INDEXING SIZES OF FERAL PIG POPULATIONS IN A VARIETY OF HAWAIIAN NATURAL AREAS

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ABSTRACT: Twelve linear models for estimating feral pig population density were generated from data on feral pig sign and densities collected in 5 habitat types in Hawaii. Densities were back-calculated from population reconstructions with data collected from pigs eradicated within fenced units. Indices to feral pig populations included frequency of pig digging, scats, tracks, plant feeding, beds, and rubs. Three age classes of sign were recorded. Sampling intensity ranged from 50 to 310 plots/km^2 in the 5 areas. Significant models for fresh digging exhibited considerable variability in the densities predicted, probably dependent on substrate available for digging. Densities predicted from fresh scat models were consistent in 2 areas, but models failed to predict densities in the other 3 areas. The model for all fresh sign encompassed variability in all habitats sampled and gave the most precise predictions across habitats. None of the models was useful at population densities of <1 pig/km^2.

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Accurate and precise indices of feral pig (*Sus scrofa*) populations are useful to those managing for sustainable yield, reduction, or eradication. Yet pigs are difficult to count because of their wide-ranging movements, preference for dense vegetation, generally low densities, highly aggregated distribution patterns, and rapidly changing densities resulting from high productivity (Barrett 1982).

Indices to feral pig numbers include area counts, spotlight strip transects, diurnal ground and aerial strip transects, bounty payments, and numbers of pigs killed in an area (Hone 1987, 1988). Indices have rarely been compared with actual pig densities determined independently (Barrett 1982, Hone 1987). In the Great Smoky Mountains National Park (USA) Bratton (1977) demonstrated large differences in rooting or digging frequencies among vegetative communities, supporting Barrett's (1982) view that optimum indices likely depend upon habitat. Hone (1988) found that digging and scat counts were repeatable measures in a given area, and that digging was a more accurate index to past pig presence than scats or counts of live pigs.

In Hawaii, pig population sizes have been estimated using dogs to flush pigs along strip census routes in several habitats, with estimates of flushing distances used to determine area surveyed (Giffin 1978). Ralph and Maxwell (1984) indexed pig densities in montane rain forest with counts of scats or dung in 2 x 10 m contiguous plots along transects and digging frequency in 1 m^2 plots at 20 m intervals along transects. The area dug up in 3 x 5 m plots along belts and the frequency of plots in which fresh digging or fresh or old scats occurred, along with other indices (tracks, plant feeding, rubbing, resting places, live pigs, or dead pigs), were used by Cooray and Mueller-Dombois (1981), also in montane rain forest. F.R. Warshauer (unpublished U.S. Fish and Wildlife Service data) used an 11-category scale for damage caused by pigs based on a combination of indicator plant species, ground cover, and digging for plants along U.S. Fish and Wildlife Service Hawaii Forest Bird Survey transects. Damage was generally a less variable index than digging (lower coefficient of variation) and a more sensitive indicator of differences in disturbance, both among vegetational communities and in distances from roads and trails. However, the botanical experience and judgment needed to apply the damage scale extensively seems prohibitive over large areas. Because "damage" is cumulative over time, it is more useful in habitat assessment than in estimating population density. No independent estimates of feral pig densities were available to compare with the various indices used in the above studies in Hawaii, with the exception of the study by Cooray and Mueller-Dombois (1981); this study will be discussed later.

In our study, data recorded during the process of complete feral pig eradication in fenced management units provides a near-absolute accounting for the standing population in a unit at any stage of control. These critical data on pig densities, integrated into linear models with different indices to pig activity, have

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been used to produce models for estimating feral pig densities in a variety of habitats in Hawaii.

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DESCRIPTION OF STUDY SITES

The study was conducted in Hawaii Volcanoes National Park (HAVO) (Fig. 1) and in the Kipahulu District of Haleakala National Park (HALE) (Fig. 2). Within HAVO, we investigated 4 fenced management units that traverse a range of elevation, topography, and vegetation representative of feral pig habitat in the Park. The National Park Service has eradicated pigs from all 4 units.

The Kipuka Kulalio management unit (22 km^2) extends from 1,500 m elevation up the slope of Mauna Loa Volcano to 2,200 m. This area is vegetated with a mosaic of koa (*Acacia koa*) forest or parkland, native shrublands, and native or alien grasslands (Fig. 3) in areas with good soil development. Nearly half the unit is covered by the sparsely vegetated Keamoku aa lava flow.

Farther downslope, from 1,200 to 1,350 m elevation, is the Kipuka Ki unit (9.2 km^2). The thick volcanic ash substrate of Kipuka Ki (Fig. 4) supports vegetation similar to that of Kipuka Kulalio. Native grasslands and much of the forest ground cover in Kipuka Ki have been replaced by introduced grasses due to the effects of cattle grazing and fire. The koa forest within Kipuka Ki contains a greater diversity of subcanopy native trees than the forested areas of the Kipuka Kulalio unit.

The remaining 2 HAVO management units are in montane rain forest. The 'Ola'a unit (2.7 km^2) ranges in elevation from 1,240 to 1,380 m, and the thick volcanic ash substrate is vegetated with very dense tree ferns (*Cibotium* spp.) and numerous other species under a sparse canopy of 'ohi'a (*Metrosideros polymorpha*) (Fig. 5). The Puhimau unit (6.2 km^2) ranges in elevation from 1,100 to 1,140 m, is drier than 'Ola'a, and is dominated by 'ohi'a with an understory of tree ferns and native shrubs (Fig. 6). The introduced tree *Myrica faya* is spreading throughout the unit and dominates the tree canopy at lower elevations. Puhimau contains substantial areas where the ground cover is dominated by uluhe (*Dicranopteris* spp.), a native fern that forms dense thickets, and introduced grasses (*Paspalum* spp., *Andropogon* spp.). The dominance of alien grasses is the result of years of forest canopy thinning caused by the digging and trampling of feral pigs.

The upper Kipahulu unit (7.8 km^2) of HALE ranges in elevation from 1,220 to 2,470 m and contains diverse, intact native 'ohi'a rain and cloud forests, native grasslands, bogs, and riparian communities (Fig. 7). The upper Kipahulu unit (Fig. 2) is the only unit in HALE where feral pigs are nearly eradicated. Unfenced boundaries are in terrain that is steep enough to prevent or severely limit pig ingress.

METHODS

Transects for monitoring pig activity as an index of population density were distributed throughout the fenced management units in HAVO and Kipahulu. The Kipuka Kulalio, Kipuka Ki, and 'Ola'a units transects were spaced systematically at intervals (150-500 m) from a randomized starting point. The Puhimau unit transects were also systematically spaced from a randomized starting point where topography and vegetation permitted. Two supplementary but non-systematically spaced transects crossed the unit in corridors where topography and vegetation permitted. Unfortunately, the sampling design for the Puhimau unit did not provide systematic coverage of pig habitat. The upper Kipahulu Valley unit is characterized by numerous steeply sloped ravines and cliffs, preventing a randomized, systematic transect network. Transects in Kipahulu were placed in major vegetation types over the range of elevations that comprised pig habitat within the Valley.

