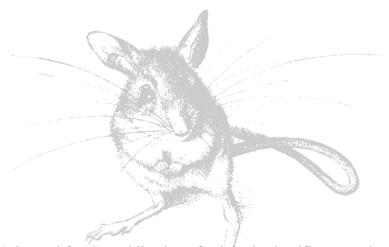
# CSIRO PUBLISHING

# Wildlife Research

Volume 24, 1997 © CSIRO Australia 1997



A journal for the publication of original scientific research in the biology and management of wild native or feral introduced vertebrates

# www.publish.csiro.au/journals/wr

All enquiries and manuscripts should be directed to Wildlife Research

**CSIRO** PUBLISHING

PO Box 1139 (150 Oxford St)

Collingwood Telephone: 61 3 9662 7622 Vic. 3066 Facsimile: 61 3 9662 7611 Australia Email: david.morton@publish.csiro.au



Published by **CSIRO** PUBLISHING for CSIRO Australia and the Australian Academy of Science



# Diggings by Feral Pigs Within the Wet Tropics World Heritage Area of North Queensland

J. Mitchell<sup>A</sup> and R. Mayer<sup>B</sup>

#### Abstract

The association of ground-digging activity of feral pigs with a range of environmental variables was examined in the wet tropics World Heritage Area of north Queensland. Approximately 4% of the surveyed ground was disturbed by digging activity of feral pigs. Significant differences in diggings were detected between highland and lowland areas and between habitat types. Diggings were more prevalent in lowland areas and coastal swamp habitats. Diggings were positively associated with roads, tracks and moist drainage lines.

### Introduction

The wet tropics World Heritage Area (WHA) region of north-eastern Queensland is a 'natural heritage of outstanding universal value' and one of the most significant regional ecosystems in the world (Anon. 1986). Feral pigs, *Sus scrofa*, are perceived to cause significant environmental damage to the WHA through the destruction of habitat, competition for food, predation, disease and weed transmission, erosion, and their influence on ecological processes (Pavlov *et al.* 1992; Mitchell 1993; McIlroy 1993). Three surveys conducted by the Wet Tropics Management Authority (1992) identified the community perception of feral pigs as a significant threat to WHA conservation. Feral pigs also cause significant economic losses to most agricultural production bordering the WHA. Feral pigs are reservoirs of numerous endemic diseases and potential vectors of exotic diseases such as foot and mouth. An exotic disease outbreak would be difficult to contain given the present knowledge of feral-pig management techniques specific to this region.

Ecological impacts of feral pigs in a range of habitats throughout the world have been documented [Bratton 1975 (US); Ralph and Maxwell 1984 (Hawaii); Lesourret and Genard 1985 (France); Coblentz and Baber 1987 (Ecuador); Thompson and Challies 1988 (New Zealand)]. Research on the detrimental impact of pigs on a tropical rainforest environment has been limited to studies in Hawaii (Baker 1976; Mueller-Dombois *et al.* 1981; Cooray and Mueller-Dombois 1981; Ralph and Maxwell 1984; Stone and Loope 1987; Stone and Anderson 1988; Katahira *et al.* 1993; Vtorov 1993) and the Northern Territory (Bowman and McDonough 1991; Caley 1993).

There is a significant lack of quantitative data on impact of feral pigs within this region, hence it is difficult to obtain an accurate picture of the true ecological damage being caused. The main visual impact of damage by feral pigs is soil disturbance caused by their digging or rooting when searching for food. This behaviour has been shown in studies outside Australia to influence soil arthropod populations (Vtorov 1993), to alter soil nutrients (Lackie and Lancia 1983; Singer *et al.* 1984; Kotanen 1994) and temperature (Kotanen 1994), to reduce plant cover (Spatz and Mueller-Dombois 1972; Bratton 1974, 1975), to effect soil erosion (Bratton 1975) and to alter plant species composition (Kotanen 1994). Disturbed ground has been used as an index of the impact of feral pigs on various environments (Bratton 1975; Mueller-Dombios *et al.* 

<sup>&</sup>lt;sup>A</sup>Department of Lands, PO Box 187, Charters Towers, Qld 4820, Australia.

