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Quantifying efficacy of feral pig (*Sus scrofa*) population management

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Abstract

Context. Feral pigs (*Sus scrofa*) are an increasing threat to agriculture and ecological communities globally. Although ground rooting is their most readily observable sign, feral pigs typically remain highly cryptic and their abundance and impacts are difficult to quantify.

Aims. The aim of the present study was to evaluate the effect of current feral pig population management practices (trapping, baiting, no feral pig management) on feral pig abundance and digging impacts, using a BACI (before–after control–impact) experimental design at a landscape scale.

Methods. A monitoring program was established to quantify both the abundance and digging impacts of feral pig populations within a temperate sclerophyll forest landscape using distance sampling. Transects were established across eight drinking water catchments where the whole catchment was the unit of replication for feral pig population management. Monitoring was carried out at 6-monthly intervals for 3 years, with no feral pig population management undertaken in the first year. In total, 367 feral pigs were trapped out of three catchments subject to trapping, and 26 were baited across two catchments subject to baiting with a commercial product (PIGOUT, Animal Control Technologies Australia, Melbourne, Vic., Australia). Three catchments were exempt from feral pig population management for the duration of this study.

Key results. Feral pig density within the overall study site was estimated as 1.127 pigs km^{-2}, resulting in 4580 diggings km^{-2} year^{-1}. There was no significant difference in feral pig density estimates observed among population management treatments or the treatment × year interaction term. An overall decrease in feral pig density across all catchments was attributed to extreme temperature and drought conditions experienced during the study.

Conclusions. Feral pig populations demonstrate high resilience to current feral pig population management practices in the present study. The annual volume of soil disturbed by the numbers of feral pigs estimated across this study area is comparable to a commercial-scale resource extraction industry. We did not find significant differences in feral pig digging density among dominant vegetation types, but larger digs were associated with swamp vegetation.

Implications. Current levels of feral pig population management did not reduce pig densities across eight catchments in the northern jarrah forest; therefore, more intensive population management is needed.

Additional keywords: bioturbation, habitat loss, invasive species, landscape ecology.

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Introduction

Feral pigs (*Sus scrofa* Linnaeus, 1758) are a significant pest species in many parts of the world, due to their invasive nature, destructive behaviour and their ability to persist across a wide range of environments. Impacts of feral pigs include loss of agricultural productivity (Gong *et al.* 2009; Bengsen *et al.* 2014) and significant public health risk (Hampton *et al.* 2006; Jay *et al.* 2007; Irwin *et al.* 2009). They degrade vegetation structure and composition via decreased seedling recruitment and survival (Hone 2002), predate on vulnerable species through selective

Table 1. Sampling effort for each water catchment in the northern and central jarrah forest
Catchments are ordered from north to south

Catchment	Location	Transects (*n*)	Total transect length (m)	Treatment	No. of pigs removed[A]
Canning	32°10′S, 116°08′E	10	5150	Bait	3
Wungong	32°12′S, 116°04′E	9	4150	Control	0
Serpentine	32°25′S, 116°07′E	12	5400	Trap	140
North Dandalup	32°31′S, 116°02′E	10	4500	Trap	102
Conjurunup	32°35′S, 116°00′E	5	2250	Bait	23
South Dandalup	32°40′S, 116°05′E	11	4200	Trap	125
Stirling Dam[B]	33°07′S, 116°02′E	8	3600	Control	0
Harris Dam[B]	33°14′S, 116°08′E	10	4300	Control	0

[A]Refers to pigs removed as part of coordinated population management efforts only; feral pig hunting in water catchments is illegal in Western Australia but is known to occur at low levels throughout the study area. Numbers of animals for baited catchments are estimated as the number of individual pigs that were viewed on cameras consuming toxic baits (PIGOUT; Animal Control Technologies Australia, Melbourne, Vic., Australia).
[B]The two most southern water catchments (Stirling and Harris) represent highly modified environments: Stirling has extensive areas of pine plantations (*Pinus radiata*) surrounding the reservoir; and Harris is a recently created water reservoir (1982) formed by flooding previously cleared grazing paddocks. As such, transects within these two catchments do not accurately reflect the habitat and soil profiles of the northern jarrah forest. Therefore, dig recordings from these two catchments were not used to generate the global model for dig density.

feeding (Melzer *et al.* 2009; Webber *et al.* 2010), alter nutrient cycling and introduce weeds and pathogens (Lynes and Campbell 2000; Li *et al.* 2013). For example, in northern Australia, feral pigs have been demonstrated to significantly affect populations of at least two freshwater and three marine turtles, due to direct predation of either the turtles themselves or their nests (Fordham *et al.* 2006; Schaffer *et al.* 2009; Whytlaw *et al.* 2013).