Sampling intensity ranged from 50 plots per km^2 in Kipahulu to 310 plots per km^2 in the 'Ola'a unit (Table 1). Periodicity of sampling ranged from every 3.8 months on the average in Kipahulu, to every 10.5 months in the Kulalio unit. Other management units were sampled at intermediate time intervals. Pig activity was sampled in continuous 5-m wide (2.5 m on

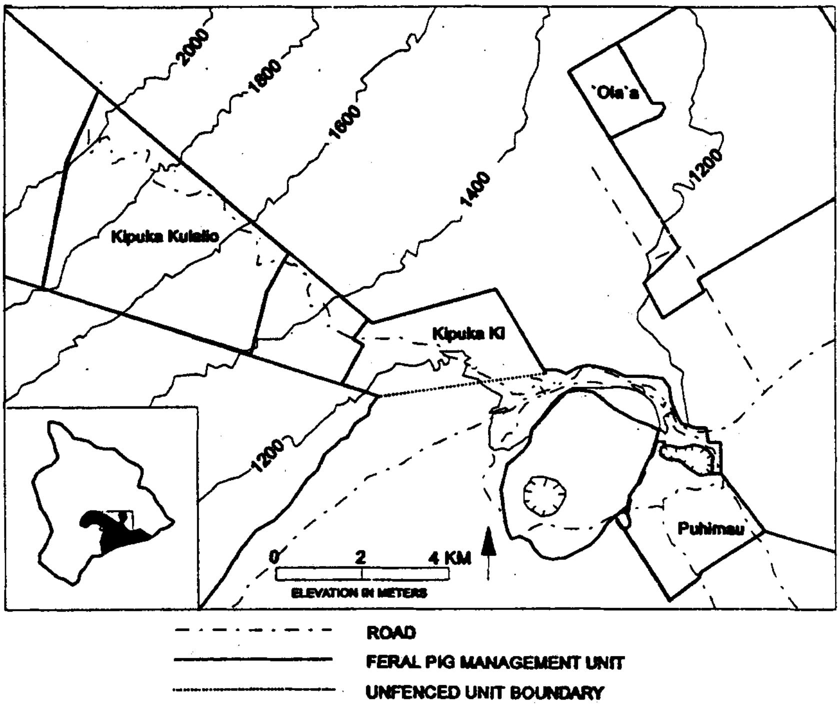


Fig. 1. Feral pig management units in Hawaii Volcanoes National Park. Four fenced units were studied.

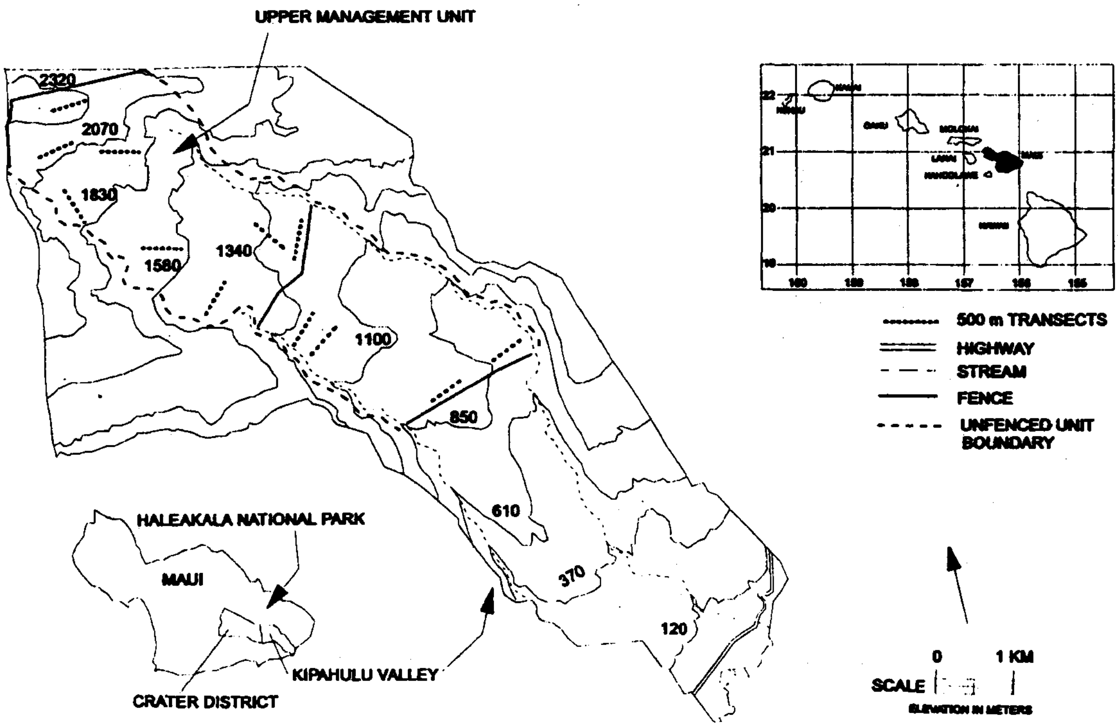


Fig. 2. Feral pig management units and pig activity transects in Kipahulu Valley, Haleakala National Park. The upper management unit is located above the upper fenceline.

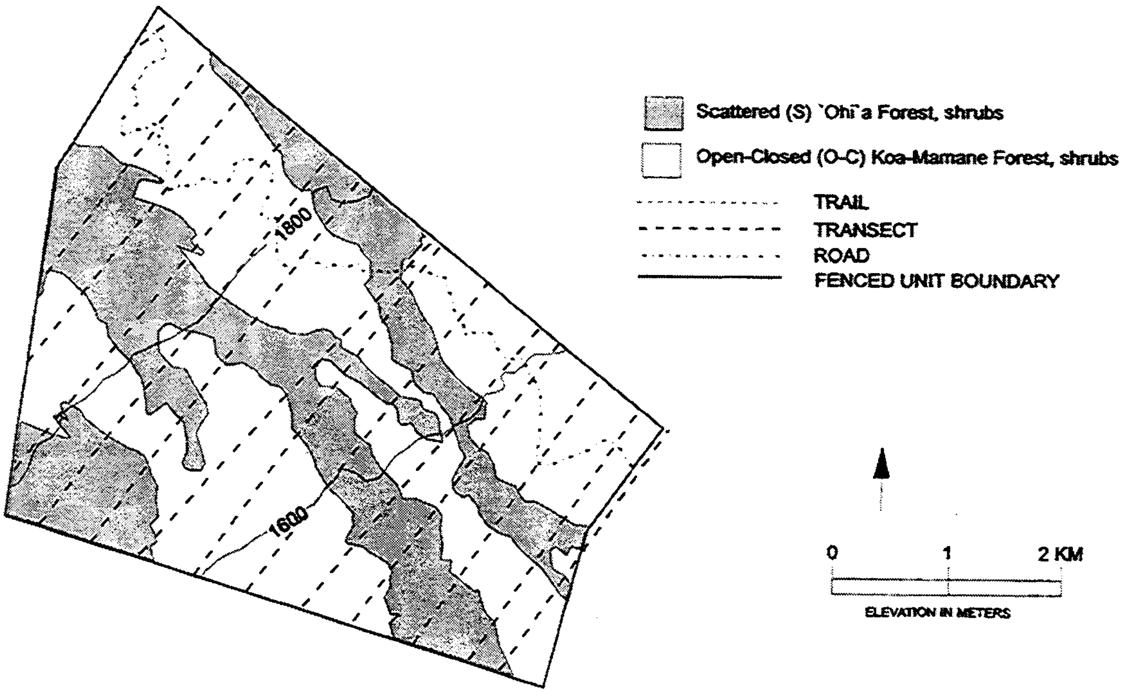


Fig. 3. Kipuka Kulalio management unit (22 km^2) in Hawaii Volcanoes National Park.

