 5,000 acre management unit at Hakalau Forest National Wildlife Refuge, island of Hawai`i, 1988–2004.

c. Feral Ungulate Activity Indices

In a general linear model, inter-observer variability, year, and management unit were all highly significant factors influencing the proportion of plots per station that had either fresh or intermediate feral pig sign ($P < 0.0001$; Table 7). Thirty-nine different observers had participated in feral pig surveys in 15 different years. Twenty observers had completed more than 5 transects and were treated separately for analysis. 19 observers were combined and treated as a single observer. Only 7 observers were significantly different than the reference observer in their detection of sign ($P < 0.0024$). Surveys in 9 years differed significantly from the reference year (1987; $P < 0.0029$). There was an apparent increase in sign from 1987 to 1990, but the 8 years from 1997–2004 had lower sign than 1987 (Figure 10). Managed units all had significantly lower sign than unmanaged areas ($P < 0.0071$).

Table 7. Coefficients and least square means from a general linear model of observers, year, and management units on the proportion of plots with fresh or intermediate feral pig activity at Hakalau Forest National Wildlife Refuge, Hawai`i 1987–2004. Reference state appears as the first level of a factor. Significant factors or levels are indicated by an asterisk.

Parameter	*n*	Parameter Estimate	Standard Error	*t* Value	*P* Value	Least Square Mean
Intercept	--	0.8984	0.0474	18.96	<0.0001*	--
Observers	--	--	--	--	<0.0001*	--
JJJ	793	0	--	--	--	0.2991
AK	579	-0.0072	0.0102	-0.71	0.4787	0.2919
AT	109	0.0673	0.0203	3.32	0.0009*	0.3664
DOD	90	-0.0398	0.0226	-1.76	0.0785	0.2593
DW	102	-0.0388	0.0196	-1.98	0.0472	0.2603
EB	103	0.0402	0.0203	1.98	0.0481	0.3393
GF	148	-0.0134	0.0177	-0.76	0.4482	0.2857
GM	66	-0.0055	0.026	-0.21	0.8332	0.2936
JLK	70	0.131	0.0242	5.42	<0.0001*	0.4301
JMY	66	-0.1985	0.0513	-3.87	0.0001*	0.1006
MB	54	-0.006	0.028	-0.21	0.831	0.2931
MW	74	-0.0041	0.0246	-0.17	0.8662	0.295
PB	40	0.0285	0.0333	0.85	0.3931	0.3276
PKH	76	-0.1389	0.0507	-2.74	0.0062	0.1602
RD	52	0.1079	0.0283	3.81	0.0001*	0.407
SA	67	-0.3218	0.0512	-6.28	<0.0001*	-0.0227
SH	271	-0.0225	0.014	-1.6	0.1088	0.2766
SK	178	-0.073	0.0174	-4.21	<0.0001*	0.2261
TVD	51	-0.0855	0.0305	-2.8	0.0051	0.2136
WO	515	0.0693	0.0109	6.37	<0.0001*	0.3684
COMBINED	665	-0.0198	0.0102	-1.94	0.0522	0.2793

Table 7, Continued. Coefficients and least square means from a general linear model of observers, year, and management units on the proportion of plots with fresh or intermediate feral pig activity at Hakalau Forest National Wildlife Refuge, Hawai`i 1987–2004. Reference state appears as the first level of a factor. Significant factors or levels are indicated by an asterisk.

Parameter	*n*	Parameter Estimate	Standard Error	*t* Value	*P* Value	Least Square Mean
Year	--	--	--	--	<0.0001*	--
1987	225	0	--	--	--	0.4192
1990	144	0.1665	0.0483	3.45	0.0006*	0.5857
1992	251	-0.1323	0.0468	-2.83	0.0047	0.2868
1993	222	-0.0108	0.047	-0.23	0.8181	0.4084
1994	228	-0.1224	0.0488	-2.51	0.0121	0.2968
1995	222	0.002	0.0472	0.04	0.9658	0.4212
1996	223	-0.0975	0.0479	-2.04	0.0417	0.3217
1997	230	-0.221	0.0472	-4.68	<0.0001*	0.1981
1998	243	-0.2268	0.0475	-4.78	<0.0001*	0.1923
1999	310	-0.1969	0.047	-4.19	<0.0001*	0.2222
2000	370	-0.2782	0.0468	-5.95	<0.0001*	0.1409
2001	378	-0.2628	0.0465	-5.65	<0.0001*	0.1563
2002	371	-0.2722	0.047	-5.8	<0.0001*	0.147
2003	375	-0.2707	0.0471	-5.75	<0.0001*	0.1485
2004	377	-0.2568	0.0473	-5.43	<0.0001*	0.1623
Management Unit	--	--	--	--	<0.0001*	--
Piha & L. Maulua	363	0	--	--	--	0.7278
Unit 1	167	-0.6808	0.0173	-39.37	<0.0001*	0.047
Unit 2	2317	-0.6301	0.0105	-59.88	<0.0001*	0.0977
Unit 3	280	-0.144	0.0148	-9.74	<0.0001*	0.5838
Unit 4	405	-0.5876	0.0136	-43.2	<0.0001*	0.1402
Unit 6	192	-0.5191	0.017	-30.47	<0.0001*	0.2087
Unit 7	445	-0.6161	0.0136	-45.48	<0.0001*	0.1117

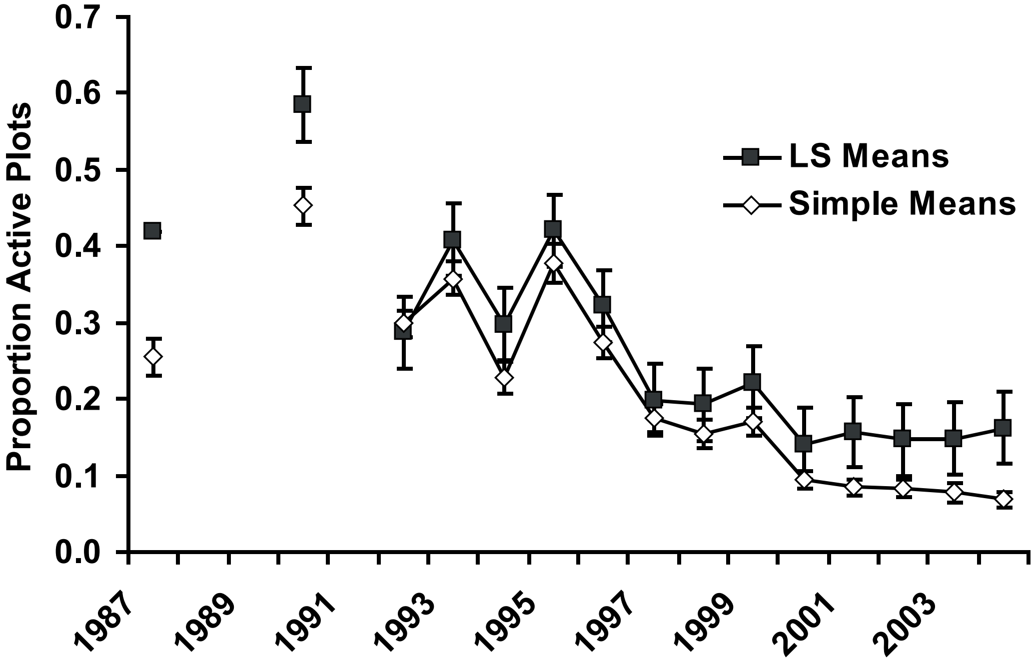

Figure 10. Simple means and least square (LS) means of pig activity surveys across all management units at Hakalau Forest National Wildlife Refuge 1987–2004. Data represent the mean proportion of stations per plot with either fresh or intermediate age feral pig sign.

d. Indexing Pig Density

Sixteen different models of pig sign were all significantly and positively related to pig density (Table 8). Models of feral pig activity with all sign, fresh sign, and intermediate sign, but without intercepts were essentially equivalent among the highest ranked by AIC_c. The highest ranked model with an intercept was > 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 (Figure 11). Year 1994 was a strong outlier in every model, having a high density of feral pigs with relatively low activity index values. A small number of pigs remained after most had been removed by the year 2000, resulting in 4 points at very low density. This caused the estimated regression intercepts to be less than zero in most cases. Because models without intercepts have rescaled R^2 values, this criterion cannot be used to make comparisons between models with and without intercepts.

