# Spatial and temporal patterns of feral pig diggings in rainforests of north Queensland

J. Mitchell<sup>A,E</sup>, W. Dorney<sup>B</sup>, R. Mayer<sup>C</sup> and J. McIlroy<sup>D</sup>

**Abstract.** Feral pigs (*Sus scrofa*) are believed to have a severe negative impact on the ecological values of tropical rainforests in north Queensland, Australia. Most perceptions of the environmental impacts of feral pigs focus on their disturbance of the soil or surface material (diggings). Spatial and temporal patterns of feral pig diggings were identified in this study: most diggings occurred in the early dry season and predominantly in moist soil (swamp and creek) microhabitats, with only minimal pig diggings found elsewhere through the general forest floor. The overall mean daily pig diggings were 0.09% of the rainforest floor. Most diggings occurred 3–4 months after the month of maximum rainfall. Most pig diggings were recorded in highland swamps, with over 80% of the swamp areas dug by pigs at some time during the 18-month study period. These results suggest that management of feral pig impacts should focus on protecting swamp and creek microhabitats in the rainforest, which are preferred by pigs for digging and which have a high environmental significance.

### Introduction

Feral pigs (Sus scrofa) have been described as a significant threat to the ecological values of the World Heritage Listed tropical rainforests of northern Queensland (McIlroy 1993; Mitchell 1993; Mitchell and Mayer 1997). Most community perceptions of the environmental impacts of pigs focus on their disturbance (digging) of the soil or soil litter/vegetation material. Feral pig diggings are thought to be responsible for causing erosion, lowering water quality, changing litter composition and distribution, affecting nutrient and water cycles, affecting soil invertebrate populations and soil seed banks, and changing species succession patterns (McIlroy 1993; Laurance and Harrington 1997; Mitchell and Mayer 1997; Tierney and Cushman 2006).

A basic knowledge of the spatial and temporal patterns of feral pig diggings is necessary to provide an insight into the degree of ecological impacts occurring. Diggings have been used as an index of ecological impact of pigs in Australia (Hone 1995; Mitchell and Mayer 1997) and elsewhere (Howe et al. 1981; Engeman et al. 2003). Mitchell and Mayer (1997) described spatial digging patterns within the Wet Tropic rainforests and identified variations in digging activity between micro- and macrohabitats. Temporal patterns of feral pig diggings have been indicated in other studies within rainforests (McIlroy 1993; Laurance and Harrington 1997) but quantitative information on the impacts of feral pigs is sparse, however, particularly in Queensland's tropical rainforests. Mitchell and Mayer (1997) described broad-scale spatial digging patterns (lowland areas had higher digging activity than highland areas) and an association of diggings with tracks and drainage lines, but their study was restricted to the tropical dry season and was broad in scope. The aim of this current study was to further quantify specific patterns of feral pig diggings at the microhabitat level. Spatial patterns were investigated to assess whether feral pigs preferred to dig in specific microhabitats and temporal patterns were investigated to assess the effect of the seasons on feral pig digging patterns.

# Methodology

Study site

The study site was situated near Cardwell (Fig. 1), north Queensland (18°16′S, 146°2′E). It was categorised into three broad macrohabitat types or 'areas' (highland, transitional and lowland). Within each area, key microhabitats or 'strata' (which represented the dominant microhabitat types available in each area) were identified. Stratum selection was based on observed pig diggings and previously documented microhabitat preferences of feral pigs (Mitchell and Mayer 1997). Three 'sites' were then randomly selected within each stratum ~2–10 km apart. Rainfall patterns within this region are markedly seasonal, with a distinct wet and dry season. Two cyclones, 'Justin' and 'Sid', caused major flooding during the study; rainfall was measured on a monthly basis within each area.