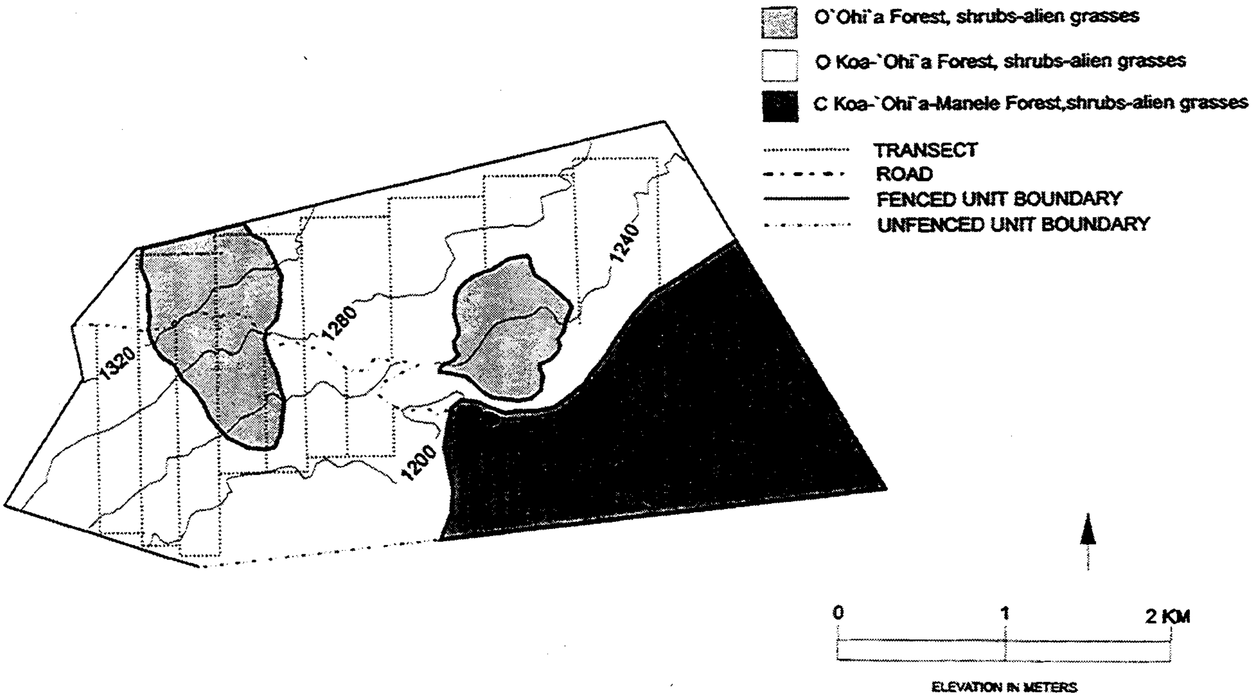


Fig. 4. Kipuka Ki management unit (9.2 km^2) in Hawaii Volcanoes National Park.

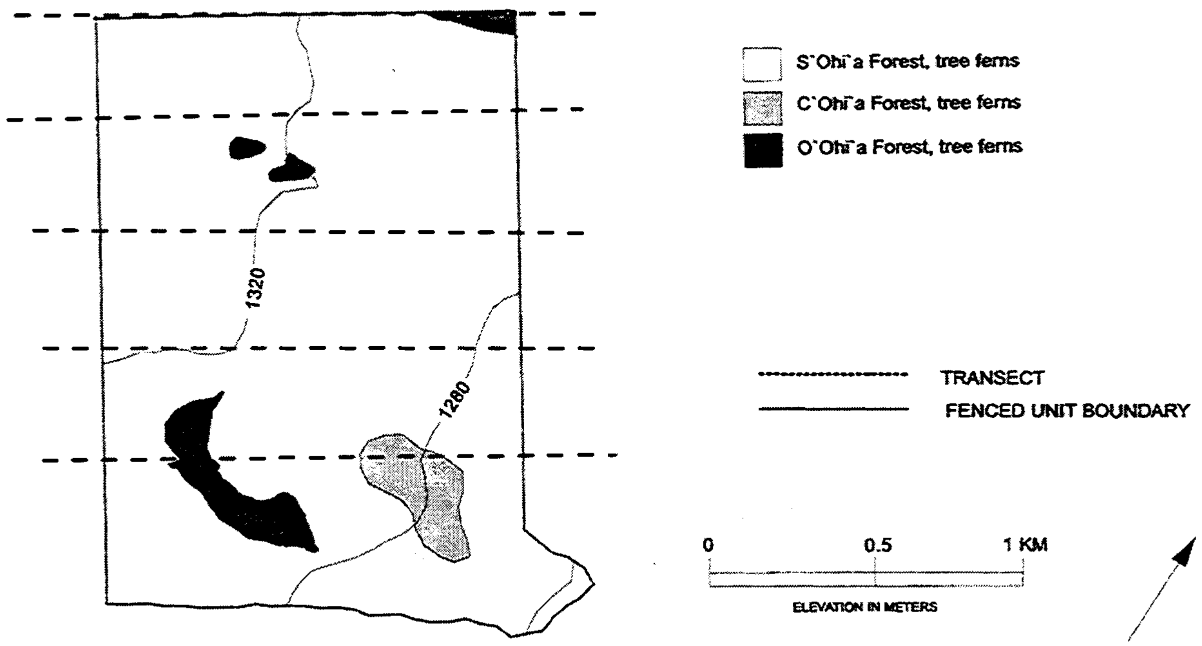


Fig. 5. 'Ola'a management unit (2.7 km^2) in Hawaii Volcanoes National Park.