<sup>&</sup>lt;sup>B</sup>Department of Primary Industries. PO Box 1085, Townsville, Qld 4810, Australia.

1981; Alexiou 1983; Ralph and Maxwell 1984; Stone and Loope 1987; Hone 1988a; Bowman and Panton 1991).

The aim of this study was to quantify the digging activity of feral pigs and to examine the relationship of this activity with a range of environmental variables within the WHA.

### Methods

Study Site

The wet tropics WHA encompasses an area of 9000 km<sup>2</sup> and lies between Townsville and Cooktown on the north-east coast of Queensland (15°30′S to 19°30′S, 145°00′E to 146°30′E. The vegetation of the area is predominantly rainforest with fringing tall to open woodlands and coastal lowlands and swamps.

The mean annual rainfall varies from 1200 mm to more than 4000 mm, 60% falling during the wet season from December to March. This survey was conducted from April to November, which corresponds with the normal dry season.

### Environmental Variables

Thirteen broad 'areas' (up to 100 km²) characterising the major habitats were initially inspected. Eight of these areas were then selected for detailed examination based on accessibility and suitable habitat (Fig. 1). Five highland areas (above 400 m in elevation) and three lowland coastal areas were assessed. The eight areas also encompassed the four broad vegetation habitats categorised below.

Within these eight areas, a total of 31 subareas or 'sites' was selected, based on accessibility during periods of wet weather, signs of feral-pig activity, and the availability of logging tracks, walking tracks and creek lines used for transect establishment.

A systematic survey method was conducted to quantify the physical impact of feral pigs, defined in this study as diggings (soil disturbance due to digging or rooting behaviour). The relationship of this digging with environmental variables was then examined.

The main variables used for analysis were the 'area', rated as a highland or lowland area based on elevation, and 'habitat', predominantly based on the dominant vegetation community (Tracey 1982) and topography. Other variables included elevation, slope and the occurrence of rocks. Microvariables such as the presence of roads or tracks and the presence of water were also used in the analysis. Environmental variables were categorised according to the criteria in Table 1.

### Transects

A total of 237 belt transects, 100–3000 m long and 5 m wide, were randomly positioned within the 31 sites. Because of the thick vegetation, a straight transect was impossible to position accurately. The procedure involved dragging a 100-m light rope into the vegetation, which was then positioned on the ground. The area up to 2·5 m from each side of the rope was then examined for pig diggings.

The area of diggings within each transect was recorded by measuring the judged average length and breadth of each digging. The age category of the diggings was also recorded according to the following criteria:

- (i) recent—fresh moist soil turned over, no leaves or vegetation in base of diggings;
- (ii) intermediate—weathered soil and some leaf litter in diggings; or
- (iii) old—diggings covered by leaf litter, plants germinating in diggings, weathered soil.

Transects were generally established perpendicular to existing access tracks. Transects from vehicle tracks were randomly selected from vehicle odometer readings. Transects from walking trails, old logging tracks and creek lines were randomly selected from counted steps of the researcher (1–1000). Some transects were also randomly established within the table drains of roads or tracks and within the beds of streams and drainage lines. Transects were categorised as follows: perpendicular to a road, logging or walking track; the actual surface of road or track; perpendicular to a stream or water course; or the bed of a stream or water course.

A problem observed during this study was the difficulty of distinguishing between the scratching activity of megapodes (the orange-footed scrub fowl, *Megapodius reinwardt*, and the Australian brush turkey, *Alectura lathami*) and pig diggings. In many cases, digging activity of pigs, scrub fowl and brush turkeys overlapped. Megapodes are attracted to freshly turned soil or leaf litter, and on many occasions megapodes were observed scratching on fresh pig activity. This scratching masked pig diggings. Diggings were recorded only where there was obvious pig sign present. Consequently, the pig-activity results presented should be regarded as conservative.