Table 8. Predictive models for estimating feral pig density derived from a reconstructed population at Hakalau Forest National Wildlife refuge, 1992–2004. All indices of activity (sign) were arcsine transformed for analysis. Precipitation represents rainfall one month prior to activity 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	20.665 * all sign
13	1	23.17	25.53	0.67	2.350	< 0.001	26.380 * intermediate sign
13	1	23.46	25.83	0.96	2.376	< 0.001	34.549 * fresh sign
13	2	23.30	28.50	3.63	2.283	< 0.001	- 1.074 + 23.408 * all sign
13	2	23.79	28.99	4.13	2.328	< 0.001	- 1.19 + 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 + 0.0072 * precipitation
13	2	24.96	30.16	5.30	2.435	< 0.001	25.7 * intermediate sign + 0.0194 * precipitation
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 + 0.0932 * precipitation
13	3	23.87	32.53	7.67	2.267	< 0.001	- 2.00 + 24.0 * all sign + 0.0610 * precipitation
13	3	25.06	33.73	8.87	2.374	< 0.001	- 1.07 + 13.7 * fresh sign + 19.7 * intermediate sign
13	3	25.46	34.13	9.26	2.482	< 0.001	34.6 * fresh sign - 0.0018 * precipitation
13	3	26.19	34.85	9.99	2.478	< 0.001	15.3 * fresh sign + 14.7 * intermediate sign + 0.0075 * precipitation
13	3	27.09	35.75	10.89	2.566	< 0.001	- 0.76 + 36.7 * fresh sign + 0.0192 * precipitation
13	4	24.42	37.42	12.56	2.261	< 0.001	- 2.80 - 2.4 * fresh sign + 33.9 * intermediate sign + 0.0977 * precipitation
13	1	47.65	50.01	25.14	6.023	0.056	0.206 * precipitation
13	2	45.33	50.53	25.67	5.330	1.000	4.68 - 0.000 * precipitation

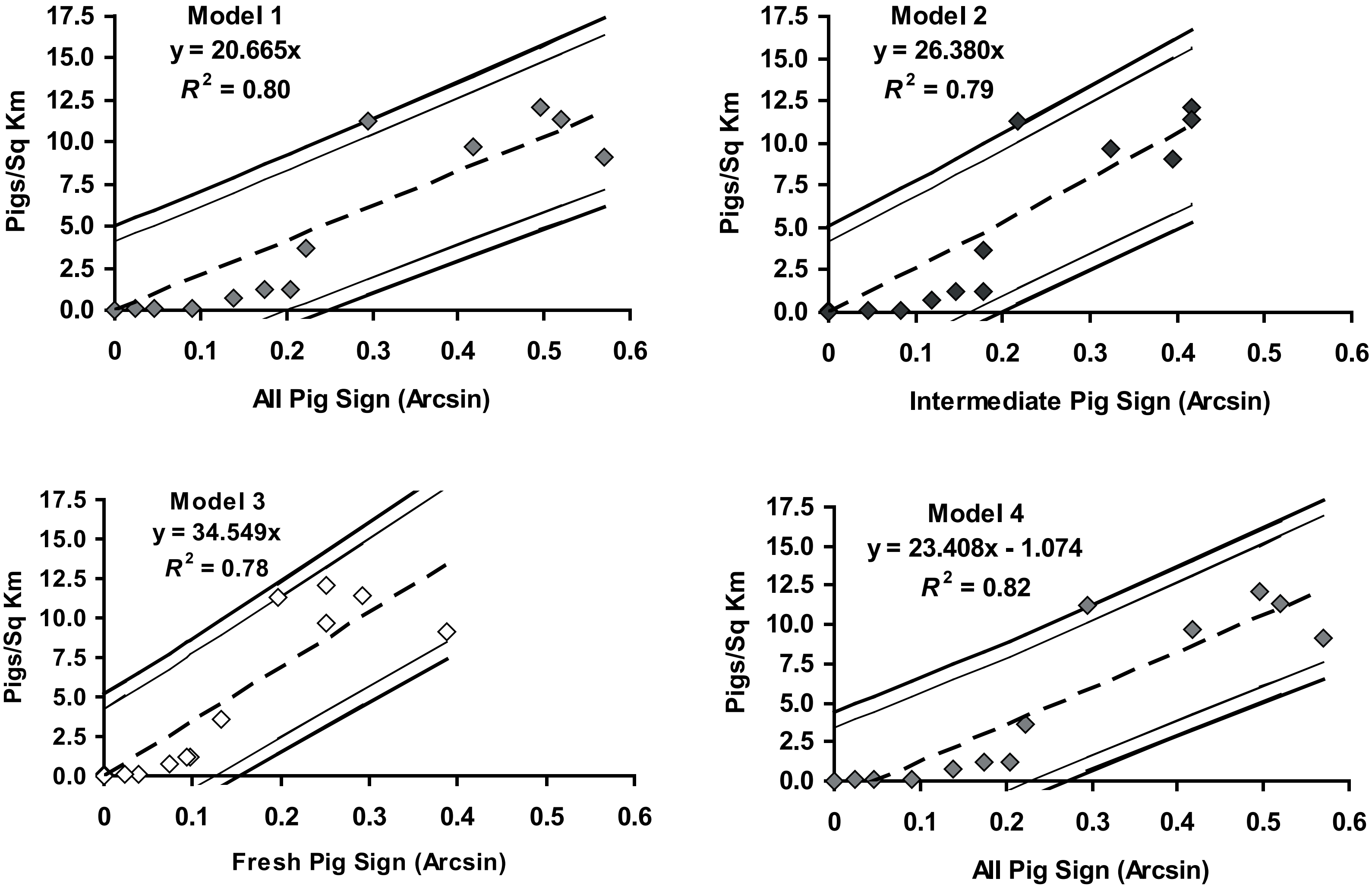

Figure 11. The 4 highest ranked predictive models for estimating feral pig density derived from a reconstructed population at Hakalau Forest National Wildlife Refuge 1992–2004. Dashed line represents model, solid light lines represent 90% prediction CI, and solid bold lines represent 95% prediction CI.

e. Predicting Density in Other Units

When applied to other management units, densities of feral pigs predicted by the model derived from the 5,000 acre unit were highly variable primarily due to annual variability in pig sign within units (Figure 12). Variability in sign may have reflected ingress in a few cases. The unmanaged area of Middle Maulau and Piha had predicted densities of feral pigs that were > 2 times higher than the Unit 2 maximum of 12.1 pigs/km^2 (Table 9). The density predicted in Unit 3 also exceeded the 5,000 acre unit maximum in several years, and Unit 4 exceeded this level in 1993. A predictive model cannot be expected to accurately estimate densities outside the range of the data used to derive the model. The predicted population of pigs in units 1 and 4 terminated at 0 in years 2002 and 2000 respectively. The predicted terminal population of Unit 3 was 118 (± 36; 90% PI) in 2004, while Unit 6 contained 24 (± 20) pigs. Unit 7 had a variable but low predicted population ranging from 17–0 between years 2000–2004.

f. Evaluating Removal Methods

In a general linear model, control method ($P = 0.001$), but not year ($P < 0.081$) or management unit ($P > 0.55$) were significant factors 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. We retained year 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 by 0.95 (SE = 0.35) pigs per person day than staff hunting ($P < 0.039$), and 1.51 (SE = 0.33) more than public hunting ($P < 0.0004$; Figure 13). There was no significant difference, however, between staff hunting and public hunting ($P > 0.10$).