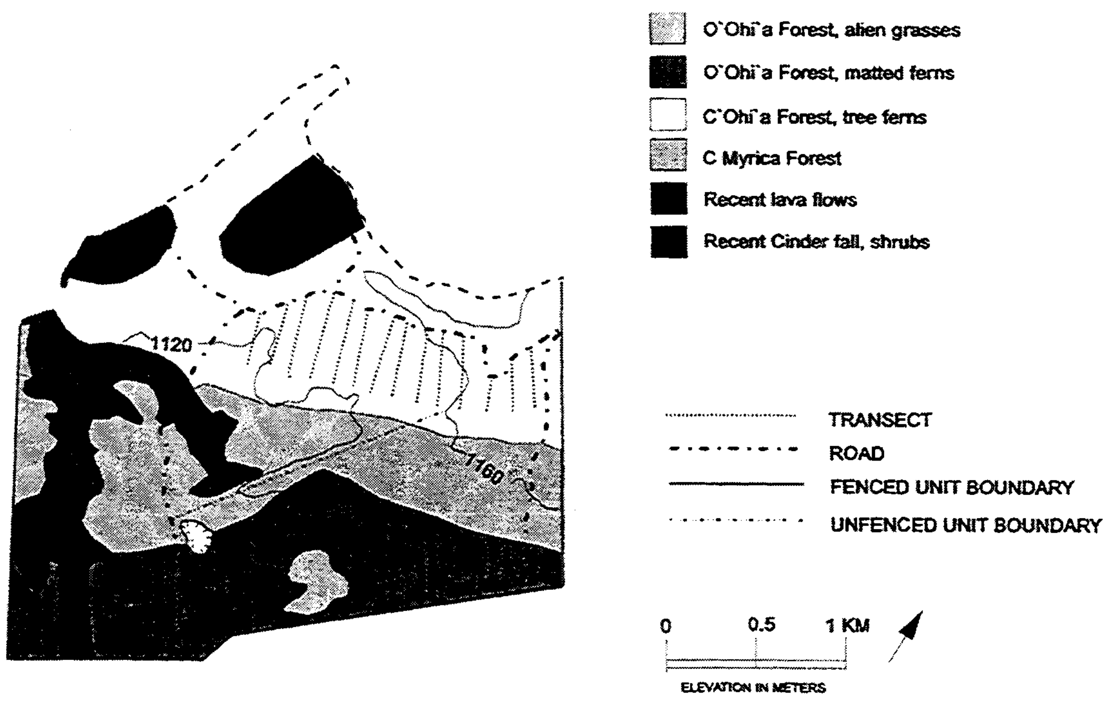


Fig. 6. Puhimau management unit (6.2 km^2) in Hawaii Volcanoes National Park.

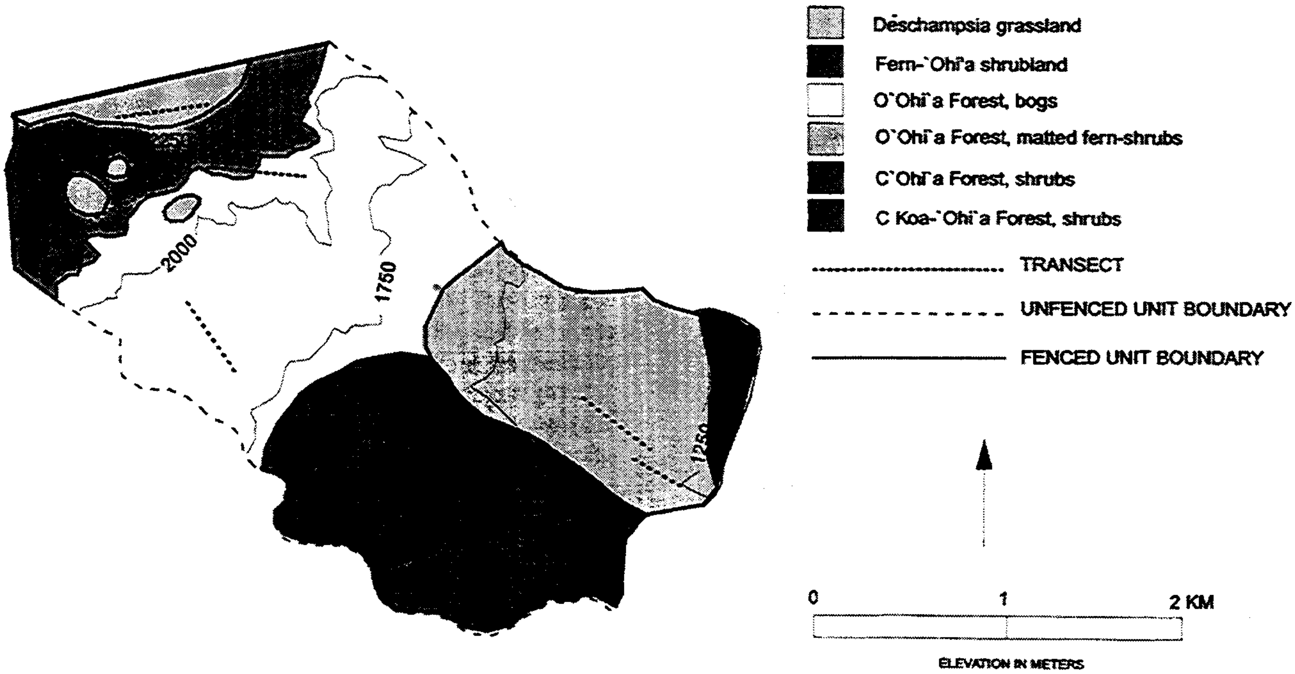


Fig. 7. Upper Kipahulu management unit (7.8 km^2) in Haleakala National Park.

Table 1. Area and sampling intensity of pig control units.

Unit	Area (km^2)	No. Plots	Plots/ km^2	Transect Spacing (m)	No. Samples	Mean Sample Interval (mo)
Kipuka Kulalio	22.0	5,580	240	150-500	3	10.5
Kipuka Ki	9.2	1,472	160	250-500	6	8.6
Kipahulu	7.8	390	50	NA[a]	9	3.8
`Ola`a	2.7	310	310	200	4	4.0
Puhimau	6.2	682	110	100[a]	4	4.3

[a] Two supplementary transects were not systematically placed. See text.

each side of the transect), 10-m long plots. Transects were marked at 10-m intervals with vinyl flagging tape, which was numbered to indicate distance from the starting point. Frequency of pig digging, scats, tracks (trails), plant feeding, beds, and rubs were recorded in 3 age classes (Table 2). The initial pig activity indices for each unit were obtained prior to or coincided with the initiation of control.

Table 2. Pig activity criteria guide.

Digging

A. Fresh - (F)

Fluffy soil; soil clumps on rootlets; digging moist in comparison to surrounding dry soil, but dependent upon weather; litter distribution uneven or different from surrounding. Dug-up plants green, not withered or wilted.

B. Intermediate - (I)

No seedlings, or seedlings with cotyledons only; litter distribution uneven, but with pockets of continuous litter layer; dug-up plants partially green with browning leaf tips.

C. Old - (O)

Seedlings emerging; litter cover uniform and/or accumulated in pits; dug-up plants drying, dead, or rerooting.

Trails and Tracks

A. Fresh - (F)

Green and broken vegetation; fresh scats; tracks well defined, edges of prints sharp or not eroded; soil in print marks moist looking, different from surrounding soils.

B. Intermediate - (I)

Broken vegetation browning, trampled; track prints slightly eroded.

C. Old - (O)

Untrampled look; regrowth of vegetation; eroded track pattern.

Scat

A. Fresh - (F)

Odor; steaming; mucus coating; wet looking (dependent upon weather); flies or other insect activity; fresh tracks or plant feeding nearby; doesn't crumble when smashed.

B. Old - (O)

Gray or black, dried; eroded; seedlings emerging; hardened; fragmented; dung beetles; fungal growth on scat.