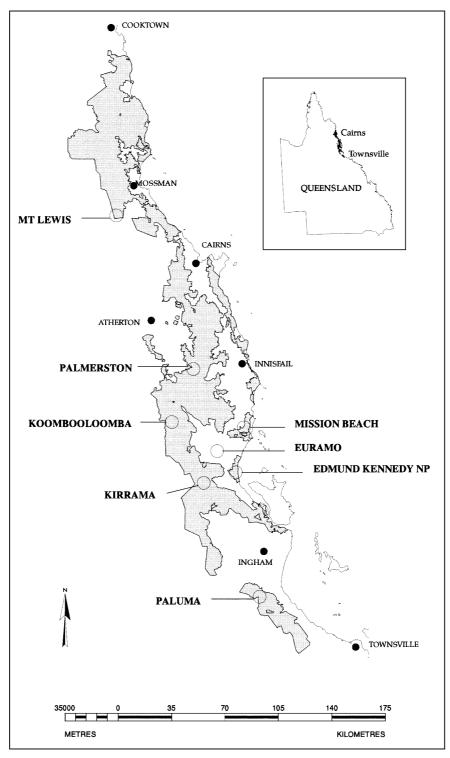


Fig. 1. Locations of the eight sites in Queensland, Australia, used in the study. Shaded areas indicate World Heritage Area.

Table 1. Environmental variable categories recorded for each transect

Variable	Category	Description			
Area	Highlands	Above 400 m: Paluma, Kirrama, Mt Lewis, Koombooloomba, Palmerston			
	Lowlands	Below 400 m: Edmund Kennedy National Park Euramo, Mission Beach			
Habitat	Highland Rainforests	Complex mesophyll and notophyll vine forests			
	Woodlands	Open forests and woodlands ( <i>Eucalyptus</i> and <i>Acacia</i> spp.)			
	Lowland Rainforests	Mesophyll vine forests with dominant palms			
	Coastal	Paperbark ( <i>Melaleuca</i> spp.) swamps and low woodlands			
Microvariables	Roads	Diggings occurring within 10 m of a road or track			
	Water	Diggings occurring with 10 m of a creek or drainage line			
	Remainder	Remainder of transect			
Elevation	1	< 100 m			
	2	101–400 m			
	3	401–800 m			
	4	> 800 m			
Slope	1	< 20°			
	2	20–45°			
	3	> 45°			
Rocks	1	No rocks present			
	2	< 25% of transect covered by rocks			
	3	25-50% of transect covered by rocks			
	4	> 50% of transect covered by rocks			

# Statistical Analysis

Within each transect, the area of pig diggings expressed as a percentage of the transect area provided the base data for analysis both on a total-transect and a microvariable basis. The relationships of total diggings and individual age categories of diggings to the environmental variables were analysed.

One-way ANOVAs were carried out to compare the environmental variables 'area', 'habitat' and 'area × habitat' and also to compare microvariables within transects. The remaining environmental variables of 'elevation', 'slope' and 'rocks' were often closely inter-related with area and habitat (all transects in the three lowland areas had identical categories for elevation, slope and rocks), so it was difficult to estimate any direct influence by these factors on pig activity. Appropriate less confounding subsets of the data (e.g. after excluding the three lowland areas) were analysed by a least-squares method for unequal subclass numbers (Harvey 1960), in which the various environmental variables were fitted in combination.

# Results

A total of  $144500~\text{m}^2$  was assessed for sign of digging activity by feral pigs. The total area of feral pig diggings recorded was  $6268~\text{m}^2$  ( $4\cdot14\%$ ) observed on 157 (67%) of the 237 established transects.

#### Areas

A significant difference ( $F_{7,229} = 2.56$ , P < 0.05) was detected in total diggings when comparing 'areas' across all combined habitat types (Table 2). The lowland area of Mission Beach was significantly different from all highland areas except for the Mt Lewis area. No significant differences were detected between the three lowland areas. The only anomaly was the Mt Lewis highland area, where the mean digging area (4.5%) was not significantly different from the lowland results. Mt Lewis recorded the highest digging rate of the five highland areas, nearly double the mean percentage of diggings in the other highland areas. Transects for the three lowland areas combined (n = 63) recorded a significantly higher mean digging percentage of (8.9%) than did those for the five highland areas (2.4%, n = 174) ( $F_{1.229} = 20.56$ , P < 0.05).

# Habitats

When habitat types were compared across all areas combined, a significant difference was detected in total diggings ( $F_{3,233} = 7$ , P < 0.01). The coastal habitat recorded significantly more diggings than did the highland rainforests and woodlands (Table 2). No differences were detected between coastal and lowland rainforests.