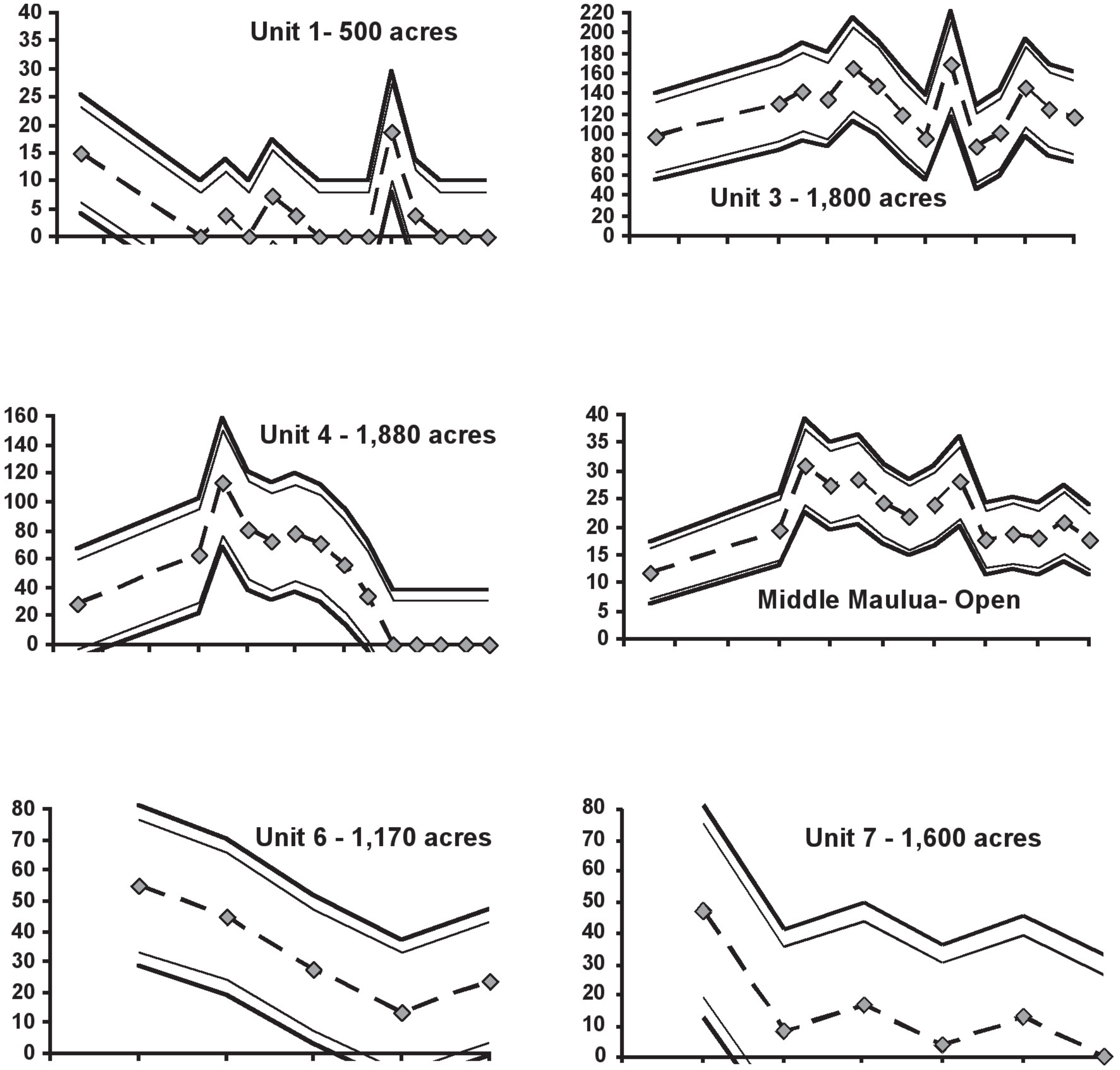

Figure 12. Predicted feral pig abundance in 5 closed management units and an unmanaged open area based on a model of all pig sign at Hakalau Forest National Wildlife Refuge 1987–2004. Dashed lines represent model predictions, solid light lines represent 90% prediction CI, and solid bold lines represent 95% prediction CI. Predictive model was based on a reconstructed population from a 5,000 acre unit (Unit 2).

Table 9. Predicted feral pig densities (pigs/km^2) based on a model of all pig sign at Hakalau Forest National Wildlife Refuge 1987–2004. Model was based on a reconstructed population from Unit 2.

Year	Unit 1	Unit 3	Unit 4	Unit 6	Unit 7	Middle Maulua	Piha
1987	7.40	13.62	3.79	-	-	11.75	27.73
1992	0.00	18.20	8.27	-	-	19.60	15.67
1993	1.87	19.70	14.87	-	-	30.92	-
1994	0.00	18.58	10.55	-	-	27.32	-
1995	3.72	22.85	9.54	-	-	28.59	-
1996	1.84	20.40	10.33	-	-	24.22	-
1997	0.00	16.43	9.40	-	-	21.76	-
1998	0.00	13.36	7.30	-	-	23.91	-
1999	0.00	23.46	4.49	-	7.25	28.17	-
2000	9.36	12.15	0.00	11.63	1.32	17.90	-
2001	1.99	14.22	0.00	9.49	2.56	18.91	-
2002	0.00	20.31	0.00	5.78	0.56	17.93	-
2003	0.00	17.27	0.00	2.88	1.97	20.79	-
2004	0.00	16.30	0.00	4.97	0.00	17.58	-
Mean	1.87	17.63	5.61	6.95	2.28	22.10	21.70

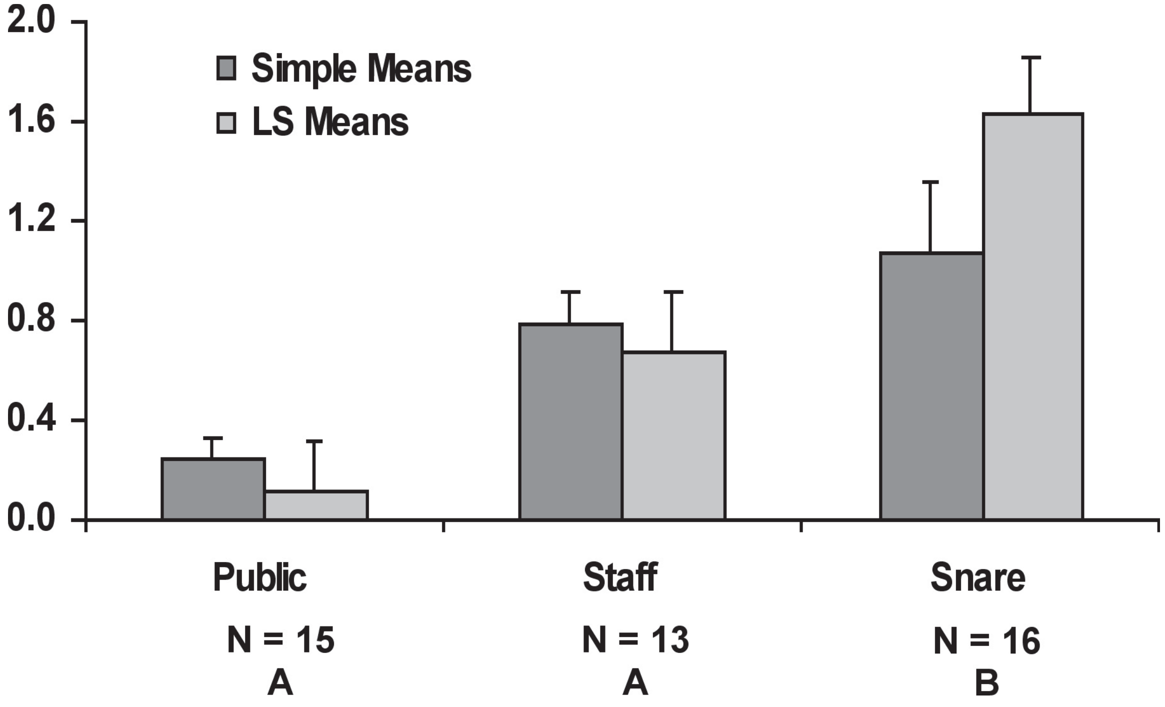

Figure 13. Simple means and least square (LS) means (+ SE) of the efficiency of 3 feral pig control methods at Hakalau Forest National Wildlife Refuge, island of Hawai`i 1989–2004. LS Means with same subscripts did not differ (Bonferroni grouping, α = 0.05).

g. Vegetation Change

Forty-one species in 9 different life-form categories were monitored by the line-intercept method. Each 50-m line-intercept transect in formerly heavily grazed locations (Table 10) and formerly lightly grazed locations (Table 11) was renumerated 4 times from 1987–2003. Not all plots were renumerated in the same year; however we treated these as 4 distinct time periods for analyses. In repeated measures ANOVA, only one of the life forms, litter, exhibited strong between subjects effects of both transect and grazing intensity ($P < 0.001$; Table 12). Native ferns were the only life form to exhibit a strong effect of increased cover over time ($P < 0.002$). Bryophytes and exposed bare soil exhibited marginally non-significant decreases in cover over time ($P < 0.071$). There were no significant interactions within subjects for the effects of time and transect or time and grazing intensity. Although not statistically significant, mean cover of native plants was generally higher in locations that were formerly lightly grazed (Figure 14), while alien grass and herb cover were generally higher in areas that were heavily grazed

(Figure 15). Measurable lichen cover was present in only 1 plot during 1 period of the 24 plot-period combinations; therefore, mean cover of lichens was not presented.