Description of study areas and selected strata

Highland area

This area is described as highland rainforest and was located at the crest of the Cardwell Range (800 m in elevation), 25 km west of the township of Kennedy. The study site was centred at

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

<sup>&</sup>lt;sup>B</sup>Department of Primary Industries and Fisheries, PO Box 20, South Johnstone, Qld 4859, Australia.

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

<sup>&</sup>lt;sup>D</sup>38 Hempleman Drive, Akaroa, 8161, New Zealand.

<sup>&</sup>lt;sup>E</sup>Corresponding author. Email: jim.mitchell@dpi.qld.gov.au

a locality known as Society Flats (18°12′30″S, 145°45′30″E). The vegetation is classified as complex notophyll vine forest with emergent rose gums (*Eucalyptus grandis*) (Tracey 1982). Five strata were selected in this area:

- 1. Swamp creek overflows or small low areas that are seasonally inundated by floodwaters with free water or saturated soil present throughout the dry season.
- 2. Track unused logging tracks with a revegetating 1–2-m shrub layer with no table drains or road formations.
- 3. Ridge forest termed the 'general forest floor' at least 250 m from all other microhabitat strata.
- 4. Road maintained formed dirt road traversing the study site.
- Creek creek bed, sand or debris adjacent to the water of perennial shallow sandy creeks, subject to seasonal flooding.

## Transitional area

598

This area forms the ecotone between the rainforest habitat and croplands on the lowlands. Two distinct locations were chosen to represent this area: Kennedy Valley (18°14′S, 145°55′E) and Upper Murray (18°6′S, 145°50′E). Riparian vegetation of complex mesophyll vine forest (Tracey 1982) dominates this area. Most of the lowland rainforest between the creeks has been cleared for sugarcane and banana production; soils were mainly alluvial. Two major strata were selected in this area:

- Creek perennial flowing creek banks or creek bed, seasonal flooding occurs.
- 3. Track unformed tracks for logging operations that usually follow the boundary between native vegetation and plantation pine (*Pinus* spp.).

# Lowlands area

This area is situated in Edmund Kennedy National Park on the coastal lowlands (18°14′S, 146°00′E). The vegetation is predominantly a mixture of mesophyll vine forests, open forest, stunted paperbark (*Melaleuca* spp.) forests, tall open forests, layered woodlands with shrubs, mangrove forests with seasonal sedge swamps and lagoons. The area has patches of mesophyll vine forests with dominant fan palms (*Licuala ramsayi*) and coastal beach ridges and swales (Tracey 1982). Soils are predominantly alluvial with beach ridge and sand sheets. Four strata were selected in this area:

- Creek perennial flowing creeks with deep waterholes (lagoons).
- Swamp low-lying areas inundated with rainfall or flooding during the wet season.
- 3. Forest open eucalypt or melaleuca forest with grass and shrub understorey.
- Track irregularly used unformed dirt tracks used in previous logging operations.

## Digging activity transects

Within each of the selected sites, five 50-m line transects were established 50–100 m apart. All transects were sampled (termed sampling events) 10 times, ranging from 37- to 100-day intervals, over a total period of 18 months. Periodic flooding and road closures dictated the timing of sampling events. Transects were marked with wooden pegs so a measuring tape could be positioned on the ground between the pegs to enable accurate repositioning of the tape for each sampling event. Each 50-m transect was divided into a continuous series of 500 10-cm increments. The total number of increments that were positioned directly over feral pig diggings and those that were classified as unavailable to pigs (owing to fallen trees or being covered by water more than 10 cm deep) were recorded for each transect for each sampling event. These recorded increments were also mapped to distinguish previous pig diggings.