Feral pig populations have largely proven resistant to eradication efforts, and in many situations their distribution continues to increase (Waithman *et al.* 1999; Spencer and Hampton 2005). In Australia, where feral pig populations are well established, realistic, cost-effective mitigation of feral pig numbers requires management of populations to limit damage. To achieve this, land managers and policymakers need information describing abundance and distribution of feral pigs and their impacts within a landscape.

Although they are large-bodied, feral pigs are highly cryptic and difficult to trap for mark–recapture estimates. Therefore, monitoring feral pigs typically relies upon indirect measures of abundance. Estimation of population size can use any cue or object produced by the target animal, so long as its production is linearly related to animal abundance (Buckland *et al.* 2001). Dung has commonly been used by previous authors as a measure of abundance for a range of species, including feral pigs (Hone 1988; Hone and Martin 1998; Marques *et al.* 2001; Walsh *et al.* 2001; Laing *et al.* 2003). Dung production typically meets this criterion, although seasonal changes in diet is one potential source of variation in rate of dung production (Ruggiero 1992; Todd *et al.* 2008), and seasonal conditions are likely to influence the rate of decay of sign, and therefore detectability (White 1995; Marques *et al.* 2001; Rivero *et al.* 2004). Ideally, these factors need to be assessed as part of validating this method for estimating population size. The most visible sign of feral pig presence is the disturbance of soil and vegetation from their rooting behaviour while foraging for subterranean food resources. However, digging activities are not ideal for population estimates because they typically vary in relation to forest type, potentially reflecting the relative availability of subterranean food resources, for example sporocarps, earthworms and other invertebrates (Laurance and Harrington 1997).

Because of discontinuity in their preferred habitat or foods, monitoring numbers of feral pigs through their sign therefore requires large-scale studies that can take into account the stochasticity of their presence and activity (Hone 2012; Elledge *et al.* 2013; Krull *et al.* 2013; Bengsen *et al.* 2014). We used a BACI (before–after control–impact) study design to test the efficacy of current feral pig population management practices within a temperate sclerophyll forest landscape in south-west Australia, comparing feral pig density and digging impact across eight drinking water catchments. We surveyed 75 monitoring transects totalling 33.5 km in length on foot, twice a year over 3 years. Feral pig dung and digging was analysed by distance sampling to calculate changes in abundance and damage in response to population management.

Materials and methods

Study sites

The northern jarrah forest covers an area of ~10 500 km^2 within the Darling Range, South-west Botanical Province, Western Australia. This area experiences a Mediterranean climate, with cool, wet winters (June–August) and hot, dry summers. This open and dry sclerophyll forest is dominated by jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) (Havel 1975).

Seventy-five monitoring transects totalling 33.5 km in length were established across eight drinking water catchments (Canning, Wungong, Serpentine, North Dandalup, Conjurunup, South Dandalup, Stirling Dam and Harris Dam), located from 32°8′S to 33°15′S latitude within the northern jarrah forest (Table 1, Fig. 1). Transect locations were identified as a desktop exercise using topographic maps, spreading transects around the periphery of water bodies within each catchment, with each transect running across the rise of the land. In the field, transect locations were shifted (as close as possible to the initial proposed site) when vegetation had been recently managed (logging, mining), or sites were not able to be accessed by vehicle. Transects were marked with metal posts located every 50 m along a compass bearing set to run from the gully bottoms to the

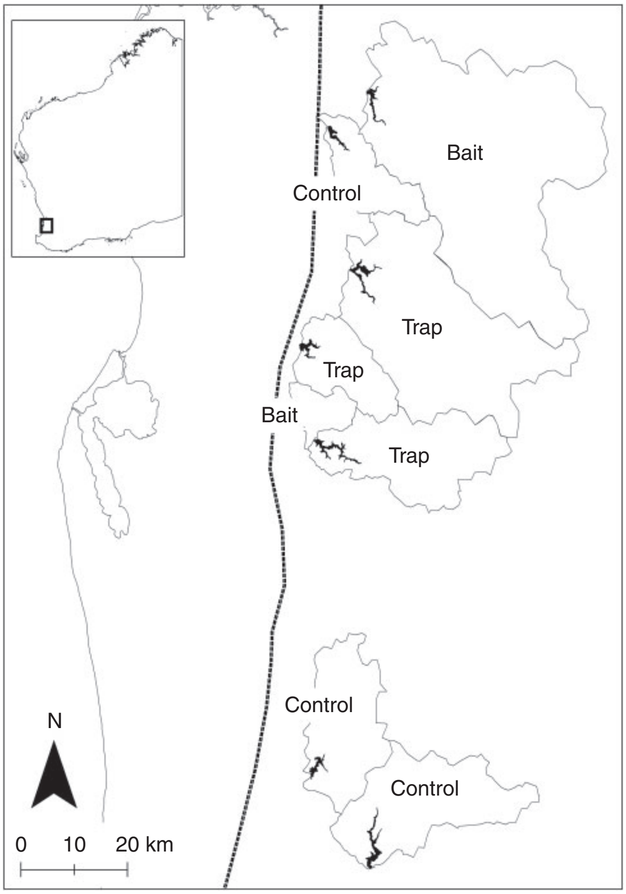

Fig. 1. Location of the eight drinking water catchments used in the study and their respective feral pig population management treatment. Dotted line represents the Darling Scarp, a geographic feature that delineates the western edge of the northern jarrah forest.