VII) Discussion

From the necropsies of feral pigs removed from HFNWR, we determined several demographic measures and vital rates of the population. Importantly, these data represent only the feral pigs that were removed; the pigs that remained over time may have systematically differed in some subtle respects. For example, we might expect pigs with cumulative exposure to hunting experiences to have remained and thus be older than the pigs that were removed. The overall sex ratio of feral pigs was essentially even and did not differ from parity. There was also no difference in sex ratios within 6 age categories although the maximum age for boars was 60 months while the maximum age for sows was 48 months.

The overall pregnancy rate of feral pigs at HFNWR was 23.5% and the overall rate of lactation was 8.3%, but lactation exhibited marked seasonality. While sows were pregnant year-round, 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 in comparison to Diong's (1982) 'November to March farrowing season' in Kipahulu Valley, Maui. Given these results, August–November is the time of year that management is likely to be most 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 occur before the annual peak period of farrowing.

Pregnancy and lactation also varied with age. Although no sows < 1 year of age were found to be lactating at the time of necropsy, we found a small number in this age category that were pregnant and others that had pregnancy scars, indicating that young sows may occasionally raise litters of piglets. Giffin (1978) reported successful breeding by sows at 10 months of age. While 2–3 years was prime age for pregnancy, the pattern for lactation was not as clear, apparently peaking at age 1–2 years. Sows with pregnancy scars reached a maximum of 60% by the age of 2–3 years, indicating that

Table 10. Percent cover by life form category in formerly heavily grazed vegetation plots at Hakalau Forest National Wildlife Refuge, island of Hawai`i, 1987–2003. Cover was determined by 50-m line-intercept method.

	Plot 1				Plot 3				Plot 5			
Category	1987	1991	1996	2003	1987	1992	1997	2003	1987	1991	1996	2002
Bare Soil	0.0	6.2	0.0	0.0	0.0	0.0	0.0	0.0	1.1	3.9	0.3	0.0
Litter	0.4	3.5	0.0	0.0	0.0	0.0	0.7	3.7	8.1	5.2	9.3	6.4
Logs	4.2	0.4	0.0	0.0	0.0	0.0	0.2	0.0	6.3	9.7	11.2	3.6
Bryophytes	0.6	1.4	0.0	0.0	3.6	0.0	0.7	0.7	5.2	5.3	2.3	1.6
Lichens	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.6	0.0	0.0	0.0
Native Ferns	8.6	10.7	7.7	19.7	3.3	14.6	20.9	24.3	7.3	8.5	15.1	18
Native Woody	0.0	0.3	3.5	8	3.1	5.4	4.2	3.6	3.4	4.9	6.7	9.3
Alien Grasses	86.2	77.2	88.8	72.3	89.8	73.7	49	57.2	63.2	62.3	53.3	59.3
Alien Herbs	0.0	0.3	0.0	0.0	0.2	6.3	24.3	10.5	1.8	0.2	1.8	1.8
Total	100	100	100	100	100	100	100	100	100	100	100	100

Table 11. Percent cover by life form category in formerly lightly grazed vegetation plots at Hakalau Forest National Wildlife Refuge, island of Hawai`i, 1987–2003. Cover was determined by 50-m line-intercept method.

	Plot 2				Plot 4				Plot 6			
Category	1987	1991	1996	2003	1987	1992	1997	2003	1987	1991	1996	2002
Bare Soil	36.2	22.3	11.5	21.4	1.4	13	1.3	1.0	2.8	5.4	0.0	0.0
Litter	12.3	11.2	18.3	7.7	9.2	9.3	7.6	25.5	45.5	34.6	27.7	13.7
Logs	0.2	3.0	4.9	1.5	0.0	0.5	2.9	1.2	0.4	0.5	3.1	2.6
Bryophytes	12.6	9.3	8.7	3.7	4.8	4.2	0.0	4.1	5.0	7.6	1.7	0.4
Lichens	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Native Ferns	20	21.8	33.8	46.8	6.3	12.2	29.6	21.6	35.7	30.4	35.2	51.9
Native Woody	1.0	10.8	4.1	5.2	9.6	7.0	4.6	3.8	2.4	4.2	11.8	13.5
Alien Grasses	17.5	21.3	17.8	13.2	68.7	53.8	54	42.7	8.2	15.8	20.5	17.9
Alien Herbs	0.2	0.3	0.9	0.5	0.0	0.0	0.0	0.1	0.0	1.5	0.0	0.0
Total	100	100	100	100	100	100	100	100	100	100	100	100

Table 12. Repeated measures ANOVA of line-intercept monitoring of 9 forest life forms at 3 formerly heavily grazed and 3 formerly lightly grazed locations at Hakalau Forest National Wildlife Refuge, island of Hawai`i, 1987–2003. Degrees of freedom are indicated in parentheses.

	Between Subjects Effects				Within Subjects Effects					
	Transect (2)		Grazing Intensity (1)		Time (3)		Time*Transect (6)		Time*Grazing Intensity (3)	
	F Value	*P* Value	F Value	*P* Value	F Value	*P* Value	F Value	*P* Value	F Value	*P* Value
Native Ferns	0.48	0.6755	5.11	0.1523	19.34	0.0017	2.67	0.1284	0.69	0.5894
Native Woody	7.80	0.1137	9.01	0.0954	2.25	0.1828	1.44	0.3346	0.43	0.7397
Bryo-phytes	0.22	0.8224	1.79	0.3132	4.17	0.0649	1.10	0.4543	0.44	0.7304
Lichens	1.00	0.5	1.00	0.4226	1.00	0.4547	1.00	0.5	1.00	0.4547
Alien Grass	0.88	0.5329	6.66	0.1231	2.01	0.2136	2.80	0.1177	1.64	0.2766
Alien Herbs	0.42	0.702	1.13	0.3989	0.81	0.5315	0.63	0.7053	0.63	0.6217
Bare Soil	1.03	0.4922	2.93	0.2289	3.98	0.0708	0.29	0.9209	0.46	0.7196
Litter	1238.70	0.0008	5562.93	0.0002	0.03	0.9934	2.29	0.1683	0.30	0.8251
Logs	1.24	0.4472	0.00	0.9875	1.33	0.3501	0.53	0.7681	2.87	0.1261