# Age of Diggings

Analyses of the age categories of the diggings (recent, intermediate or old) between the areas revealed that significantly ( $F_{7,229} = 2.27$ , P < 0.05) more recent diggings occurred in the lowland Edmund Kennedy National Park (NP) than in all other areas except for the lowland Euramo area (Table 2). A significant difference ( $F_{7,229} = 3.85$ , P < 0.05) in the old category was detected for

Table 2. Percentage area of the transects showing pig diggings for 'area' (highlands and lowlands) and 'habitat'

Diggings are categorised according to age. n = number of transects sampled. For highlands, lowlands and habitat, column values followed by different letters are significantly different (P < 0.05)

Variables	n		Age of diggings	·	Total area of diggings	
		Recent	Intermediate	Old	uiggiiigs	
Area						
Highlands						
Paluma	36	0.72a	1·11 <sup>a</sup>	0.59a	2·42a	
Kirrama	28	0.64a	0.85a	0·77a	2·26a	
Mt Lewis	20	0.82a	2·57a	1·11 <sup>a</sup>	4·50ab	
Koombooloomba	45	1·04a	0.61a	0.25a	1.91a	
Palmerston	45	0.62a	0.94a	0.53a	2·09a	
Mean	174	0.78	1.06	0.58	2.41	
Lowlands						
Edmund Kennedy	19	7·23 <sup>b</sup>	0.04a	0·49 <sup>a</sup>	7⋅76 <sup>ab</sup>	
Mission Beach	37	0.01a	3·44a	6·56 <sup>b</sup>	10·02 <sup>b</sup>	
Euramo	7	1·34 <sup>ab</sup>	1·20a	3.65a	6·19 <sup>ab</sup>	
Mean	63	2.34	2.17	4.41	8.91	
Habitat						
Highland forests	159	0.81a	1.08a	0.54a	2·43a	
Woodlands	15	0.43a	0.86a	1·01a	2·30a	
Lowland forests	18	0.52a	1.64a	2·15ab	4·30ab	
Coastal	45	3·07a	2·38a	5·31b	10⋅75 <sup>b</sup>	
Mean	237	1.19	1.36	1.6	4.14	

the coastal swamp habitat of Mission Beach when compared with all other areas. No significant difference was detected between areas for the intermediate age category. When ages of diggings were compared across habitat categories, only in the old digging category was a significant difference detected ( $F_{3,233} = 6.2$ , P < 0.05), where coastal habitats were different from the highland rainforest and woodland habitats. Age of diggings was also compared between the highland and lowland areas. Significantly ( $F_{1,235} = 17.9$ , P < 0.05) more old diggings occurred in the lowlands (4.41%) than in the highlands (0.58%).

## Area × Habitat Interactions

Analyses compared the habitat groupings within each area (Table 3). The coastal habitat of the lowland Mission Beach area recorded a significantly higher ( $F_{10,226} = 2.44$ , P < 0.01) percentage area of diggings than all five highland areas that had a rainforest habitat category. Percentage area of diggings in highland rainforest (five areas) was also significantly higher than that in the woodland habitat in the highland Paluma area and in the lowland rainforest habitat within the same Mission Beach area.

#### Microvariables

Analyses within the transects, aggregated over area and habitats, were used to test for any association between diggings and microvariables, that is, the presence of roads or drainage lines. A total of 2965 m<sup>2</sup> or 47% of all recorded pig diggings were within 10 m of a road or track, 1336 m<sup>2</sup> (22%) were within 10 m of surface water or drainage line and 1937 m<sup>2</sup> (31%) occurred on the remainder of the inspected area.

A significant difference in percentage area of diggings was detected between the three microvariables ( $F_{2,424} = 14.94$ , P < 0.01) (Table 4). For transects (n = 202) within 10 m of or on a road or track, 8.1% of the ground surface was affected by pig diggings. The highest record of road damage was 20% in the Mt Lewis area. Pig diggings affected 16% of the surface area on transects (n = 18) placed along the beds of water courses or associated with a drainage line. Edmund Kennedy NP recorded a 100% digging disturbance on one transect in a Marina plains swamp. A general average of 2.4% diggings was recorded on transects (n = 207) for the general forest floor not associated with any road, track or creek line. The three microvariables for the different-aged diggings are compared in Table 4. Only in the intermediate age group was a significant difference (P < 0.05) observed.