nearest ridge top. Because of differences in size of catchments, the number and length of transects varied accordingly, with transects ranging from 250 to 700 m in length (mean 447 m ± 82 s.d.) (Table 1).

All catchments were surveyed in the first year when no organised feral pig population management was undertaken. For years 2 and 3, each catchment was designated one of three treatments: control (no feral pig removal; $n = 3$ catchments), trapping (removal of feral pigs via trapping only; $n = 3$ catchments) or bait (removal of feral pigs by poison baiting only; $n = 2$ catchments) (Table 1, Fig. 1). Feral pig trapping involved pre-feeding potential trap sites with apples over ~2 weeks to gauge feral pig presence, determined by removal of bait and feral pig sign (dung and tracks), followed by placement of wire cage traps (1.5 × 1.5 × 1.5 m; apple bait). On average, 10 traps per catchment were set over 4 nights (weekdays) and wired open on weekends. Traps were moved depending on feral pig activity such that ~25 trap locations were trapped in a season. Trapping was typically continued at each site from November until April. Baiting was carried out by deploying PIGOUT, Animal Control Technologies Australia, Melbourne, Vic., Australia) baits in clearings at five bait stations in Canning catchment and three bait stations in Conjurunup catchment. Baits were monitored by IR camera traps (HC500; Reconyx, Holmen, WI, USA) deployed on trees located 2–3 m from the baits to monitor feral pig bait take and non-target species interference. Pre-feeding with non-toxic PIGOUT baits was continued until either consistent bait take by feral pigs occurred for three consecutive nights, or non-target bait interference caused the bait station to be abandoned (four bait stations at Canning catchment had to be discontinued due to non-target bait interference, leaving a single bait station). In total, ~60 toxic PIGOUT baits were deployed.

Illegal, recreational hunting of feral pigs is known to have occurred within these areas but could not be effectively excluded or monitored, and as such was assumed to be consistent across all catchments.

Transect monitoring

Transects were monitored every 6 months (Austral summer: November–December; winter: June–July) for 3 years (total of six sampling events, December 2009 to June 2012). Seasonal feral pig population management occurred during drier (summer) months, the results of which would therefore be captured in the winter sampling period.

To quantify their numbers and impact, all feral pig sign (dung and diggings) along transects were simultaneously recorded. For each monitoring survey, a team of two observers walked the entire length of each transect at an approximate speed of 0.5 km h^{-1}, carefully searching the ground to either side of the transect (to an approximate distance of 3–4 m). The search pattern of both observers was such that they overlapped on the centre line of the transect to maximise detection on or close to the centre line (Buckland *et al.* 2001). Feral pig dung was identified by the unique shape, appearance and smell associated with it. Feral pig digging was distinguished from that of other species by the unique characteristics associated with the pig's snouting or rooting behaviour. Diggings were characterised by disturbance of topsoil (<5 cm depth), mixing of soil profile, uprooting of plant(s) or major disturbance to plant root systems. In addition to counting each dig, the area (to the nearest 0.1 m^2) of each dig was recorded; for a subset of diggings, we also recorded approximate depth (to the nearest 0.01 m) to allow an estimate of dig volume. Once recorded, dung was removed from the transect and diggings were marked with white ground-marking paint (we did not analyse decay rates for digging; instead, all observed digs were marked, and paint-marked digs were still discernible at the completion of the 3-year project). The perpendicular distance of the dung from the transect centre line was measured to the nearest 0.1 m and the distance along the transect was approximated (±10 m).

Dung deposition and decay rates

Direct observation of dung deposition by free-ranging feral pigs was not feasible. Therefore, to relate dung densities to feral pig abundance, dung deposition rates (number of dung piles h^{-1}) were calculated for $n = 23$ trapped feral pigs held in large pen style cages (~30 m^2) for varying time periods (10–24 h) (Table S1, available as Supplementary material to this paper).