Plant Feeding*

A. Fresh - (F)

Damaged plant material green, fresh looking; uprooted plants green; soil still clinging to exposed rootlets.

B. Intermediate - (I)

Affected plant material browning.

C. Old - (O)

Plant material brown and dead; eaten plant shoots regenerating; regrowth of shoots from tubers, rhizomatous or corm plants; uprooted plants dead or rerooted; vertical plant growth from horizontally lying plants.

* Edible plants for pigs (dry habitats): *Vaccinium* fruits, *Styphelia* fruit, *Dianella* fruit and leaves, *Machaerina* leaves, *Myrica faya* fruit, *Sadleria* spp.

Pigs were eradicated in each management unit area through hunting, trapping, and snaring as part of control methodology research and resource management programs. The ages of removed pigs were estimated using tooth eruption and wear (Matschke 1967). Dates of birth were back-calculated from the dates of kill and age of each animal. Standing populations were estimated for each time period during which pig activity data were recorded by using estimated birth dates to determine how many animals had been born into the population and not removed by the date of the pig activity sample. Estimated feral pig densities and frequencies of fresh sign during initial sampling for each unit are shown in Table 3 as an example of some relationships examined.

Table 3. Relationship of feral pig density to frequency of fresh feral pig sign in five management units.

Control unit	Estimated Density (pigs/km^2)	Total Sign Frequency (AF)	Scat Frequency (SF)	Digging Frequency (DF)
Kipuka Ki	1.86	2.08	0.00	0.27
Kulalio	2.63	1.73	0.54	1.28
`Ola`a	5.26	6.92	0.12	6.55
Kipahulu	6.01	8.64	2.50	2.95
Puhimau	6.53	4.39	0.15	2.05

Data Analysis.—Frequencies of pig activity in sample plots were tallied separately for presence of digging, scats, and all sign combined. From 3 age classes of sign recorded in the field, 4 categories were chosen for analysis, as follows: Plots with fresh and intermediate sign were counted separately; a third category of plots that had either fresh or intermediate sign were then counted. Finally, a fourth count of plots with fresh or intermediate sign was performed by weighting plots that had both fresh and intermediate sign. If a plot contained both fresh and intermediate sign, it was given a value of 2; plots with only fresh or intermediate were given a value of 1. Because fresh and intermediate sign were not well defined in Puhimau, the first unit sampled, they were categorized as fresh for analysis. Subsequent monitoring emphasized training and calibrating observers in aging and identifying sign. Frequency count categories that were tallied for the periodic samples obtained from each control unit and abbreviations that will be used in subsequent figures and for discussion are given in Table 4.

Table 4. Frequency count categories for analyses performed on the periodic samples of feral pig activity.

Type of Sign	Fresh	Intermediate	Fresh and Intermediate	Fresh and Intermediate (Weighted)
Digging	DF	DI	DFI	DFAI
Scat	SF	SI	SFI	SFAI
All Sign	AF	AI	AFI	AFAI

Twelve linear models (Table 4) were generated for each of the 5 units to explore the potential predictive value of types, ages, and combinations of the recorded pig sign for the reconstructed pig population densities. Pig activity frequencies were transformed to arcsin values in radians to normalize distributions. Twelve additional linear models were constructed using the combined data from all units, to check for similarity among units and determine whether any single model had predictive value for all of the habitats studied. Plots of residuals against predicted values did not reveal that data transformation or inclusion of additional terms would improve fit of any of the models. The "REG" procedure of the SAS software system for personal computers was used to perform statistical analyses (Anonymous 1985), and the "CLI" option was specified to determine the 95% confidence limits for individual predicted values.

RESULTS

A plot of R^2 vs. standard error of the y estimate for all of the models provides a means of determining the fit and relative predictive values of the models (Fig. 8). For simplicity, the plot axes were truncated at 0.60 for R^2 and 6 for standard error (Fig. 8); models falling outside these limits (n = 41) are not discussed here. (Components for all models are available from the authors.) The models for fresh digging (DF) as an indication of pig density provided the best fit (highest R^2 with lowest standard error of the y estimate) for all units (KDF, OLDF, KKDF, PDF) except for the Kipuka Kulalio unit, which has shallow, rocky soils or aa lava flows not easily dug by pigs. Kipuka Kulalio was sampled only 3 times, twice at zero density, but the model (KUSF) generated from occurrence of fresh scats indicates a correlation (R^2 = 0.96) with feral pig density. The frequency of fresh scats provides a good model for the upper Kipahulu rain forest unit (KSF).

Combining tallies of fresh and intermediate digging (DFAI) decreased the standard error in the Kipuka Ki model from 5.3 to 2.4 but increased the error and decreased the R^2 in the models for digging in the other units. The model generated from tallies of fresh and intermediate scat (SFAI) in the Kipuka Kulalio unit did not provide as good a fit as the model for fresh scat alone (SF). Combining fresh and intermediate scat (SFAI) for the Kipahulu unit resulted in a better fit than that for fresh scat alone (SF); the standard error of the y estimate was decreased from 3.4 to 2.0. Overall, little or no improvement of fit was realized by combining occurrence of different ages of sign in either digging or scat models. Fresh sign alone provided the most consistent method of indexing pig population density (Table 5).

Digging

Of the control units where linear models for digging were significant (Table 5), the Kipuka Ki unit provided the model with best fit (Fig. 9a). The regression equation for Kipuka Ki is $y = 0.19 + 36.65x$, where y = pig density/km^2 and x = frequency of fresh pig digging (arcsin transformed in radians). The model predicts pig density within the 95% individual prediction bound to be within ±0.70 to ±0.80 pigs/km^2 of the actual pig density.

The Kipahulu fresh digging model (Fig. 9b) $y = 0.23 + 30.45x$ predicts pig density within the 95% confidence interval to be between ± 1.3 and

± 1.6 pigs/km^2 of the actual pig density for any given prediction.

Table 5. Significant correlation coefficients between frequencies of fresh digging, fresh scat, and all fresh sign and reconstructed pig densities.

Control unit	Degrees of Freedom	Fresh Digging	Fresh Scat	Fresh All Sign
Kulalio	1	NS	0.96*	NS
Kipuka Ki	4	0.90***	NS	0.68**
Puhimau	2	0.81*	0.78*	0.81*
`Ola`a	2	0.92**	NS	0.79*
Kipahulu	7	0.95***	0.93***	0.92***
Kulalio and Kipahulu	8	–	0.93***	–
All Combined	24	0.72***	0.56***	0.81***

* $p < 0.1$
** $p < 0.05$
*** $p < 0.01$
NS = not significant.

The predictive value of the `Ola`a digging model (Fig. 9c) is diminished by a low sample size (n = 4). The model equation is y = 0.62 + 16.98x. The range of error expected for individual predictions is between ±4.8 and ±5.1 pigs/km^2. The correlation coefficient for the model is 0.92 ($p < 0.05$), which indicates that the predictive error of the model is due to the low sample size and that the error associated with the model is probably less than that predicted.

The Puhimau unit was sampled only 4 times, and the predictive value of the digging model is also low (Fig. 9d). The model equation is y = 2.03 - 19.12x, and the error associated with an individual prediction is approximately ±6.5 pigs/km^2. The negative y intercept of the model (-2.03 arcsin value) indicates that digging was recorded in plots until eradication.