# Other Variables

The analyses for subsets of elevation and rocks detected no significant differences. Analysis for slope was restricted to the highland rainforest habitat, which possessed all slope categories. A significant trend (P < 0.05) of decreasing diggings associated with increasing slope was demonstrated. Transects where slopes were less than 20° recorded mean diggings of 2.99% (n = 103), a value significantly different from that from transects of slopes more than 45°, which recorded mean diggings of 0.29% (n = 15).

### Discussion

Diggings by feral pigs appear to be widespread throughout the WHA. All 31 sites recorded some pig digging, with 67% of all transects recording pig diggings. Ground disturbance by feral pigs averaged 4% of the surface area of the surveyed transects. Alexiou (1983) found 32% of susceptible land in his ACT study disturbed, whereas Katahira *et al.* (1993) recorded an average digging rate of 0.7% in Hawaii's rainforests.

Diggings by feral pigs occurred more in the coastal lowlands than in the highland rainforest areas for this dry-season study. This could be due to a range of environmental factors; however, favourable food and water-supply conditions on the lowlands during the dry season may be responsible. The soft soils, bulb-producing plant species, availability of soil moisture and high soil-invertebrate populations (particularly earthworms) in lowland swamp areas would

Table 3. Percentage of the transect area showing pig diggings for each area and habitat group

Percentage areas of diggings for each digging age are presented, as are total percentage areas. n = number of transects sampled. The average ratings for elevation, slope and rocks categories are also presented. Column values followed by different letters are significantly different (P < 0.05)

Area	Habitat	n	Average variable rating			Area (%) of different-aged diggings			Total area of
			Elevation	Slope	Rocks	Recent	Intermediate	Old	diggings
Paluma	Highland Rainforest	25	4.0	1.9	1.3	0.8a	1·1ª	0.5a	2·4ª
	Woodland	11	3.5	1.0	1.6	0.6a	1.Oa	0.8a	2·4a
Kirrama	Highland Rainforest	24	2.8	1.5	1.3	0·7a	0.9a	0.6a	2·3a
	Woodland	4	3.0	1.7	1.0	0·1a	0·4 <sup>a</sup>	1.6a	2·0a
Mt Lewis	Highland Rainforest	20	3.9	1.3	1.5	0.8a	2.6a	1·1a	4.5a
Koombooloomba	Highland Rainforest	45	3.2	1.2	1.0	1·0a	0.6a	0.2a	1.9a
Palmerston	Highland Rainforest	45	3.2	1.5	1.1	0.6a	0.9a	0.5a	2·1a
Edmund Kennedy	Coastal	19	1.0	1.0	1.0	7·2 <sup>b</sup>	0.0a	0.5a	7·8ab
Mission Beach	Lowland Rainforest	11	1.0	1.0	1.0	0.0a	1.9a	1·2a	3·1a
	Coastal	26	1.0	1.0	1.0	0.0a	4·1a	8.8p	12·9 <sup>b</sup>
Euramo	Lowland Rainforest	7	1.0	1.0	1.0	1·3a	1·2a	3.6ab	6·2ab

**Table 4. Percentage of the transect area in different microvariables** Percentage areas of diggings for each digging age are presented, as are total percentage areas. n = number of transects where microvariable occurs. Column values followed by different letters are significantly different (P < 0.05)

Microvariable	n	Area (%)	Area (%) of different-aged diggings				
		Recent	Intermediate	Old	diggings (%)		
Roads	202	2·05a	3·29a	2·73ª	8·06a		
Drains	18	1.64a	9·33b	5·08a	16·05 <sup>b</sup>		
Remainder	207	0·84a	0·42°	1·15a	2·41°		

encourage digging activity of feral pigs. Bratton *et al.* (1982) found intense digging activity (80%) in some of the wet areas in their study. Kotanen (1994) also found that diggings were associated with damp ground or seeping water. The significantly high recent diggings in the lowland Edmund Kennedy NP suggests that more digging activity was occurring during this dry-season study than in the highland areas.