To estimate the decay rate of feral pig dung, feral pig dung ($n = 37$ dung from 16 deposition dates – collected during summer trapping and known to be less than 48 h old at time of collection) was positioned within the vicinity of monitoring transects, where they were monitored regularly. Dung was deemed to have 'decayed' when it had degraded beyond being recognisable as feral pig dung, or leaf litter had accumulated to the extent that the dung sample was no longer detectable. The number of days each dung sample took to decay was recorded.

Statistical analyses

Because detection of sign varies with distance from transect, vegetation type, time of year and observer, we used a distance-sampling framework to estimate dung and dig densities. Using Distance 5.0 (Buckland *et al.* 2001), a global detection function was estimated from all recordings of dung or digs across all sampling intervals and locations, assuming 100% detection on the centreline. Selection of global detection functions were guided by chi-square model-fit statistics and visual inspection of detection probability and probability density plots (Buckland *et al.* 2001), and best fit functions were ranked by Akaike's Information Criterion (Akaike 1973; Burnham and Anderson 1998). Tests for estimation of separate detection functions by season and/or different observer combinations (Buckland *et al.* 2001) indicated that specific detection probability functions were not warranted. Recorded observations for both dung and dig were right-truncated by 5% to remove extreme observations, because these records provide little information for estimating the detection function [$f(0)$] and do not improve model fit (Buckland *et al.* 2001). Distance-sampling analyses yielded estimates of the annual unconditional probability of detection (P_a – the probability that a randomly selected object within the survey area is detected). Measures of P_a provide an unbiased means to directly assess the issue of constant detectability, if key assumptions are adequately met (Buckland *et al.* 2001).

Feral pig density $\left(\hat{D}\right)$ was estimated from dung observations within the Distance 5.0 statistical software using calculations as per Buckland *et al.* (2001). The estimated dung density $\left(\hat{R}\right)$, divided by the estimated mean time to decay (in days) of the dung $\left(\hat{\xi}\right)$, provides an estimate of the dung production per day per unit area ($\hat{G}$):

$$\hat{G} = \frac{\hat{R}}{\hat{\xi}} \text{ (Buckland } et\ al. \text{ 2001, eqn 6.4, p. 185)}$$

Dividing $\hat{G}$ by $\hat{\eta}$, the estimated daily production of dung by one animal (number of dung piles per day), gives $\hat{D}$, the estimate of feral pig density:

$$\hat{D} = \frac{\hat{G}}{\hat{\eta}} = \frac{\hat{R}}{\hat{\xi}\hat{\eta}} \text{ (Buckland } et\ al. \text{ 2001, eqn 6.5, p. 185)}$$

Once we estimated dung and digging densities, we then tested for effects of feral pig control. We analysed feral pig sign density estimates (both BoxCox-transformed to meet the assumptions of normal distribution; dung: Shapiro–Wilk $W = 0.98$, $P = 0.766$; diggings: $W = 0.98$, $P = 0.615$), using the six bi-annual estimates as separate dependent variables for each transect using repeated-measures ANOVA. We included experimental treatment as the categorical factor. As a *post hoc* analysis, we analysed feral pig density estimates over time for each catchment using non-parametric ANOVA. We compared density estimates derived from dung and for diggings by Spearman rank-order correlation.

Studies of feral pig foraging in tropical and sub-tropical environments of northern Australia have reported large differences in digging activities among vegetation types, with pigs showing a particular preference for wetland communities and/or drainage features (Bowman and McDonough 1991; Bowman and Panton 1991; Laurance and Harrington 1997; Mitchell and Mayer 1997; Mitchell *et al.* 2007). We therefore set out to analyse dig density estimates by dominant vegetation type. All 75 transects within the eight catchments were segregated using ArcGIS (version 10.4) to the nearest 50 m, into four respective vegetation complexes using the Vegetation Complexes – South West forest region of Western Australia (DBCA-047) shapefile (Mattiske and Havel 1998): (1) Swamp – closed scrub, heath and/or sedgelands on seasonally wet or moist soils; (2) Murray – open forest on valley slopes (i.e. vegetation on incised or erosion prone landforms); (3) Yarragil – open forest on valley floors (i.e. vegetation on flat or depositional landforms); and (4) Dwellingup – open forest on lateritic uplands. These four complexes represent ~72% (or 7578 km^2) of the northern jarrah forest (Mattiske and Havel 1998). Dig densities and the area of each dig were compared among the four vegetation complexes using Kruskal–Wallis ANOVA. Dig volume estimates were only used to calculate overall soil displacement caused by feral pig digging.

Values are reported as the mean ± 1s.d. throughout.