The fresh digging and reconstructed population density data from the periodic samples of all units were consolidated to overcome the differences in error associated with small sample size in some of the units and to test if a significant model could be generated for all of the habitats encompassed within the control units. The model for fresh digging in all units combined (Fig. 9e) is y = 0.45 + 15.59x and has an error for any individual prediction of about ±2 pigs/km^2.

Scats

Two significant models (Table 5) were generated for the frequency of fresh scats found on the activity transects. The Kulalio unit was sampled the least frequently of all the units (n = 3), and no pig scats were found in the plots for 2 of the 3 samples. The model (Fig. 10a) is y = 0.25 + 32.38x. Individual predictions using this model are subject to gross error (±5 pigs/km^2).

The fresh scat model from the Kipahulu unit (Fig. 10b) is y = 0.53 + 34.49x, where y = predicted pig density/km^2 and x is the frequency of fresh pig scat (arcsin transformed). The confidence of an individual prediction (95%) using this model is between ±1.45 and ±1.82 pigs/km^2. A combined model frequency of fresh scat in all units was calculated and resulted in a low correlation coefficient of 0.56; this relationship was not grouped.

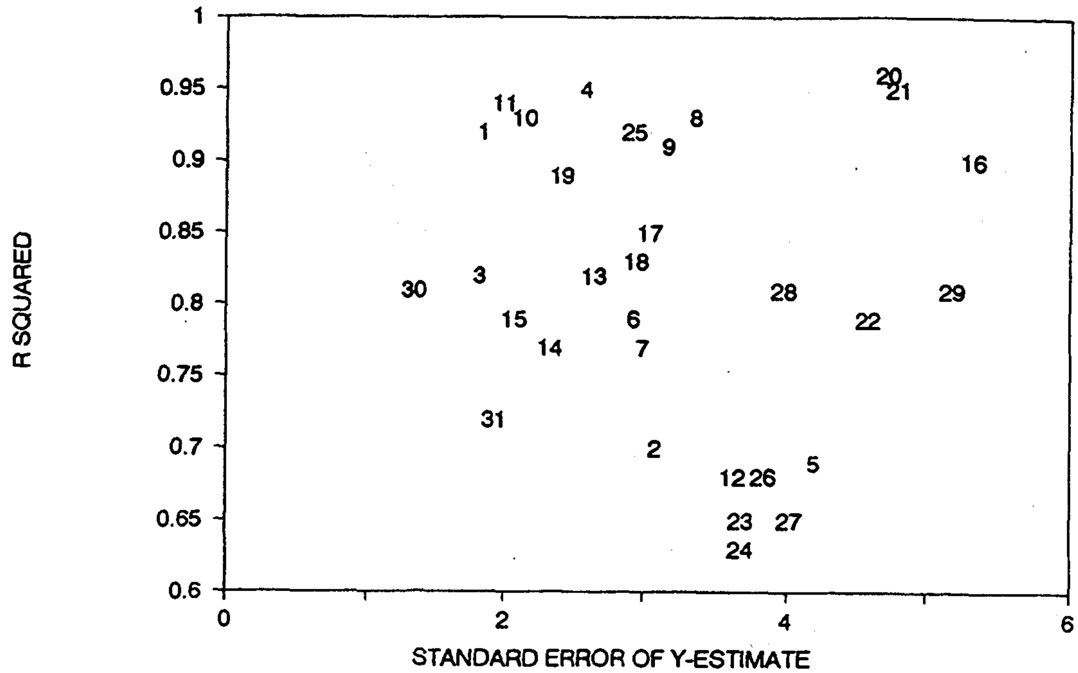
An additional model used the frequency of fresh scat data from Kipahulu and Kipuka Kulalio, the 2 units that had significant correlations between fresh scat frequency and pig density. The correlation coefficient for this model is 0.93 ($p < 0.01$). The equation for the model is y = 0.46 + 34.16x, and the confidence interval of individual prediction (95%) using this model is between ±1.1 and ±1.4 (Fig. 10c).

All Sign

A final model was developed using the frequency of any kind of fresh pig sign in all of the units for all of the periods sampled with the corresponding reconstructed pig densities. The all fresh-sign model (Fig. 10d), y = 0.28 + 13.85x, predicts pig density ±1.5 to 1.8 pigs/km^2 (95% confidence).

DISCUSSION

The sampling frequency in this study is low (Table 1), but the number of plots read for each of the samples is quite large (390-5,580), lending confidence to each individual sample. The significant models (Table 5) for fresh digging exhibited variability in the number of pigs predicted for each management unit per observed frequency of sign. The Kipuka Ki model predicts the greatest density of pigs from the least amount of digging (slope = 36.7). No measure was made of the amount of ground available for digging, but of the units where pig digging has predictive value, Kipuka Ki certainly has the least amount of diggable soil. The unit is transversed by the Keamoku lava flow, a partially vegetated aa or rough flow of clinker lava.



1-KIPAHULU ALL SIGN FRESH
2-KIPAHULU ALL SIGN INTERMEDIATE
3-KIPAHULU ALL SIGN FRESH & INTERMEDIATE
KIPAHULU ALL SIGN FRESH & INTERMEDIATE (WEIGHTED)
4-KIPAHULU DIGGING FRESH
5-KIPAHULU DIGGING INTERMEDIATE
6-KIPAHULU DIGGING FRESH & INTERMEDIATE
7-KIPAHULU DIGGING FRESH & INTERMEDIATE (WEIGHTED)
8-KIPAHULU SCAT FRESH
9-KIPAHULU SCAT INTERMEDIATE
10-KIPAHULU SCAT FRESH & INTERMEDIATE
11-KIPAHULU SCAT FRESH & INTERMEDIATE (WEIGHTED)
12-KIPUKA KI ALL SIGN FRESH
13-KIPUKA KI ALL SIGN INTERMEDIATE
14-KIPUKA KI ALL SIGN FRESH & INTERMEDIATE
15-KIPUKA KI ALL SIGN FRESH & INTERMEDIATE (WEIGHTED)
16-KIPUKA KI DIGGING FRESH
17-KIPUKA KI DIGGING INTERMEDIATE
18-KIPUKA KI DIGGING FRESH & INTERMEDIATE
19-KIPUKA KI DIGGING FRESH & INTERMEDIATE (WEIGHTED)
20-KULALIO SCAT FRESH
21-KULALIO SCAT FRESH & INTERMEDIATE
KULALIO SCAT FRESH & INTERMEDIATE (WEIGHTED)
22-OLAA ALL SIGN FRESH
23-OLAA ALL SIGN FRESH & INTERMEDIATE
24-OLAA ALL SIGN FRESH & INTERMEDIATE (WEIGHTED)
25-OLAA DIGGING FRESH
26-OLAA DIGGING FRESH & INTERMEDIATE
27-OLAA DIGGING FRESH & INTERMEDIATE (WEIGHTED)
28-PUHIMAU ALL SIGN FRESH
29-PUHIMAU DIGGING FRESH
30-ALL AREAS ALL SIGN FRESH
31-ALL AREAS DIGGING FRESH

Fig. 8. Plot of R^2 vs Standard error of y estimate for linear models of predicting feral pig density from feral pig sign.