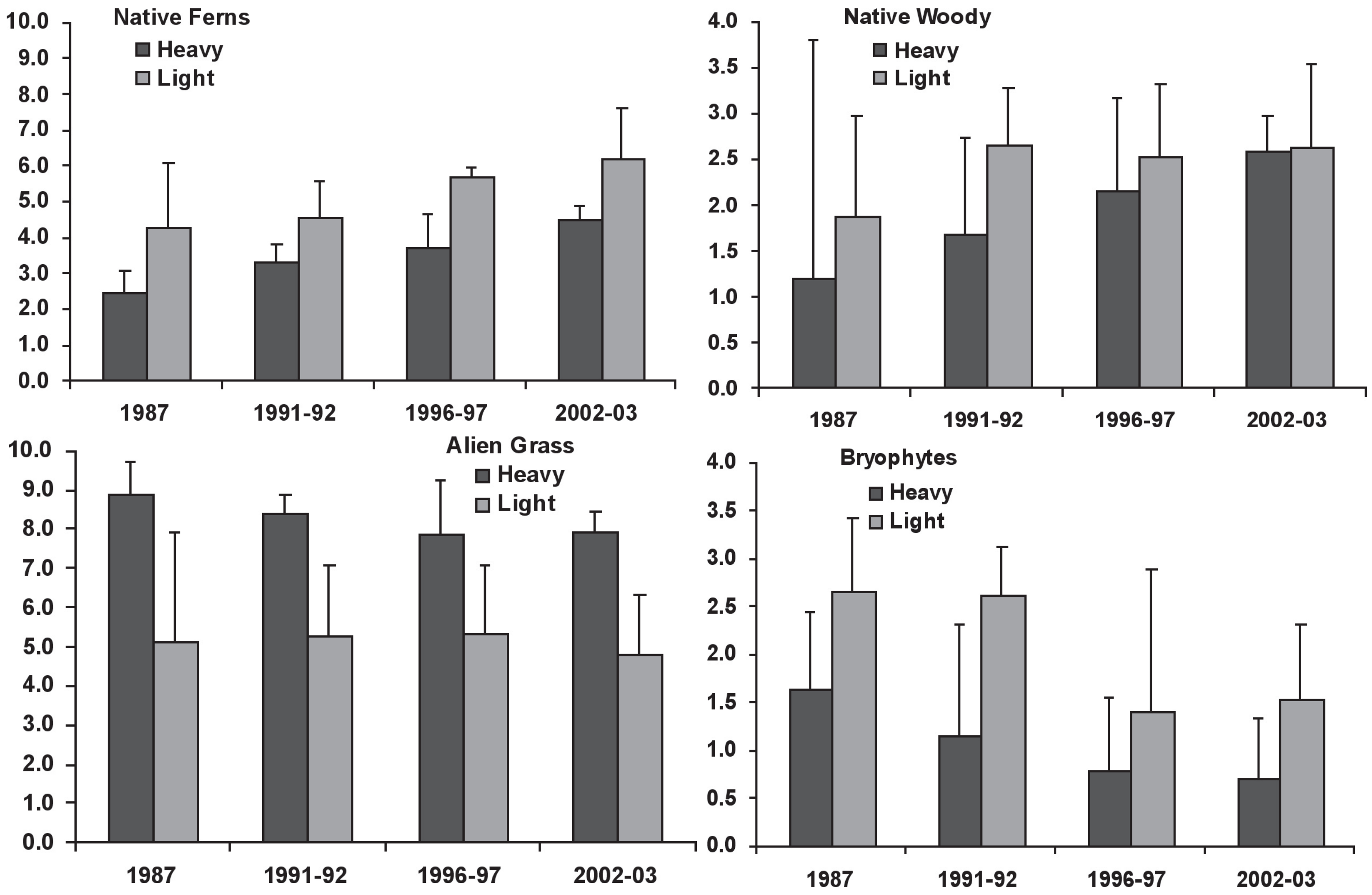

Figure 14. Mean (+SD) square-root transformed percent cover of native ferns, alien grass, native woody plants, and bryophytes at Hakalau Forest National Wildlife Refuge, island of Hawai`i, 1987–2003.

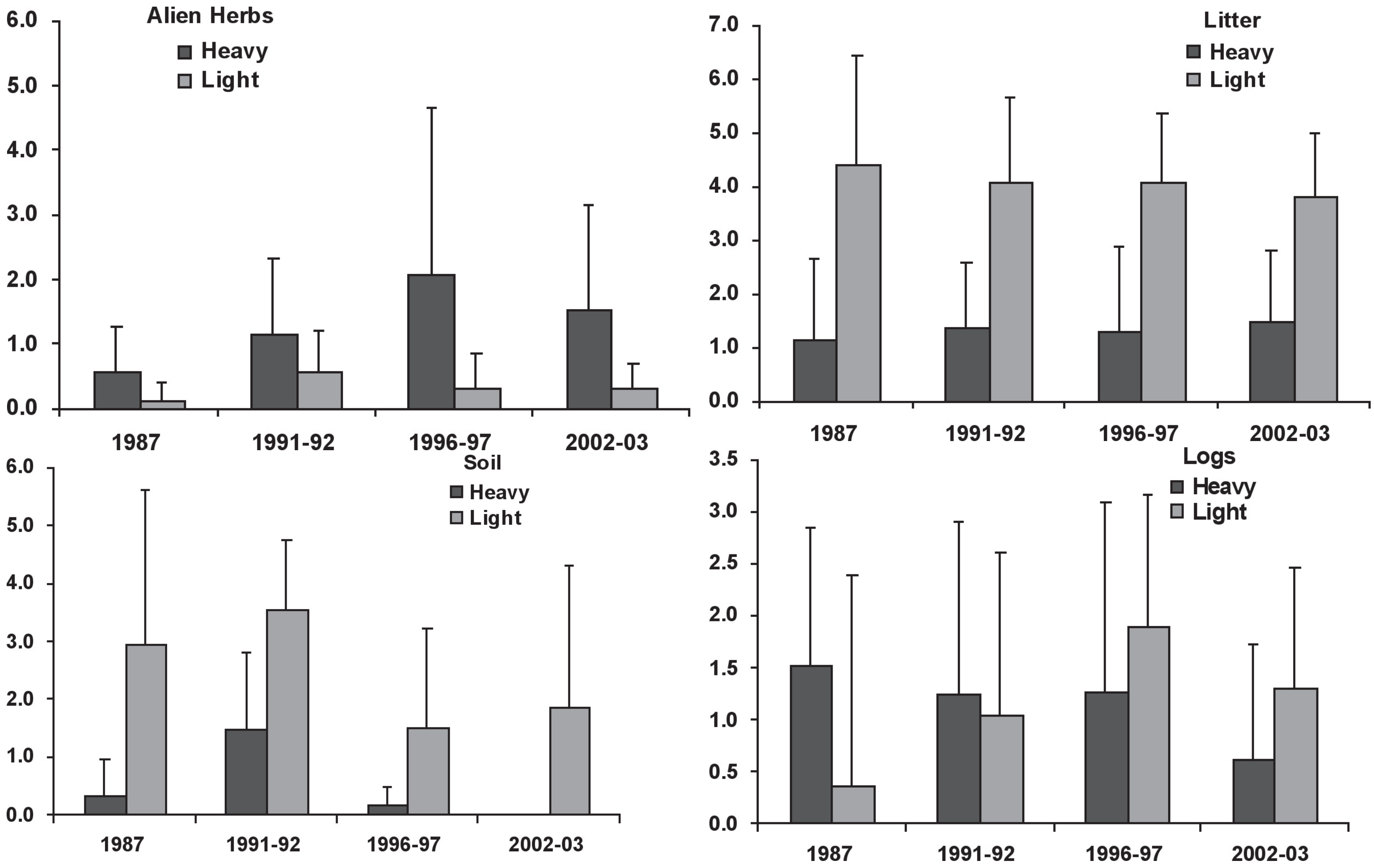

Figure 15. Mean (+SD) of square-root transformed percent cover of alien herbs, soil, litter, and logs at Hakalau Forest National Wildlife Refuge, island of Hawai`i, 1987–2003. Values determined by line-intercept vegetation monitoring at 3 formerly heavily grazed and 3 lightly grazed locations.

approximately 40% of sows may never become pregnant during their lives, which apparently does not frequently exceed > 4 years of age. Nonetheless, number of embryos per pregnancy ranged from 2–12 with an overall median of 7, and the median number of lactating teats was 5, demonstrating the potential for high reproductive capacity. Therefore, when new management units are enclosed, removals should commence immediately and all available resources should be committed to the unit without interruption.

These data represent the largest reported sample of reproductive rates for feral pigs from Hawai`i, offering more precise and accurate estimates than previously available. Diong (1982) found that 21.9% of 41 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, if we considered only the 216 sows >1 year of age, the pregnancy rate at HFNWR was 31.5%, while lactation was 16.9%. Because there was a strong seasonal component to lactation in particular, seasonally unbalanced samples can result in strongly biased estimates of overall reproductive rates. The larger sample from HFNWR varied from 75–94 sows per 3 month period, and correcting for seasonal differences in sample size resulted in < 0.25% difference in our quarterly estimates of pregnancy and lactation rates.