Results

Feral pig density

Dung deposition rate for $n = 23$ feral pigs of a range of body mass (18.1 ± 14.0 kg; 5–40 kg), held as four groups in traps, averaged 5.83 ± 2.65 dung pig^{-1} day^{-1} (Table S1). The average time to disappearance for feral pig dung (322 ± 238 days, range 48–691 days; Table S2) was twice the length of time between monitoring periods (approximately every 6 months). Given that once identified, feral pig dung was removed from each transect during monitoring, we assumed a maximum length for individual samples of 6 months (the interval between monitoring periods). As such, we calculated a figure of 142.4 ± 56.1 days as the average time until dung decay or disappearance from the transects (Table S2).

In total, 873 feral pig dung were recorded across the 75 transects surveyed during this study. The detection probability for feral pig dung (whole study overall) was 0.54 in the central strip (~3 m width, effective strip width = 1.5 m); i.e. we were certain of detecting more than half of all dung present across the central strip. Combining the dung counts with the deposition and decay rates (estimated above), distance-sampling analysis produced an overall population estimate of 1.127 individual feral pigs km^{-2} (95% CI: 0.899–1.413).

There was no significant main effect of treatment (i.e. catchments subject to no feral pig control, baiting or trapping)

Table 2. Summary of repeated-measures ANOVA for feral pig density estimates derived from dung counts
SS, sum of squares; d.f., degrees of freedom; MS, mean square; F, ANOVA test statistic; *P*, probability. Bold indicates statistical significance

	SS	d.f.	MS	*F*	*P*
Intercept	0.41	1	0.41	0.19	0.678
Treatment	8.07	2	4.03	1.91	0.242
Error	10.55	5	2.11		
Year	**4.52**	**2**	**2.26**	**4.69**	**0.037**
Year × treatment	1.91	4	0.48	0.99	0.457
Error	4.83	10	0.48		
Season	**1.10**	**1**	**1.10**	**11.87**	**0.018**
Season × treatment	0.80	2	0.40	4.33	0.081
Error	0.46	5	0.09		
Year × season	0.21	2	0.10	0.37	0.701
Year × season × treatment	0.97	4	0.24	0.87	0.514
Error	2.80	10	0.28		