Hone (1988b) also found a significant relationship between pig diggings and elevation, correlated with low altitude in winter and spring, and high altitude during summer. Hone's study in Namadgi National Park near Canberra may have been influenced by low temperatures during winter, which is not applicable to this study. Bratton *et al.* (1982) found pig digging to be widespread in the Great Smoky Mountains National Park and present at all elevations.

The seasonal nature of diggings by feral pigs has been reported in the Northern Territory by Hone (1990), who suggested that seasonal flooding may be responsible. Seasonal distribution patterns from other studies have been attributed to rainfall and temperature patterns in Malaysia (Diong 1973), and in the USA to food availability (Kurz and Marchington 1972; Graves and Graves 1977; Brisbin *et al.* 1977). Barrett (1978) related density of cover to distribution.

Other factors that could influence seasonal pig diggings are dry soil conditions in highland areas during the dry season, which force worm populations into deeper soil horizons, beyond the reach of pig diggings (Lee 1985). This unavailability of earthworms coupled with the compounding influence of the seasonal fruiting cycle would encourage pigs to move to the lowlands. This is possibly linked to nutritional requirements: worms are an important source of protein, although the importance of earthworms in the diet of feral pigs is unknown in this region. McIlroy (1993) believed that nutrition is the dominant factor influencing pig movements in this area. Caley (1993) also found that the seasonally available cereal crops in the Northern Territory increased pig populations four-fold in cropping areas. The elevated sugar content in sugar cane prior to harvesting (at the end of the dry season) may also influence pig distribution and hence digging activity in this region.

The significant relationship of diggings with road and tracks indicates that pigs use these as travel corridors. Pigs forage as they travel along the roads and tracks, occasionally venturing into the surrounding vegetation. Table drains would accumulate fallen fruit and leaf litter; moisture and soil invertebrates would also tend to concentrate within these table drains. Thus, food-searching behaviour on roads and tracks would contribute to increased digging activity. Similarly, the significant association of diggings with drainage lines may be due to their use as travel corridors and/or to the increased availability of food in the moist environment.

The other measured environmental variables, elevation, slope and the presence of rocks, appeared to have little influence on pig digging activity. No significant associations were detected between the elevation categories in this study.

However, Hone (1988b) found that the presence of rocks was significantly related to pig diggings; diggings were more prevalent when rocks were abundant and less when rocks were

very abundant. He suggests that this was due to the accumulation of leaf litter and bark around rocks under trees; in this study, the localised effect of leaf-litter collection around rocks did not occur as leaf litter is prevalent throughout the forest floor.

The influence of slope on digging activity was logical: feral pigs tended to dig less on steep slopes. Hone (1995) also found less digging activity on steep slopes. Pigs do move through these areas, but appear to limit their time in unsuitable terrain.

The effect of soil or litter-layer disturbance by diggings on ecological processes in this study site is unknown. Studies outside Australia have found that pig diggings influence organic-matter levels and cation-exchange capacity (Lackie and Lancia 1983), mineral nitrogen and soil surface temperatures (Kotanen 1994) and soil-invertebrate population levels and decomposition rates (Vtorov 1993). These hidden influences on ecological processes within the WHA need to be quantified if a more accurate picture of the impact of pigs due to digging activity is to be acquired. The observed digging patterns appear to be influenced by microvariables, as more diggings occur in a small number of favourable microhabitats. Large areas of less favourable microhabitats are associated with lower levels of diggings. Hone (1988a) also found this negative exponential frequency distribution of diggings: many sites with little or no activity and few sites with high digging activity.

Some generalised associations of diggings with environmental variables have been derived from this study. However, the complex inter-relationships of these variables tend to conceal individual variable influences on digging activity, and these assertions are valid only for the dry season. The importance of 4% of the WHA surface being dug up by feral pigs is difficult to quantify. Simple measurements of digging area are inadequate in understanding the 'true' damage being imposed on the ecological processes in this ecosystem. However, the knowledge of this level of impact of feral pigs will give the management of the WHA an insight into the possible ecological damage being caused and to facilitate research programmes to collect the required information.