Using the ages of feral pigs removed from a 5,000 acre management unit, we reconstructed the annual standing population and examined several population processes including pig density, annual change in population, the proportion of the population removed each year, and the point of stability. These data provided a rare opportunity for understanding demography during removals and also a 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 finer than one year where pigs were removed but no necropsy was performed. Therefore, all removal analyses were conducted by calendar year.

Although management removals of feral pigs commenced in 1988 enclosure of the 5,000 acre unit was not completed until 1992. Therefore, reliable estimates for the population could not be determined for the period 1988–1991; 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, reliable population estimates could be reconstructed, the number of removals continued to increase, and the reconstructed population declined except in one year. In 1995, management efforts were temporarily halted for several months due to 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 roughly 6.5% from 1995 to 1996 despite the removal of 60 pigs, or about 32.8% of the population in 1995.

We were able to use information on the standing population and the 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, such an analysis is valuable and there are no other means to examine these processes. Plotting these data showed an excellent linear pattern and close relationship between the proportion removed and the population change, indicating that the population reconstruction appeared to be reliable. This analysis showed that > 43.2% of the population would need to be removed on an average annual basis to cause a trajectory of decline. Four data points from the period prior to enclosure were used to derive this estimate, however, using only data from the closed period resulted in only a minor difference in the estimate, > 41.3% (i.e., approximately 41–43% of the population per year could have been removed from this management unit indefinitely). Using the same regression equation, approximately 70–71% of the population would have to be removed to reduce the population by half 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 half their equilibrium density. Attempting to reduce densities in unenclosed areas is not likely to be as successful or lasting at achieving this goal as high levels of removals from enclosed areas.

Annual surveys of feral pig sign showed significant variability between years and management units, but also variability between observers in comparison to an experienced reference observer. The survey design was not balanced in a manner where observers were rotated or randomized among the units each year. Several observers participated in only a few surveys and had to be grouped together for analysis. Additionally, surveys of units 7 and 6 were annexed in years 1999 and 2000 respectively. These design imbalances limited rigorous inferences about the causes of variability between surveys, however, there appears to have been substantial year-to-year variability during periods when feral pigs were abundant in 1987–1997 followed by a period of significantly lower sign and less year-to-year variability from 1997–2004 relative to unmanaged areas. The source of high-level annual fluctuations cannot be adequately explained from this analysis. Intense rainfall immediately preceding surveys may have eliminated tracks, eroded signs of digging, and washed away scat (Hone and Martin 1998). High rainfall combined with warmer temperatures may have also favored ground-level plant regrowth and faster scat decomposition that further obscured evidence of pig activity. Continuous, detailed data on environmental conditions during surveys were not available for this analysis; therefore it was difficult to determine these effects in a meaningful manner.

Our attempt to index pig density had mixed results because of high variability in pig sign at high levels of pig density. Models without intercepts consistently ranked high, supporting a constant proportion index (Lancia 1994). Constant proportion indices have high utility because 1) they predict zero density when there is no sign, and 2) they are simple to employ. Models with all sign were as good as models with fresh or intermediate sign alone. While the data points may appear to follow a non-linear sigmoidal pattern, non-linear regression models are not warranted; some of the data points themselves do not appear to correspond to appropriate levels of pig density. We found that a high density of feral pigs left relatively little sign in one year, an intermediate density left large amounts of sign in another year, and low densities of feral pigs left virtually no sign over the course of several years. In 1994, a year that had relatively high feral pig density, excessive rainfall or other environmental conditions immediately preceding the survey may have washed away sign. Because this was the only year in which high rainfall corresponded with high pig density, precipitation was not a significant factor in any of the highest ranked regression models. Nonetheless, future index surveys should not be conducted immediately after or during periods of intense rainfall.

We also considered the hypothesis that particular observers during the 1994 survey of Unit 2 biased the activity data downwards; however, our examination of inter-observer variability did not support this. None of the 1994 observers had significant negative coefficients relative to the reference observer. Nonetheless, observers should participate in training sessions prior to surveys to better recognize pig scat, tracks, and browse; however, it is not necessary to distinguish fresh versus intermediate sign during surveys. This may simplify field procedures and circumvent problems with classifying sign as fresh or intermediate.

The predictive model of pig density is unique and important in that the 5,000 acre unit was larger in area, had higher densities of feral pigs, data was collected over a much longer period of time, and there were higher levels of sign than reported by Anderson and Stone (1994). The highest density of feral pigs reported by Anderson and Stone (1994) was at the Puhimau study area with 6.53 pigs/km^2 whereas the 5,000 acre unit of Hakalau had a maximum density of 12.12 pigs/km^2 in 1992. Although limited to a single area, this data extends indices of feral pig abundance almost twofold and is therefore extremely valuable. More sophisticated 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 applied in Hawai`i or calibrated with known densities of pigs as the method developed by Anderson and Stone (1994). Adapting any such new index method would require calibration with rigorously estimated feral pig abundance to be useful in setting management goals.

When applied to other management units, the predictive model of pig density showed units 1 and 3 remaining pig-free for several years, and Unit 7 in the terminal year of 2004. The model also predicted a small terminal population remaining in Unit 6. The predictive model probably did not estimate accurate densities for Unit 3 and the unmanaged area of Middle Maulua where sign values were outside of the range of the generating model, but was useful in confirming high densities of feral pigs remaining in these areas. Although feral pigs were eradicated from Unit 4 without the use of snares, this was exceptional in that dense, closed-canopy forest did not dominate the unit whereas other units had substantially denser forest vegetation.

Comparing the efficiency of control methodology was difficult for three reasons: 1) the effort expended in deploying snares was not recorded separately from staff hunting effort prior to 1998; 2) multiple methods were used in units within calendar years; and, 3) pig densities had decreased in most units by the time high-effort snaring was initiated in 1998. The effect of the first issue precluded any analysis of snaring efficiency prior to 1998, but also inflated the amount of effort expended in staff hunting in the same period. Therefore, our estimate of staff hunting efficiency was likely biased lower than the actual value. The effect of the second issue may have also biased low our estimate of staff hunting efficiency because public hunting preceded staff hunting within years, reducing pig density prior to staff hunting. This, however, occurred in only 3 of the 28 cases. The last issue may have also biased low the estimated efficiency of snaring because pig density within units had been reduced by the other methods. There was, however, only one case in which (public) hunting and snaring were conducted in a unit within a calendar year. Ideally, pig density could have been used as a covariate in the analysis of control efficiency; however, this was not available for 2 of the 8 management units, as activity surveys were never conducted. Least square means of the general linear model controlled for some of the imbalances between years by providing estimates of efficiency as if all methods had been conducted in a common year. Although there was no significant difference in efficiency between public and staff hunting, snaring was significantly more efficient in terms of the number of pigs removed per unit effort than either hunting method.

Although some humane groups in Hawai`i oppose snaring (Jenkins *et al*. 1996), it is clearly more effective than hunting as a technique for eradicating remnant populations of feral pigs. Reliance on hunting alone to eradicate feral pigs could result in persistent small numbers of pigs that may reestablish larger populations and require repetitive control. Marks (1996) stated that, "strategies used to control pests for a particular outcome should be adequate and effective in order to reduce the need for unnecessary and repetitive control involving increased numbers of animals. Efforts must be taken to monitor control activities to ensure that the desired outcome of vertebrate pest control is achieved." If HFNWR had not collected detailed data on all of these control techniques, there would have been no means to understand the relative effectiveness of each technique. Logistical considerations limited HFNWR to this suite of specific techniques, but new methods may become available and used for future control efforts.