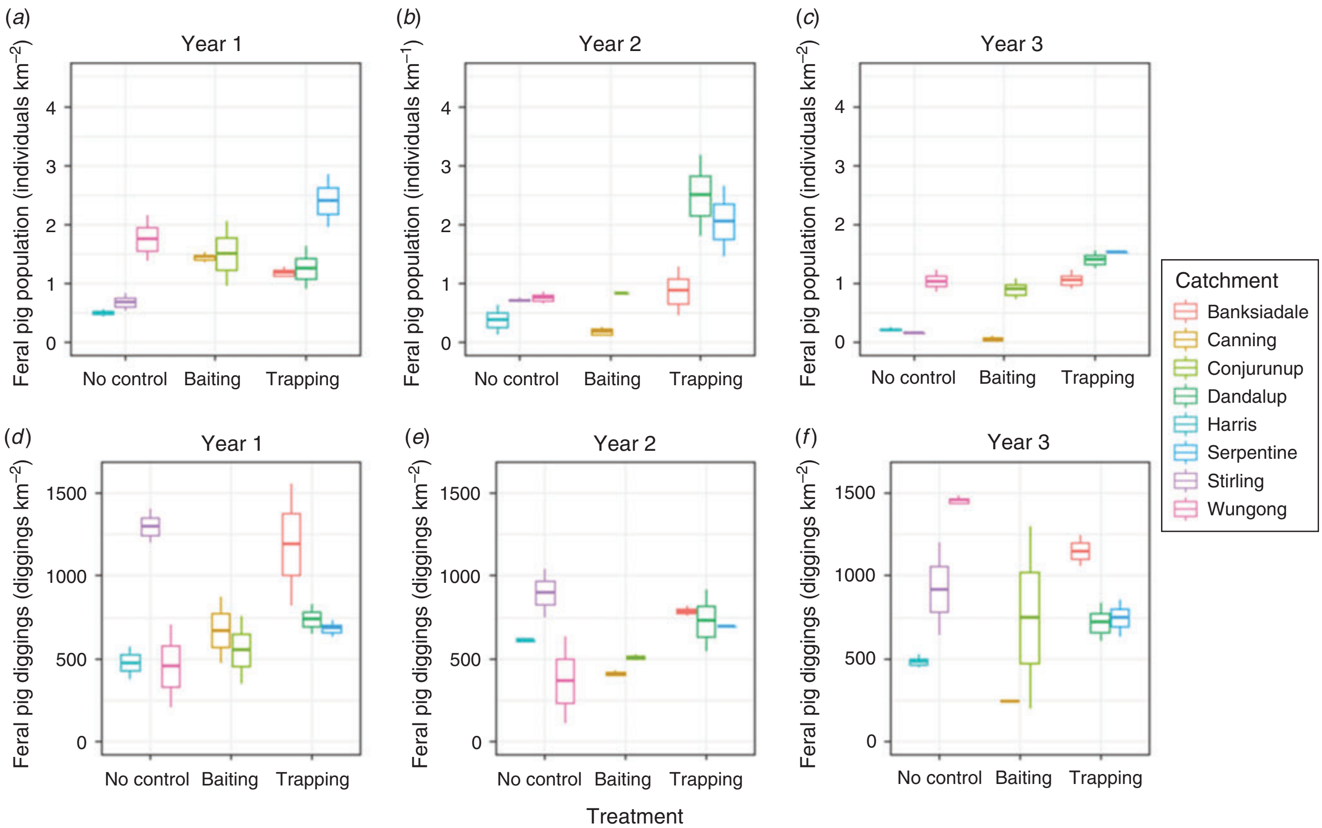

Fig. 2. Comparison of feral pig population density estimates derived from dung counts (pigs km^{-2}) (*a–c*) and feral pig digging density (diggings km^{-2}) (*d–f*) for 3 years across eight catchments subject to varying levels of feral pig population control: no feral pig control ($n = 3$ catchments); baiting at the commencement of Year 2 ($n = 2$ catchments); or trapping across all 3 years ($n = 3$ catchments). Although BoxCox-transformed values were used for statistical analyses, raw data are presented here for clarity.

on feral pig population estimates derived from dung counts (Table 2; Fig. 2*a*–c), and no significant treatment × year interaction term. We therefore conclude that there was no statistically significant effect of feral pig control management on their population estimates. There was a season effect (Table 2; $F_{1,5} = 11.87$, $P = 0.018$), with lower feral pig population for winter compared with summer surveys. There was also a significant annual effect on feral pig population (Table 2, Year: $F_{2,10} = 4.69$, $P = 0.037$, Fig. 3*a*), with significantly lower overall density estimated for Year 3 compared with Year 1 (Table 3). This annual change was significant only for the Canning catchment (Fig. 3*c*, Friedman ANOVA $\chi^2_{n=10,\text{d.f.}=2} = 12.67$, $P = 0.002$), where four feral pigs were known to have taken baits; there was no significant annual change observed for the

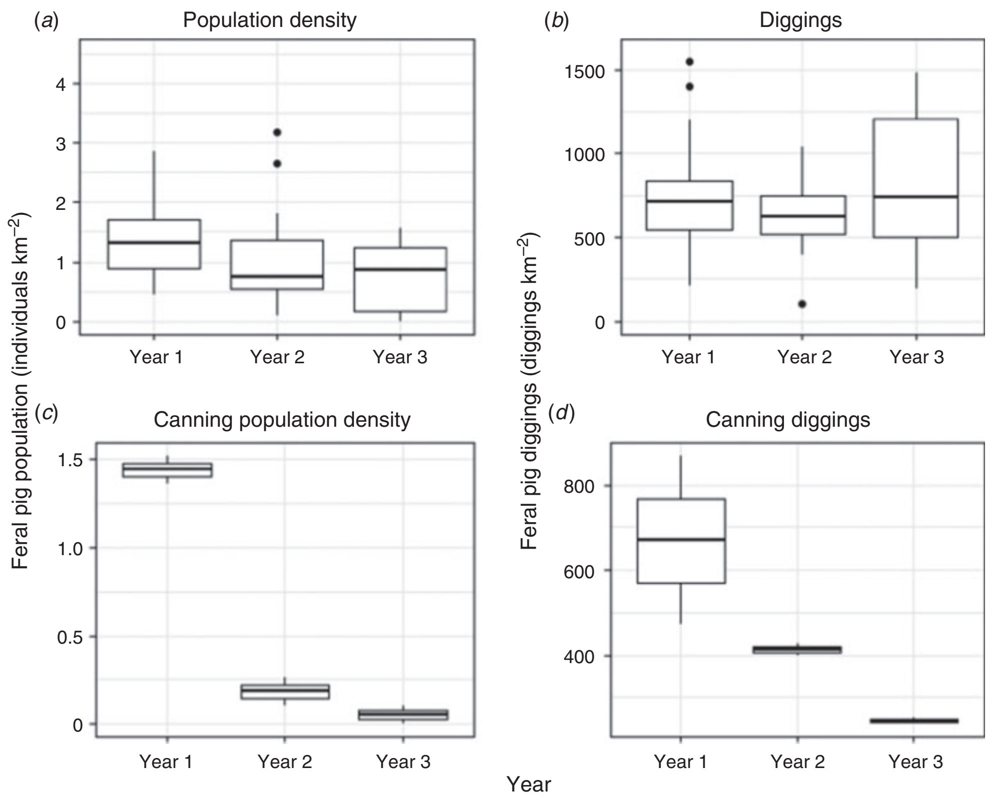

Fig. 3. Comparison of feral pig population density estimates derived from dung counts (*a*, *c*) and feral pig digging density (*b*, *d*) across 3 years for all catchments (top), and for Canning catchment, subjected to feral pig baiting at the commencement of Year 2 (bottom). Although BoxCox-transformed values were used for statistical analyses, raw data are presented here for clarity.