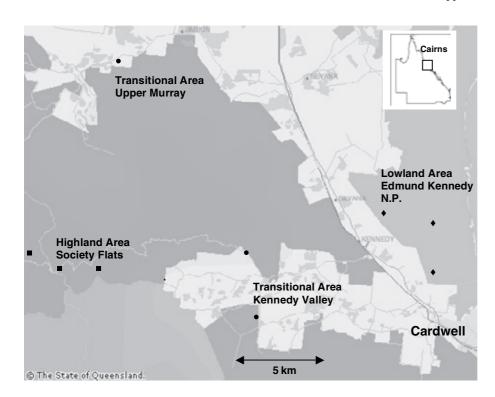


Fig. 1. Location of the Cardwell study site showing the three study areas and location of the transect sites for the highland (■), transitional (●) and lowland (●) areas. Shaded sections represent rainforest/native vegetation habitats; unshaded sections are agricultural zones.

Table 1. The mean daily digging index (DDI) for feral pigs in each stratum for each sampling event within each of the three areas

Superscripts indicate where significant differences between strata values were detected. Values followed by the same superscript letter are not significantly different (P > 0.05)

Area	Stratum	Sampling events and days (n) between the next sampling event									
		1 (100)	2 (56)	3 (48)	4 (37)	5 (61)	6 (77)	7 (57)	8 (57)	9 (47)	10 (63)
Track	$0.05^{bc}$	$0.01^{b}$	0.0	$0.0^{b}$	0.07	0.09	$0.08^{b}$	0.0	0.03	0.11	
Ridge	$0.002^{c}$	$0.02^{b}$	0.0	$0.0^{b}$	0.01	0.0	$0.0^{b}$	0.0	0.0	0.0	
Road	0.61a	$0.0^{b}$	0.0	$0.0^{b}$	0.0	0.22	$0.04^{b}$	0.0	0.01	0.0	
Creek	$0.36^{ab}$	$0.0^{b}$	0.2	$0.27^{a}$	0.02	0.22	$0.25^{ab}$	0.08	0.01	0.07	
Transitional	Creek	0.07	$0.52^{a}$	0.05	0.01	$0.04^{a}$	0.1	0.09	$0.27^{a}$	0.22	0.07
	Track	0.01	$0.0^{b}$	0.00	0.00	$0.01^{b}$	0.01	0.03	$0.01^{b}$	0.02	0.01
Lowland	Creek	0.33	0.02	0.0	0.07	0.14	0.0	$0.26^{ab}$	0.0	0.07	0.06
	Swamp	0.22	0.25	0.1	0.04	0.04	0.09	$0.14^{b}$	0.2	0.13	0.05
	Forest	0.03	0.00	0.0	0.01	0.0	0.03	$0.01^{c}$	0.0	0.0	0.01
	Track	0.11	0.0	0.01	0.04	0.1	0.05	$0.39^{a}$	0.03	0.01	0.03

Diggings observed at each subsequent sampling event could then be identified as old (previously recorded) or as new (occurring since previous sampling events).

The percentage of available increments disturbed by new pig diggings between successive sampling events on each transect was termed the 'digging index' and provided the basic data for analysis. Rain, leaf litter and the scratching activity of scrub turkeys (*Alectura lathami*) and scrub fowls (*Megapodius reinwardt*) sometimes masked diggings caused by feral pigs. Only diggings clearly identified as pig diggings were recorded. In total, 195 transects, totalling 9.75 km in length, were established and monitored.

#### Analysis

The amount of new feral pig diggings in each transect between each sampling event is also related to the length of time available to cause these diggings. Because the number of days between sampling events varied owing to weather and logistic considerations, a standardised 'daily digging index' (DDI) was calculated to represent the amount of new diggings that occurred in a standardised period of one day. The DDI was calculated for each transect using the following equation:

$$DDI = ((x / (500 - n)) / d) \times 100,$$

where x = the number of increments positive to new pig diggings, n = the number of increments unavailable, and d = the number of days since the previous sampling event.

One-way ANOVA was used to test for significance differences (to identify spatial variation) in the DDI between the strata within each area at each sampling time. For these analyses, sites were used as independent experimental units and transects were samples. Repeated-measures ANOVA compared patterns across all sampling events. Plots were constructed to illustrated temporal trends of DDI for each area.