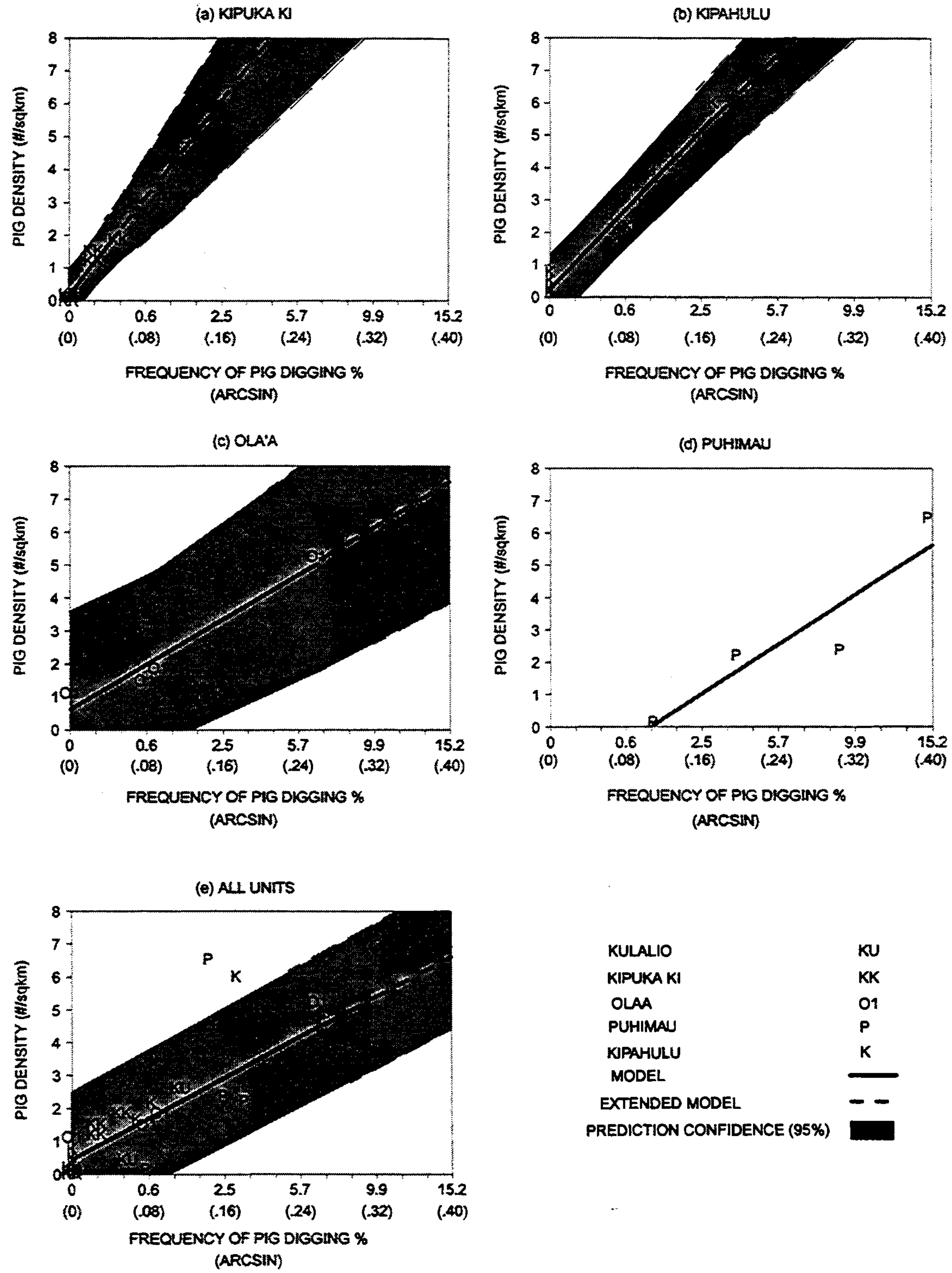


Fig. 9. Significant relationships of frequency of fresh feral pig digging and pig density in 4 management units and all units combined.

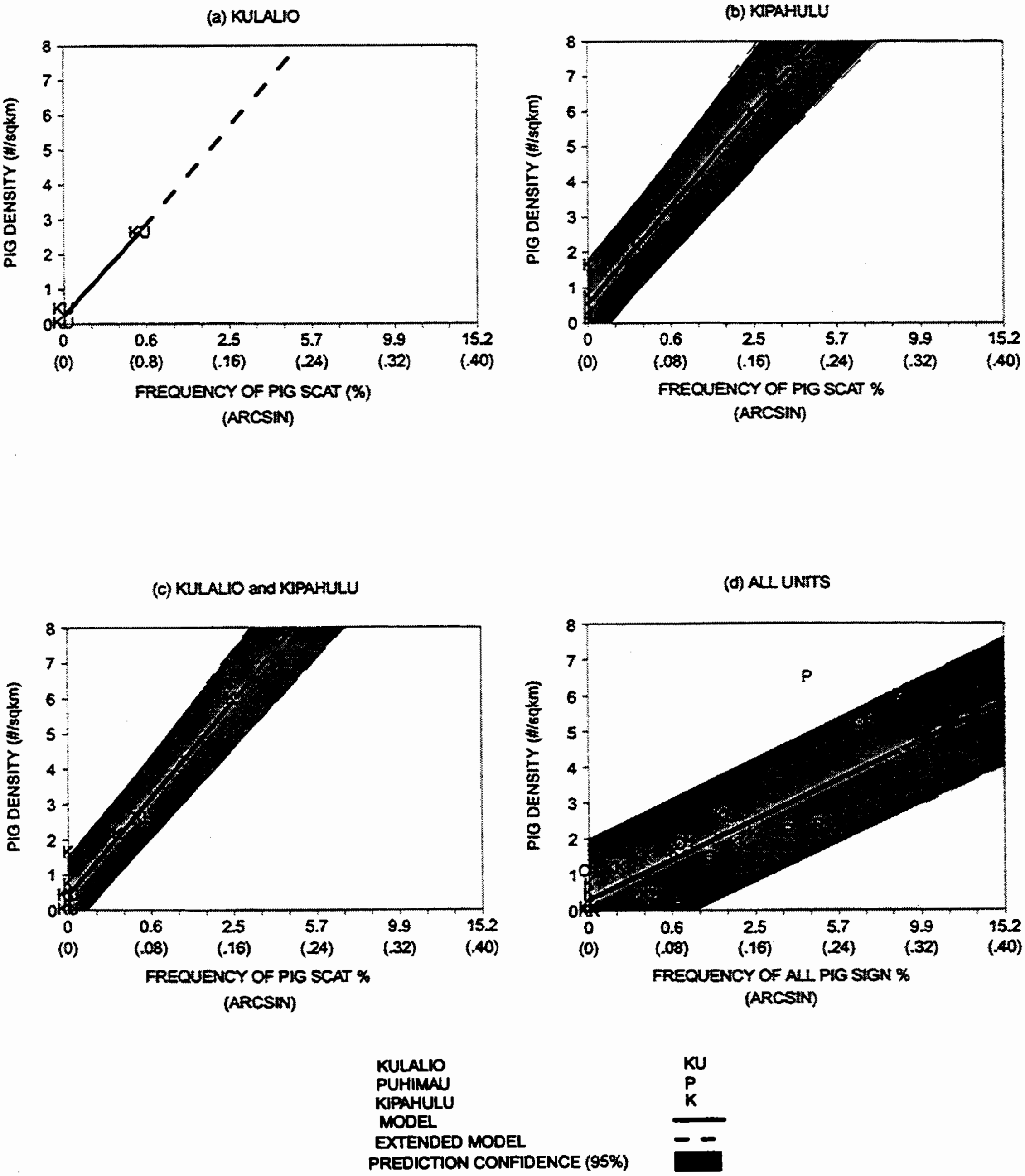


Fig. 10. Significant relationships of frequency of feral pig scat and pig density in 2 management units and 2 units combined, and relationship of all fresh sign to density in 5 management units.