Table 3. Feral pig density estimates derived from dung counts across eight catchments subject to varying levels of pig control: no feral pig control ($n = 3$ catchments); baiting at the commencement of year 2 ($n = 2$ catchments); or trapping across all 3 years ($n = 3$ catchments)

Last column indicates the results of non-parametric ANOVA testing for a treatment effect of feral pig management on population density estimates

Year	Feral pig density estimates (data pooled by year for each transect)											Treatment effect (Kruskal–Wallis test)
	N transects	Mean	Median	Min	Max	Lower quartile	Upper quartile	Range	s.d.	–95% CI	+95% CI	
Year 1	75	1.36	0.67	0.00	9.59	0.00	1.93	9.59	1.83	1.58	2.19	$H_{2,n=75} = 0.96$ $P = 0.619$
Year 2	75	1.14	0.49	0.00	8.34	0.00	1.35	8.34	1.71	1.47	2.04	$H_{2,n=75} = 8.83$ $P = 0.012$
Year 3	74	0.82	0.30	0.00	5.01	0.00	1.35	5.01	1.13	0.98	1.35	$H_{2,n=74} = 16.90$ $P < 0.001$

other catchments (Table S3). Although the relationship between change in feral pig population estimates and removal efforts (number of feral pigs removed; Table 1) was statistically significant ($r^2_7 = 0.6285$, $P = 0.019$), the relationship was the converse of that expected (Fig. 4*a*). The greatest decreases in feral pig numbers were evident for those catchments where there had been little or no feral pig control management, while the catchment where most feral pigs were removed actually demonstrated an increase in population density between Year 3 and Year 1.

Feral pig diggings

In total, 2197 feral pig diggings were recorded across the 75 transects surveyed during this study. Although feral pig numbers derived from dung records required inclusion of an estimate of the longevity of the cue (i.e. average time to disappearance for feral pig dung), diggings were marked and therefore not re-counted during this study. Analysis of all digging data together produced an average estimate of 4580 diggings km^{-2} year^{-1} (95% CI: 1803–13 315). The median area of disturbed soil associated with individual pig diggings was 0.40 m^2 (range 0.01–39.20 m^2), and the median volume of soil disturbed per individual pig digging was 0.29 m^3 (range 0.10–0.99 m^3) (Table 4). The majority of pig diggings were created in previously undisturbed soil, with 6.98% of previously disturbed digs showing signs of being reworked by pigs within 12 months of their creation.

There were no significant main effects of experimental treatment (Fig. 2*d*–*f*) or treatment × year interaction term on