The relationship of seasonal rainfall patterns with the DDI was quantified by time-lag correlation analysis. The value of the dependent variable (the mean combined DDI for strata within each area) at time *t* was expressed as a linear function of

rainfall measured at times t, t-1, t-2 etc, from one to eight months previously.

#### Results

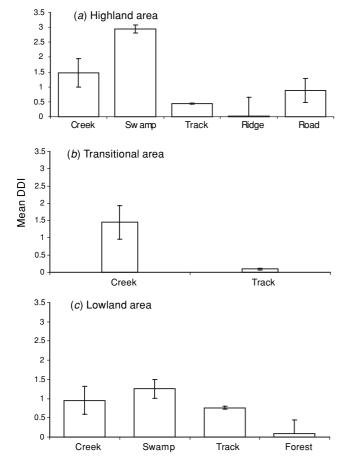
The DDI for each stratum within each of the three areas for each sampling event is shown in Table 1. Significant differences in the DDI between strata were found in some sampling events. Significant differences in the mean (combined across all sampling events) digging indices were found between the strata within the three areas (Fig. 2). For the highland area, swamps had more pig diggings than all other strata ( $F_{4,10}=9.95$ , P<0.01). Differences in mean DDI between the creek and track strata were also detected in the transitional areas ( $F_{1,10}=8.03$ , P<0.05). No significant differences were detected between the four strata in the lowland area. The mean DDI for all strata combined was  $0.115\pm0.036\%$  in the highland area,  $0.077\pm0.034\%$  in the transitional area and  $0.076\pm0.038\%$  in the lowland area. The overall mean DDI for all strata in all areas was 0.09%.

Digging patterns varied with seasons: generally less digging occurred during the wet season and, conversely, most diggings occurred during the dry season (Fig. 3). Temporal differences in the amount of digging activity in each area (all strata combined) were identified in the highland area ( $F_{3,11} = 5.22$ , P < 0.01), the transitional area ( $F_{2,2} = 4.43$ , P < 0.05) and the lowland area ( $F_{3,9} = 4.43$ , P < 0.05). A significant interaction effect was detected only in the transitional area ( $F_{2,20} = 4.55$ , P < 0.05). For all three areas, a significant correlation of the mean DDI of each stratum with antecedent rainfall was found. The extent of diggings was significantly correlated with rainfall that had occurred three months (r = 0.69, P < 0.05) and four months (r = 0.8, P < 0.05) earlier in the highland area and five months earlier in the transitional (r = 0.68, P < 0.05) and lowland (r = 0.62, P < 0.05) areas.

#### Discussion

The most obvious visual impact of feral pigs on the rainforest environment is their foraging activity or diggings associated with soil or surface vegetation disturbance. Spatial and tempoWildlife Research

J. Mitchell et al.



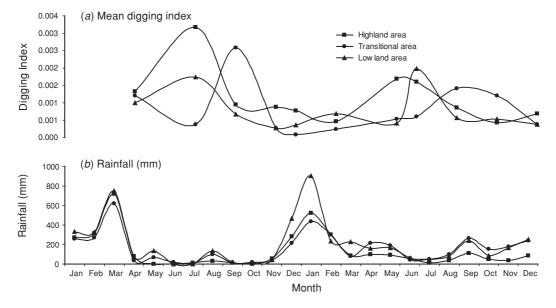
600

**Fig. 2.** Mean daily digging index (and s.e.) of each stratum over all sampling events for the (a) highland area, (b) transitional area and (c) lowland area.

ral patterns of feral pig diggings were identified in this study. Feral pigs preferred to dig in moist microhabitats where soil moisture persists into the dry season (swamps and creeks) and most diggings occur during the early dry season.