Vegetation monitoring by 50-m line-intercept transects at 6 locations was not entirely conclusive for several reasons. First, although feral pig sign and feral cattle sign were both quantified, we were not able to separate the effects of these two ungulates on vegetation. The potential effects of feral cattle removal on vegetation recovery may have been greater than that of feral pig removal, but more detailed experimental manipulation would have been be required to separate and quantify these effects. Second, the power to detect trends in life form cover with repeated measures ANOVA may have low due to a small number of replicate surveys. There were also insufficient error degrees of freedom to perform multivariate hypothesis tests due to the small number of replicate surveys. A retrospective power analysis of these data would be useful in determining the ability to detect trends given their existence. Thirdly, although plots were designated as heavily grazed or lightly grazed, there was no designed experimental manipulation and control; the removal of feral pigs and cattle proceeded without specific regard to the arrangement of these plots. It is also instructive to note that pig density in plot 4, which was located in management Unit 3 (Lower Honohina), was never reduced to levels as low as the other units, and plot 2 was completely outside of any managed area, thus possibly introducing a confounding effect on the ability to measure recovery in this type of analysis. There was, however, a strong trend of increased cover over time in native ferns, primarily represented by *Drypoteris wallichiana, D. glabra, and D. hawaiiensis*. There were also marginally non-significant decreases in the cover of bryophytes and exposed soil cover, both of which may have resulted from seral processes in forest regeneration following the removal of feral ungulates. A strong difference between subjects was detected in litter cover between transects and between formerly heavily grazed and lightly grazed areas, but this effect did not change over time. Mean cover of native plants was generally higher in locations that were formerly lightly grazed, while alien grass and herb cover was generally higher in areas that were heavily grazed, although these effects were not statistically significant.

VIII) Management Recommendations

There are a number of considerations from our analyses that can improve the ability to manage feral pigs at HFNWR and other similar protected natural areas in

Hawai`i regardless of whether the goal is reduction or eradication. First, to avoid the additional effort of controlling large numbers of new-born pigs, new management units should be enclosed and control implemented prior to the peak of farrowing season, which is April–June at HFNWR. Seasonality in farrowing at other locations may vary. Control is likely to be most effective from August-November; however, once control efforts have commenced, they should proceed with all deliberate speed to avoid being outpaced by reproduction, which occurs throughout the year.

Second, control efforts need to remove more than 41–43% of the population within closed units in order to affect declines in those units. Mangers should attempt to reduce populations by > 70% each year to ensure that populations decrease by half in successive years. We recommend that control efforts not be divided among many units simultaneously if this results in ineffective (i.e., < 41–43%) annual removal. By applying the index model to sign surveys of units where management will be initiated, pig populations can be estimated and removal targets can be assigned to reduce densities by these desired goals. The model's value may be greater for use across multiple years rather than in single years due to the inherent year-to-year variability in sign, particularly at high pig densities.

Thirdly, using estimated removal rates, managers can also determine the amount of effort in person-days that can be expected to achieve management goals with different techniques. Combinations of control techniques may be more effective than single techniques immediately after the enclosure of new management units. When small numbers of pigs remain in a management unit, snaring is the most effective removal technique and it is recommended in addition to any other techniques being used.

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Appendix I

Summary of feral pig control effort by management unit at Hakalau Forest National Wildlife Refuge 1988–2004.

Table A. Unit 1 - Middle Honohina.

	Effort (Person Days)[a]			Pigs Removed			
Year	Staff	Public	Total	Staff	Snare	Public	Total
1988	-	-	0	-	-	-	0
1989	6	-	6	6			6
1990	-	-	0	-	-	-	0
1991	-	-	0	-	-	-	0
1992	-	-	0	-	-	-	0
1993	1	-	1	1	-	-	1
1994	4	-	4	3	-	-	3
1995	3	-	3	4	-	-	4
1996	1	-	1	1	-	-	1
1997	-	-	0	-	-	-	0
1998	-	-	0	-	-	-	0
1999	2	-	2	-	-	-	0
2000	3	-	3	1	2	-	3
2001	2	-	2	-	2	-	2
2002	-	-	0	-	-	-	0
2003	-	-	0	-	-	-	0
2004	-	-	0	-	-	-	0
Total	22	0	22	16	4	0	20

[a] Staff hunting and snaring effort not differentiated.

Table B. Unit 2 – Shipman.

	Effort (Person Days)[a]				Pigs Removed			
Year	Staff	Snare	Public	Total	Staff	Snare	Public	Total
1988	3	-	-	3	-	6	-	6
1989	-	-	11	11	-	11	-	11
1990	44	-	9	53	-	44	9	53
1991	37	-	-	37	57	5	-	62
1992	28	-	-	28	69	21	-	90
1993	114	-	-	114	81	26	-	107
1994	101	-	-	101	110	16	-	126
1995	32	-	-	32	55	5	-	60
1996	130	-	-	130	138	-	-	138
1997	115	-	-	115	58	-	-	58
1998	31	1	-	32	13	2	-	15
1999	-	30	-	30	2	7	-	9
2000	-	18	-	19	-	12	-	12
2001	-	1	-	1	-	-	-	0
2002	-	-	-	0	-	-	-	0
2003	-	-	-	0	-	-	-	0
2004	-	16	-	16	-	3	-	3
Total	702	65	20	722	583	158	9	750

[a] Staff hunting and snaring effort not differentiated prior to 1998.

Table C. Unit 3 - Lower Honohina.

	Effort (Person Days)[a]			Pigs Removed			
Year	Staff	Public	Total	Staff	Snare	Public	Total
1988	-	-	0	-	-	-	0
1989	1	-	1	1	-	-	1
1990	-	-	0	-	-	-	0
1991	-	-	0	-	-	-	0
1992	-	-	0	7	1	-	8
1993	11	-	11	9	-	-	9
1994	7	-	7	2	-	-	2
1995	-	-	0	-	-	-	0
1996	3	-	3	5	-	-	5
1997	8	-	8	7	58	-	65
1998	-	-	0	-	20	-	20
1999	-	-	0	-	63	-	63
2000	-	-	0	-	-	-	0
2001	-	-	0	-	-	-	0
2002	-	-	0	-	-	-	0
2003	-	-	0	-	-	-	0
2004	-	-	0	-	-	-	0
Total	30	0	30	31	142	0	173

[a] Staff hunting and snaring effort not differentiated.

Table D. Unit 4 - Upper Maulua.

	Effort (Person Days)[a]			Pigs Removed			
Year	Staff	Public	Total	Staff	Snare	Public	Total
1988	-	-	0	-	-	-	0
1989	-	-	0	-	-	-	0
1990	-	-	0	-	-	-	0
1991	-	-	0	-	-	-	0
1992	-	105	105	-	-	38	38
1993	-	82	82	-	-	18	18
1994	-	80	80	-	-	25	25
1995	-	84	84	-	-	36	36
1996	-	49	49	-	-	17	17
1997	-	101	101	-	-	56	56
1998	13	36	49	7	-	14	21
1999	20	-	20	25	-	-	25
2000	3	-	3	-	27	-	27
2001	4	-	4	-	-	-	0
2002	-	-	0	-	-	-	0
2003	-	-	0	-	-	-	0
2004	-	-	0	-	-	-	0
Total	40	537	577	32	27	204	263

*Staff hunting and snaring effort not differentiated.

Table E. Unit 5 - Upper Honohina.

	Effort (Person Days)[a]			Pigs Removed		
Year	Staff	Public	Total	Staff	Public	Total
1988	-	-	0	-	-	0
1989	-	-	0	-	-	0
1990	-	-	0	-	-	0
1991	-	-	0	-	-	0
1992	-	-	0	-	-	0
1993	-	-	0	-	-	0
1994	-	-	0	-	-	0
1995	-	-	0	-	-	0
1996	20	-	20	7	-	7
1997	6	-	6	1	-	1
1998	-	-	0	-	-	0
1999	-	-	0	-	-	0
2000	-	-	0	-	-	0
2001	-	-	0	-	-	0
2002	-	-	0	-	-	0
2003	-	-	0	-	-	0
2004	-	-	0	-	-	0
Total	26	0	26	8	0	8

[a] No snaring was conducted in this unit.

Table F. Unit 6 - Middle Hakalau.