Information on digging patterns is required for developing management plans for feral pigs. The optimum timing and placement of control strategies is critical in maximising effectiveness and reducing costs. The seasonality of diggings (lowlands during the dry season) and preferred microhabitats (creeks and tracks) may allow the feral-pig managers in this region (the Wet Tropics Management Authority) to maximise control effectiveness. The information obtained in this study is the preliminary information required in developing a feral-pig management plan for this region.

# Acknowledgments

We greatly acknowledge John McManus for his assistance in the field. We also thank Joe Vitelli for constructive criticism of the manuscript. The Wet Tropics Management Authority provided financial support for this study and we thank Bill Laurance for his support. Also, we thank John McIlroy, who provided advice and support throughout the study.

## References

Alexiou, P. N. (1983). Effects of feral pigs (Sus scrofa) on subalpine vegetation at Smokers Gap, ACT. Proceedings of the Ecological Society of Australia 12, 135–142.

Anon. (1986). Tropical rainforests of north Queensland; their conservation significance. A report to the Australian Heritage Commission by the Rainforest Conservation Society of Queensland. Special Australian Heritage Publication Series No. 3. (Australian Government Publishing Service: Canberra.)

Baker, J. K. (1976). The feral pig problem in Hawaii National Parks. In 'Proceedings of the First Conference on Scientific Research in National Parks'. (Ed. R. M. Linn.) pp. 365–367. (New Orleans.)

Barrett, R. H. (1978). The feral hog on the Dye Creek ranch, California. *Hilgardia* 46, 283–355.

Bowman, D. M. J. S., and Panton, W. J. (1991). Sign and habitat preference of banteng (*Bos javanicus*) and pig (*Sus scrofa*), Cobourg Peninsula, northern Australia. *Australian Journal of Ecology* **16**, 15–17.