Differences in the extent of diggings between the three study areas were apparent, with more diggings occurring in the highland area than in the transitional or lowland areas. This may indicate that either pig population densities were higher or that diggings were a more prominent foraging activity in this highland area. The amount of diggings has been positively associated with pig population densities in studies in Hawaii (Katahira et al. 1993) and on mainland USA (Ralph and Maxwell 1984). Hone (1988a) found that the amount of recent or fresh diggings was positively related to pig population levels. As fresh diggings were directly measured in this study, a relationship between the digging index and population density may be relevant although no direct association was tested.

Dunning et al. (1992) defined a landscape as a mosaic of habitat patches (termed microhabitats in this study) with landscape composition being the relative amount of each microhabitat within the landscape. Rainforest complexity made calculating the relative amount of each study stratum within the landscape difficult and beyond the scope of this study. However, differences in the utilisation of these microhabitat strata by feral pigs may be described by the differences in the amount of diggings between the strata. Significant differences in the utilisation of these strata by feral pigs were found in the highland and transitional areas of this study. Most diggings occurred in strata that were small in size or uncommon compared with the rainforest landscape. For example, most diggings occurred in swamp and creek strata, which represent only a very small proportion of the total rainforest area. In comparison, the strata that represent the largest portion of the total rainforest area, the ridge in the highlands and forests in the lowlands, had significantly



**Fig. 3.** Comparison of the mean daily digging index for (a) all strata within each of the three areas, and (b) the recorded rainfall (mm) for the entire study period.

fewer diggings. The amount of diggings in the common ridge stratum in the highland area was less than 1% of the DDI for the other strata.

Choquenot and Ruscoe (2003) suggested that the quality of a location or microhabitat stratum where a large herbivore such as a feral pig may prefer to spend time will be determined by the availability and quality of food resources and the degree that local conditions may limit the rate that this food can be assimilated for reproductive and survival purposes. The preference of feral pigs to spend more time in some microhabitats was also described by Mitchell and Mayer (1997), who found that most pig diggings also occurred in small microhabitats, such as drainage lines and roads, compared with the larger area of the general forest floor. Hone (1988b) described this spatial digging pattern of many sites with few diggings and few sites with many diggings as fitting a negative exponential frequency distribution. Thus the ecological impacts of pig diggings seem to be concentrated within small-area microhabitats and may not be an important ecological impact to the general rainforest macrohabitat.

Seasonal patterns of digging were also observed in this study, with a relationship between digging activity and antecedent rainfall. The digging peak occurred 3–4 months after the rainfall peak in the highlands and 5 months in the transitional and lowland areas. Thus, from the highest-rainfall events of the wet season (usually February) the peak in diggings were generally in the dry-season months of May/June in the highlands and July/August in the transitional and lowland areas. Engeman *et al.* (2003) also described seasonal patterns of feral pig diggings in their study in Florida.

Studies in other areas have demonstrated that rainfall patterns, particularly in dry areas, have a major influence on pig population levels (Choquenot *et al.* 1996) and that food and water availability affect pig distribution patterns (Caley 1997; Dexter 1998). This study demonstrated a correlation of digging activity with seasonal rainfall patterns in rainforests and implies that rainfall has a substantial influence on the ecological factors that indirectly influence feral pig ecology.

Factors such as the seasonality of available above-ground food resources (e.g. fruits), in comparison with the availability of below-ground food resources (e.g. earthworms), would influence the distribution, scale and timing of diggings. Pig distribution can be driven by variations in locally or seasonally abundant food sources (Choquenot *et al.* 1996). For example, D. Westcott (unpubl. data) demonstrated a seasonal fruiting cycle at a Mount Bartle Frere site, with the peak of fallen fruit biomass occurring in March and a smaller peak in November; he found a distinct lack of fruit on the ground during the dry season (May to October). The absence of fallen fruit at this time may cause pigs to forage more within the soil, increasing the amount of diggings during the dry season, as found in the present study.