	Effort (Person Days)				Pigs Removed			
Year	Staff	Snare	Public	Total	Staff	Snare	Public	Total
1988	-	-	-	0	-	-	-	0
1989	-	-	-	0	-	-	-	0
1990	-	-	-	0	-	-	-	0
1991	-	-	-	0	-	-	-	0
1992	-	-	-	0	-	-	-	0
1993	-	-	-	0	-	-	-	0
1994	-	-	-	0	-	-	-	0
1995	-	-	-	0	-	-	-	0
1996	-	-	-	0	-	-	-	0
1997	9	-	151	160	12	-	1	13
1998	8	-	25	33	5	-		5
1999	-	-	26	26	-	-	1	1
2000	-	-	22	22	-	-	2	2
2001	-	38.5	-	38.5	-	-	-	0
2002	-	9.3	-	9.25	-	59	-	59
2003	-	6.5	-	6.5	-	20	-	20
2004	-	-	-	0	-	-	-	0
Total	17	54.3	224	295.3	17	79	4	100

Table G. Unit 7 - Middle Papaikou.

	Effort (Person Days)				Pigs Removed			
Year	Staff	Snare	Public	Total	Staff	Snare	Public	Total
1988	-	-	-	0	-	-	-	0
1989	-	-	-	0	-	-	-	0
1990	-	-	-	0	-	-	-	0
1991	-	-	-	0	-	-	-	0
1992	-	-	-	0	-	-	-	0
1993	-	-	-	0	-	-	-	0
1994	-	-	-	0	-	-	-	0
1995	-	-	-	0	-	-	-	0
1996	-	-	-	0	-	-	-	0
1997	-	-	135	135	-	-	5	5
1998	-	45	13	58	-	75	-	75
1999	-	-	-	0	-	47	-	47
2000	-	6	-	6	-	9	-	9
2001	-	8	-	8	-	1	-	1
2002	-	-	-	0	-	-	-	0
2003	-	-	-	0	-	-	-	0
2004	-	7.5	-	7.5	-	7	-	7
Total	-	66.5	148	214.5	0	139	5	144

Table H. Unit 8 - Pua Akala.

	Effort (Person Days)				Pigs Removed			
Year	Staff	Snare	Public	Total	Staff	Snare	Public	Total
1988	-	-	-	0	-	-	-	0
1989	-	-	-	0	-	-	-	0
1990	-	-	-	0	-	-	-	0
1991	-	-	-	0	-	-	-	0
1992	-	-	-	0	-	-	-	0
1993	-	-	-	0	-	-	-	0
1994	-	-	-	0	-	-	-	0
1995	-	-	-	0	-	-	-	0
1996	-	-	-	0	-	-	-	0
1997	-	-	-	0	-	-	-	0
1998	-	1.5	-	1.5	-	1	-	1
1999	-	0.8	-	0.8	-	2	-	2
2000	-	0.3	-	0.3	-	-	-	0
2001	-	3.5	-	3.5	-	2	-	2
2002	-	-	-	0	-	-	-	0
2003	-	-	-	0	-	-	-	0
2004	-	1	-	1	-	-	-	0
Total	0	7	0	7	0	5	0	5

Appendix II

Percent of plots with feral ungulate sign at Hakalau Forest National Wildlife Refuge 1987-2004.

Table A. Percent of plots with fresh feral pig sign.

Year	Unit 1	Unit 2	Unit 3	Unit 4	Unit 6	Unit 7	Middle Maulua	Piha
1987	5.00	2.96	26.29	1.31	-	-	26.34	59.12
1990	-	25.14	-	-	-	-	-	-
1992	0.00	6.21	31.30	5.38	-	-	31.83	30.21
1993	0.46	8.29	39.73	21.65	-	-	87.04	-
1994	0.00	3.81	51.88	12.93	-	-	91.36	-
1995	0.53	14.25	53.28	7.88	-	-	75.63	-
1996	0.90	6.21	37.18	7.67	-	-	48.74	-
1997	0.00	1.75	32.03	8.03	-	-	57.21	-
1998	0.00	0.96	17.95	9.27	-	-	58.77	-
1999	0.00	0.89	59.00	3.00	-	4.41	75.64	-
2000	2.35	0.53	17.57	0.00	9.23	0.00	25.40	-
2001	0.44	0.15	19.44	0.00	6.13	0.24	27.79	-
2002	0.00	0.00	51.17	0.00	2.32	0.00	40.00	-
2003	0.00	0.06	39.79	0.00	0.87	0.00	47.88	-
2004	0.00	0.00	23.36	0.00	0.36	0.00	37.83	-
Mean	0.69	4.75	35.71	5.51	3.78	0.77	52.25	44.67

Table B. Percent of plots with intermediate feral pig sign.

Year	Unit 1	Unit 2	Unit 3	Unit 4	Unit 6	Unit 7	Middle Maulua	Piha
1987	5.83	9.52	15.43	3.66	-	-	20.00	34.31
1990	-	21.63	-	-	-	-	*	-
1992	0.00	16.57	27.98	10.07	-	-	34.20	15.72
1993	0.46	16.33	29.46	21.82	-	-	12.39	-
1994	0.00	4.65	11.88	10.86	-	-	2.47	-
1995	3.19	14.79	27.92	12.09	-	-	20.92	-
1996	0.00	10.15	32.96	15.33	-	-	36.18	-
1997	0.00	3.15	19.78	11.50	-	-	16.44	-
1998	0.00	3.14	17.38	3.03	-	-	24.83	-
1999	0.00	2.13	21.88	1.76	-	7.30	19.92	-
2000	19.25	1.39	15.20	0.00	13.31	0.00	32.20	-
2001	0.00	0.67	20.56	0.00	11.56	0.47	37.05	-
2002	0.00	0.20	16.67	0.00	4.76	0.09	18.20	-
2003	0.00	0.00	13.00	0.00	1.12	0.86	21.38	-
2004	0.00	0.00	25.72	0.00	4.50	0.00	18.44	-
Mean	2.05	6.95	21.13	6.44	7.05	1.45	22.47	25.02

Table C. Percent of plots with fresh feral cattle sign.

Year	Unit 1	Unit 2	Unit 3	Unit 4	Unit 6	Unit 7	Middle Maulua	Piha
1987	7.50	14.54	6.86	21.41	-	-	0.00	10.22
1990	-	5.98	-	-	-	-	-	-
1992	0.00	0.00	0.28	4.86	-	-	0.00	1.77
1993	0.00	0.04	0.00	1.43	-	-	0.00	-
1994	0.00	0.00	0.00	0.17	-	-	0.00	-
1995	0.00	0.07	0.00	0.55	-	-	0.00	-
1996	0.00	0.00	0.00	0.00	-	-	0.25	-
1997	0.00	0.00	0.00	0.00	-	-	0.00	-
1998	0.00	0.00	0.00	0.00	-	-	3.87	-
1999	0.00	0.00	0.00	0.00	-	2.97	0.00	-
2000	0.00	0.00	0.00	0.00	0.48	0.58	0.00	-
2001	0.00	0.00	0.00	0.00	0.47	0.00	0.24	-
2002	0.00	0.00	0.00	0.00	1.59	0.00	0.00	-
2003	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
2004	0.00	0.00	0.00	0.00	0.00	0.00	3.78	-
Mean	0.54	1.38	0.51	2.03	0.51	0.59	0.58	5.99

Table D. Percent of plots with intermediate feral cattle sign.

Year	Unit 1	Unit 2	Unit 3	Unit 4	Unit 6	Unit 7	Middle Maulua	Piha
1987	5.83	29.08	1.14	15.14	-	-	0.49	6.57
1990	-	10.38	-	-	-	-	-	-
1992	0.00	0.00	1.94	9.38	-	-	0.00	0.88
1993	0.00	0.00	0.81	3.40	-	-	0.00	-
1994	0.00	0.00	0.00	1.90	-	-	0.00	-
1995	0.00	0.68	0.00	0.73	-	-	0.23	-
1996	0.00	0.00	0.00	0.00	-	-	0.25	-
1997	0.00	0.00	0.00	0.00	-	-	0.00	-
1998	0.00	0.00	0.00	0.00	-	-	1.37	-
1999	0.00	0.00	0.00	0.00	-	0.72	0.64	-
2000	0.00	0.00	0.00	0.00	1.56	0.00	0.00	-
2001	0.00	0.00	0.00	0.00	0.59	0.16	0.00	-
2002	0.00	0.00	0.00	0.00	1.10	0.00	0.00	-
2003	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
2004	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Mean	0.42	2.68	0.28	2.18	0.65	0.15	0.21	3.73