- Bowman, D. M. J. S., and McDonough, L. (1991). Feral pig (Sus scrofa) rooting in a monsoon forest-wetland transition, northern Australia. Wildlife Research 18, 761–765.
- Bratton, S. P. (1974). The effect of the European wild boar *Sus scrofa*, on the high elevation vernal flora in the Great Smoky Mountains National Park. *Bulletin of the Torrey Botanical Club* **101**, 198–206.
- Bratton, S. P. (1975). The effect of the European wild boar *Sus scrofa*, on grey beech forest in the Great Smokey Mountains. *Ecology* **56**, 1356–1366.
- Bratton, S. P., Harmon, M.E., and White, P.S. (1982). Patterns of European wild boar rooting in the western Great Smoky Mountains. *Castanea* **47**, 230–242.
- Brisbin, I. L., Smith, M. W., and Smith, D. M. H. (1977). Feral swine studies at the Savannah River Ecological Laboratory: an overview of program goals and designs. In 'Research and Management of Wild Hog Populations'. (Ed. G. W. Wood.) pp. 71–90. (Belle Baruch Forest Institute: Georgetown, South Carolina.)
- Caley, P. (1993). Population dynamics of feral pigs (Sus scrofa) in a tropical riverine habitat complex. Wildlife Research 20, 625–636.
- Coblentz, B. E., and Baber, D. W. (1987). Biology and control of feral pigs on Isla Santiago, Galapagos, Ecuador. *Journal of Applied Ecology* 24, 403–418.
- Cooray, R. G., and Mueller-Dombois, D. (1981). Feral pig activity. In 'Island Ecosystems: Biological Organisation in Selected Hawaiian Communities'. (Eds D. Mueller-Dombois, K. W. Bridges and H. L. Carson.) pp. 309–319. (Hutchinson Ross: Stroudsburg, Pennsylvania.)
- Diong, C. H. (1973). Studies on the Malayan wild pig. Malaya Nature Journal 26, 120-151.
- Graves, H. B. and Graves, K. L. (1977). Some observations on biobehavioural adaptations of swine. In 'Research and Management of Wild Hog Populations'. (Ed. G. W. Wood.) pp. 71–90. (Belle Baruch Forest Institute: Georgetown, South Carolina.)
- Harvey, W. R. (1960). Least squares analysis of data with unequal subclass numbers. United States Department of Agriculture, Agricultural Research Service. No. ARS-20-8.
- Hone, J. (1988a). Evaluation of methods for ground survey of feral pigs and their sign. Acta Theriologica 33, 451–465.
- Hone, J. (1988b). Feral pig rooting in a mountain forest and woodland: distribution, abundance and relationships with environmental variables. Australian Journal of Ecology 13, 393–400.
- Hone, J. (1990). Note on seasonal changes in population density of feral pigs in three tropical habitats. Australian Wildlife Research 17, 131–134.
- Hone, J. (1995). Spatial and temporal aspects of vertebrate pest damage with emphasis on feral pigs. Journal of Applied Ecology 32, 311–319.
- Katahira, L. K., Finnegan, P., and Stone, C. P. (1993). Eradicating feral pigs in montane mesic habitat at Hawaii Volcanoes National Park. Wildlife Society Bulletin 21, 269–274.
- Kotanen, P. (1994). Effects of feral pigs on grasslands. Fremontia 22, 14-17.
- Kurz, J. C., and Marchington, R. L. (1972). Radio-telemetry studies of feral hogs in South Carolina. Journal of Wildlife Management 36, 1240–1248.
- Lackie, M. J., and Lancia, R. A. (1983). Changes in soil properties of forests rooted by wild boar. Proceedings of the Annual Conference of the South-East Association of Fish and Wildlife Agencies 37, 228–236.
- Lee, K. E. (1985). 'Earthworms: their Ecology and Relationship with Soils and Land Use.' (Academic Press: Sydney.)
- Lesourret, F., and Genard, M. (1985). Search for signs of feeding and investigations of the summer habitat used in the wild boar, *Sus scrofa scrofa*, in the Herault Department. *Gibier Faune Sauvage* 1, 63–73.
- McIlroy, J. C. (1993). Feral pig management in the Wet Tropics of Queensland World Heritage Area. Final report to the Wet Tropics Management Agency Cairns.
- Mitchell, J. (1993). Systematic assessment of feral pig damage and recommended pig control methods in the wet tropics World Heritage Area. Final Report to the Wet Tropics Management Authority, Cairns.
- Mueller-Dombois, D., Bridges, K. W., and Carson, H. L. (Eds) (1981). 'Island Ecosystems: Biological Organisation in Selected Hawaiian Communities.' (Hutchinson Ross: Stroudsburg, Pennsylvania.)
- Pavlov, P. M., Crome, F. H. J., and Moore, L. A. (1992). Feral pigs, rainforest conservation and exotic disease in north Queensland. Australian Wildlife Research 19, 179–195.
- Ralph, C. J., and Maxwell, R. D. (1984). Relative effects of human and feral hog disturbance on a wet forest in Hawaii. *Biological Conservation* 30, 291–303.
- Singer, F. J., Swank, W. T., and Clebsch, E. E. C. (1984). Effects of wild pig rooting in a deciduous forest. Journal of Wildlife Management 48, 464–473.

- Spatz, G., and Mueller-Dombois, D. (1972). Succession patterns after pig diggings in grassland communities on Mauna-Loa, Hawaii. *Phytocoenologica* **3**, 346–373.
- Stone, C. P., and Loope, L. L. (1987). Reducing negative effects of introduced animals on native biotas in Hawaii: what is being done, what needs doing, and the role of national parks. *Environmental Conservation* 14, 245–258.
- Stone, C. P., and Anderson, S. J. (1988). Introduced mammals in Hawaii's natural areas. In 'Proceedings of the 13th Vertebrate Pest Conference, Monterey, California'. (Eds A. C. Krabb and R. E. Marsh.) pp. 134–140. (University of California: Davis.)
- Thompson, C., and Challies, C. N. (1988). Diet of feral pigs in the podocarp–tawa forests of the Urewera Ranges. *New Zealand Journal of Ecology* **11**, 73–78.
- Tracey, J. G. (1982). 'The Vegetation of the Humid Tropical Region of North Queensland.' (CSIRO: Melbourne.)
- Vtorov, I. P. (1993). Feral pig removal: effects on soil microarthropods in a Hawaiian rainforest. *Journal of Wildlife Management* **57**, 875–80.
- Wet Tropics Management Agency (1992). Wet Tropics Plan: Strategic Directions.

Manuscript received 10 April 1996; revised 27 November 1996; accepted 20 December 1996