Significant seasonal variations in the amount of diggings between the strata (in all three areas) was also evident in the dry season. In general, strata with higher soil moisture levels had significantly higher digging levels than other drier strata. This variation in soil moisture levels may cause a preference for pigs to dig where it is easier to dig and food sources such as underground plant bulbs and earthworms are abundant. Rainfall events such as cyclones wash large amounts of rainforest debris

(including fruits) into creeks and swamps, which may also attract foraging pigs to these microhabitats when fruits become scarce in other strata during the dry season. During the wet season no difference in strata preferences was evident as there were only small differences in soil moisture levels between the strata as the soil was close to saturation.

Mitchell and Mayer (1997) found similar seasonal differences in digging activity between microhabitats, with a preference by pigs to dig in moist soil microhabitats in the dry season. Vernes *et al.* (2001) also found significantly more pig diggings in swamps than in dry ridge habitats during the dry season. The preference for pigs to dig in wet areas has also been reported in the USA (Bratton *et al.* 1982) and in France (Dardaillon 1987).

McIlroy (1993) believed that earthworms might influence pig diggings in this region. He suggested that rainfall may force earthworm populations closer to the surface, thereby making them easier prey for feral pigs. He also suggested that the high protein requirements of female pigs for reproduction and lactation purposes may cause them to actively search for a high-protein source, such as earthworms.

Other factors that may influence pig diggings were found in studies in the Northern Territory, where seasonal variations in the distribution of pig populations (and associated pig digging levels) were caused by seasonal flooding (Hone 1990) and by the availability of seasonal cereal crops (Caley 1993). Overseas studies have reported seasonal population distribution patterns being attributed to rainfall and temperature patterns in Malaysia (Diong 1973), to food availability (Graves 1984) and to the density of available cover (Barrett 1978) in the USA.

Although large-scale ecological impacts of digging have not been reported in this study, the amount of diggings in the small-scale microhabitat was severe. Excessive diggings within small microhabitats may not have much influence on the ecology of the rainforests as a whole, but may have a severe ecological impact on the individual microhabitats. The clear preference of pigs to dig in swamps and creeks may have particularly important ramifications if these habitats are refuges for rare or endangered plant and animal species. High levels of digging disturbance may influence the survival of rare and endangered species or influence the ecological process involved in these small microhabitats. The timing of pig diggings may also have important implications: maximum disturbance at a vulnerable phase of the endangered species' life cycle may have a devastating impact.

Management strategies for feral pigs in this region should be prioritised to reducing the ecological impacts of feral pigs on the relatively small microhabitats that are preferred by feral pigs for foraging activities, rather than to the rainforest landscape as a whole. Management needs to be specific in targeting those microhabitats or species that have high conservation values and that have been identified as at risk from feral pig activities. Additional studies on the ecological impacts of feral pigs on the rainforest landscape are necessary to help prioritise management options.

## Acknowledgements

We acknowledge Dr Chris Johnson for his support. The Rainforest CRC and the Department of Natural Resources and Water provided financial support for this study. Several University students assisted – thanks go to Geoff

Wildlife Research

J. Mitchell et al.

Andersson, Steve Locke, Leon Hill and Cathy Brennan. Thanks go to the staff of the Queensland Parks and Wildlife Service at Edmund Kennedy National Park