The model for the Kipahulu rain forest unit (slope = 30.5) predicts fewer pigs for a given frequency of plots dug than Kipuka Ki. Although most of the Kipahulu unit contains diggable soil, portions of the unit contain topography too steep for pigs to root. Additionally, the thickly vegetated, relatively pristine nature of Upper Kipahulu makes pig-rooting more difficult than in degraded forests.

The `Ola`a and Puhimau models (slopes: 17, 19.1) predict even fewer pigs in relation to the amount of digging observed than the Kipahulu model. Nearly 100% of the substrate in these units is suitable and available to pigs for digging. The vegetation in the Puhimau unit is the most disturbed, with most of the area easily dug by pigs. The number of pigs predicted for a given frequency of scat observed was consistent (slopes: 34.5, 32.4) for the Kipahulu and Kipuka Kulalio units, but scat models failed to predict pig densities in the other 3 units studied.

Application of Models to Other Areas

Previous studies of feral pig activity indices have been conducted in a variety of habitats with different methods, including variation in size and arrangement of plots and transects, sampling intensity and periodicity, and types and ages of sign recorded. Pig densities have also been estimated by various methods less definitive than complete eradication of animals, as achieved in this study. Nonetheless, it is useful to compare densities obtained from appropriate models developed in the present study and density estimates from other studies in which indices are also available.

Barrett et al.'s (1988) study of feral pigs in Annadel State Park in California resulted in population estimates based on population reconstruction, using age and removal data from nearly complete eradication. However, he did not attempt to correlate feral pig sign to population density. Reconstructing the population for early stages of control provided a maximum estimate of 90 pigs (4.5 pigs/ km^2) for the 2,000-ha park. The frequency of occurrence of all sign for the same time period was 25%. Prediction of density from our all fresh sign model developed in the present study ($y = 0.28 + 13.85x$) is 7.5 pigs/km^2. The fresh digging model for all units in this study ($y = 0.45 + 15.59x$) provides a better estimate (6.3 pigs/km^2) for the 13.5% digging frequency reported. The Annadel data were characterized as fresh or old in the field, but the distinction was not retained in analysis. Fresh scat models from the present study grossly overestimated (8.2-9.1 pigs/km^2) the reconstructed population (4.5 pigs/km^2) for the 6% scat frequency reported at Annadel. Barrett et al. (1988) noted that pig sign was definitely more abundant in certain vegetation types defined by Wainwright and Barbour (1984), irrespective of type abundance in Annadel. Clearly, models developed in this study will be most functional in habitats similar to those in which they were developed, especially if similar methodologies and sampling schemes are used.

Cooray and Mueller-Dombois (1981) found recent (fresh) scats in 4.0 to 17.5% of plots in a 4-year study of a Hawaiian rain forest. Feral pig density estimated by flush counts with dogs along a strip transect in the area ranged from 25 to 100 pigs/km^2. Density estimates for the fresh scat model developed in our study ($y = 0.46 + 34.16x$; Kipahulu and Kulalio) ranged from 7.3 to 15.2 pigs/km^2. In their study, recent digging occurred in 49.3 to 92.0% of sample plots. Our digging model from the adjacent `Ola`a Tract ($y = 0.62 + 16.98x$) predicted 13.8 to 22.4 pigs/km^2, higher than those obtained from the scat model. The high estimate obtained with our digging model approaches the lower density they estimated by flush counts. However, based on our experience in areas where pigs have eventually been eradicated, flush counts produce inflated estimates. Fewer animals than expected can do extensive damage over time.

Hone (1988) found digging in 18.1 to 26.6% of plots and that the percentage of plots with fresh scats varied from 1.4 to 8.3% in a dry _Eucalyptus_ woodland in Australia. The density (visual counts) of feral pigs in the study area was 0.89 pigs/km^2. Habitat in our study was not similar to _Eucalyptus_ woodland, but the Kipuka Ki digging model ($y = 0.19 + 36.5x$) predicted densities of 16.3 to 20.1/km^2, whereas the `Ola`a digging model ($y = 0.62 + 16.98x$) predicted 8.1 to 9.8 km^2. The combined fresh scat model from Kipuka Kulalio and Kipahulu ($y = 0.25 + 32.38x$) predicted densities of 4.1 to 9.7 pigs/km^2. This model predicted fairly low density from few scats, but still higher density than observed for _Eucalyptus_ woodland, as did digging models. Hone (1988) suggested that his pig densities in Namadgi National Park in Australia were underestimates because the relationship of observed density to dung counts would require defecation rates of 300 pellets/day. Pen studies at HAVO suggest that defecation rate would be closer to 30/day. If the observed density in Namadgi (0.89 pigs/km^2) is increased by a factor of 10 (to

8.9 pigs/km^2), the population estimate is within the variation predicted by the model.

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

The model for all fresh sign may be the most useful management tool. It encompasses the variability of all the habitats sampled in the study and provides estimates within ± 2 pigs per km^2. Habitats sampled include a broad spectrum, from sparsely vegetated lava flows through grasslands and shrublands to densely vegetated rain and cloud forests. This model allows the habitat to dictate the sign observed and thus is not biased by conspicuousness of a certain type of sign. Frequency of digging is apparently quite variable in relation to habitat, so models used for digging will be most useful if they match the habitat, especially in availability of diggable substrate and abundance of starchy roots and tubers or soil invertebrates. Models generated for fresh scats seem least useful. Variability in defecation rates in different habitats, and differences in rate of disappearance with temperature, rainfall, and decomposition organisms, make these models less accurate.

None of the models provide much predictive value at population densities below 1 pig/km^2. When populations are below this threshold, sampling on frequency transects generally results in little or no recorded activity. The maximum estimated density available for comparison with pig activity data was 6.5 pigs/km^2 in the Puhimau unit. Extrapolation of the models beyond the highest pig density that was known for a unit is conjecture because the relationship of variables in the model may not be linear outside of the range of real data. Models were extended to densities beyond those recorded by extrapolating the prediction line along the same slope. There is less potential for error in extrapolation than in using the other methods available for estimating feral pig population density. Further verification of the models should be ongoing as pigs are removed from areas and more data are available.

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