#### References

602

- Barrett, R. H. (1978). The feral hog on the Dye Creek ranch, California. *Hilgardia* **46**, 283–355.
- 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.
- Caley, P. (1993). Population dynamics of feral pigs (Sus scrofa) in a tropical riverine habitat complex. Wildlife Research 20, 625–637. doi:10.1071/ WR9930625
- Caley, P. (1997). Movements, activity patterns and habitat use of feral pigs (Sus scrofa) in a tropical habitat. Wildlife Research 24, 77–87. doi:10.1071/WR94075
- Choquenot, D., and Ruscoe, W. A. (2003). Landscape complementation and food limitation of large herbivores: habitat-related constraints on the foraging efficiency of feral pigs. *Journal of Animal Ecology* **72**, 14–16. doi:10.1046/j.1365-2656.2003.00676.x
- Choquenot, D., McIlroy, J. C., and Korn, T. J. (1996). 'Managing Vertebrate Pests: Feral Pigs.' (Bureau of Resource Sciences & Australian Government Publishing Service: Canberra.)
- Dardaillon, M. (1987). Seasonal feeding habits of the wild boar in a Mediterranean wetland, the Camargue (southern France). Acta Theriologica 32, 389–401.
- Dexter, N. (1998). The influence of pasture distribution and temperature on habitat selection by feral pigs in a semi-arid environment. *Wildlife Research* **25**, 547–560. doi:10.1071/WR97119
- Diong, C. H. (1973). Studies of the Malayan wild pig in Perak and Johore. *Malayan Nature Journal* **26**, 120–151.
- Dunning, J. B., Danielson, B. J., and Pulliam, H. R. (1992). Ecological processes that affect populations in complex landscapes. *Oikos* 65, 169–175. doi:10.2307/3544901
- Engeman, R. M., Smith, H. T., Shwiff, S. A., Constantin, B., Woolard, J., Nelson, M., and Griffin, D. (2003). Prevalence and economic value of feral swine damage to native habitat in three Florida State parks. *Environmental Conservation* 30, 319–324. doi:10.1017/ S037689290300033X
- Graves, H. B. (1984). Behaviour and ecology of wild and feral swine (Sus scrofa). Journal of Animal Science 58, 482–492.
- 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. doi:10.1111/j.1442-9993. 1988 tb00987 x
- Hone, J. (1990). Note on seasonal changes in population density of feral pigs in three tropical habitats. *Australian Wildlife Research* 17, 131–134. doi:10.1071/WR9900131
- Hone, J. (1995). Spatial and temporal aspects of vertebrate pest damage with emphasis on feral pigs. *Journal of Applied Ecology* 32, 311–319. doi:10.2307/2405098
- Howe, T. D., Singer, F. J., and Ackerman, B. B. (1981). Forage relationships of European wild boar invading northern hardwood forest. *Journal of Wildlife Management* 45, 748–754. doi:10.2307/3808713
- 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.
- Laurance, W. F., and Harrington, G. N. (1997). Ecological associations of feeding sites of feral pigs in the Queensland wet tropics. Wildlife Research 24, 579–591. doi:10.1071/WR96029
- McIlroy, J. C. (1993). Feral pig management problems in the wet tropics of Queensland World Heritage Area. Cairns. Report to Wet Tropics Management Agency, Cairns.
- Mitchell, J. L. (1993). Systematic assessment of feral pig damage and recommended pig control methods in the Wet Tropics World Heritage Area. Report to Wet Tropics Management Agency, Cairns.
- Mitchell, J. L., and Mayer, R. (1997). Digging by feral pigs within the Wet Tropics World Heritage Area of north Queensland. *Wildlife Research* **24**, 591–603. doi:10.1071/WR96041
- Ralph, C. J., and Maxwell, B. D. (1984). Relative effects of human and feral hog disturbance on a wet forest in Hawaii. *Biological Conservation* 30, 291–303. doi:10.1016/0006-3207(84)90048-X
- Tierney, T. A., and Cushman, J. H. (2006). Temporal changes in native and exotic vegetation and soil characteristics following disturbance by feral pigs in a California grassland. *Biological Invasions* 8, 1073–1089. doi:10.1007/s10530-005-6829-7
- Tracey, J. G. (1982). 'The Vegetation of the Humid Tropical Region of North Queensland.' (CSIRO: Melbourne.)
- Vernes, K., Johnson, C. N., and Mitchell, J. L. (2001). The effectiveness of trapping in reducing pig abundance in the wet tropics of north Queensland. In 'Feral Pigs: Pest Status and Prospects for Control'. (Ed. C. N. Johnson.) pp. 51–56. (James Cook University: Cairns.)

Manuscript received 6 June 2006, accepted 2 October 2007