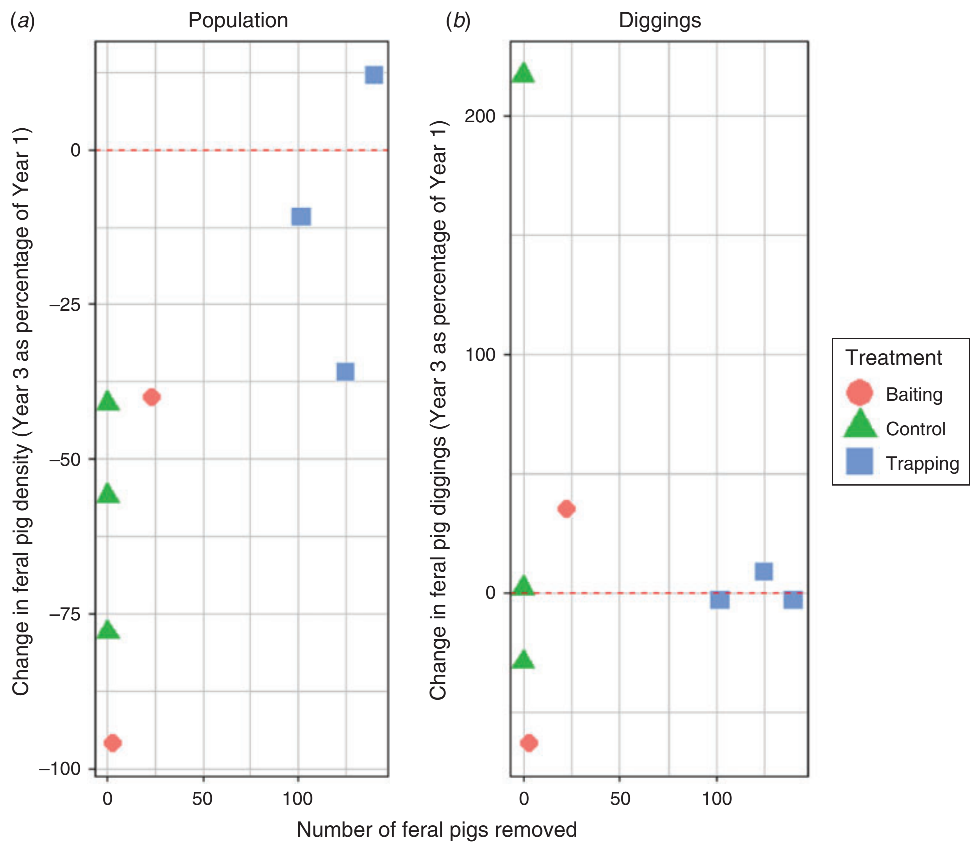

Fig. 4. Comparison of control effort (number of feral pigs removed) with change in (*a*) feral pig population density estimates and (*b*) digging density between Year 3 (after population control management) and Year 1 (before population control management).

Table 4. Feral pig digging disturbance summarised by total area and volume of soil disturbed

	N	Mean	Median	Min	Max	Lower quartile	Upper quartile	Range	s.d.	−95% CI	+95% CI
Area (m^2)	2726	1.05	0.40	0.01	39.20	0.18	0.96	39.19	2.49	2.43	2.56
Volume (m^3)	585	0.36	0.29	0.10	0.99	0.17	0.51	0.89	0.24	0.22	0.25

feral pig digging density estimates (Table 5). The density of feral pig digging varied across catchments (dig density estimates for each catchment are given in Table S4). There was also a significant season × treatment interaction term (Table 5; $F_{2,10} = 6.06$, $P = 0.046$); there was no difference between summer and winter for the control and trapping removal catchments, but for the baited catchments there was less digging recorded in winter (i.e. digging activity over summer, when feral pig population management was carried out) compared with sampling during summer (i.e. winter activity).

There was no statistically significant relationship between the change in feral pig digging estimates and removal efforts (number of feral pigs removed; $r^2_7 = 0.0376$, $P = 0.6456$). Catchments where trapping was carried out showed reasonably consistent amounts of digging between Year 3 and Year 1, while one catchment where no feral pig management was carried out showed the greatest increase in digging disturbance (Fig. 4*b*). The relationship between feral pig population estimates derived from dung and digging density estimates was also not significant ($R_{s\ 46} = 0.208$, $P = 0.156$).

We expected heterogeneity in digging impacts across the landscape, which we observed. There was no significant annual (Friedman ANOVA: $\chi^2_{n=97,\ \mathrm{d.f.}=2} = 5.83$, $P = 0.054$; Table 6) or seasonal ($\chi^2_{n=99,\ \mathrm{d.f.}=1} = 0.01$, $P = 0.917$) difference in feral pig dig density analysed by vegetation complexes; the data were therefore pooled for all surveys across each vegetation complex for further analyses. There was no significant difference in feral pig digging density recorded between the four main vegetation complex types (Kruskal–Wallis ANOVA: $H_{3,n=24} = 1.98$, $P = 0.576$; Fig. 5*a*), but there were differences in the area of diggings recorded by vegetation type ($H_{3,n=2261} = 13.46$, $P = 0.004$; Fig. 5*b*), with the largest diggings recorded in Swamp vegetation.

Table 5. Summary of repeated-measures ANOVA for feral pig digging density estimates
SS, sum of squares; d.f., degrees of freedom; MS, mean square; *F*, ANOVA test statistic; *P*, probability. Bold indicates statistical significance

	SS	d.f.	MS	*F*	*P*
Intercept	139 231.81	1	139 231.81	325.80	<0.001
Treatment	1603.67	2	801.83	1.88	0.247
Error	2136.75	5	427.35		
Year	302.65	2	151.33	0.53	0.606
Year × treatment	476.19	4	119.05	0.41	0.795
Error	2872.92	10	287.29		
Season	64.28	1	64.28	1.06	0.351
Season × treatment	**734.96**	**2**	**367.48**	**6.06**	**0.046**
Error	303.44	5	60.69		
Year × season	557.50	2	278.75	2.08	0.176
Year × season × treatment	654.12	4	163.53	1.22	0.363
Error	1343.09	10	134.31		

Table 6. Average density of feral pig digging impacts in each sampled vegetation complex within a 12-month period estimated using Distance 5.0
LCL, lower confidence limit; UPL, upper confidence limit

Vegetation complex	Area of northern jarrah forest (km^2)	Density (diggings km^{-2})	95% LCL	95% UCL
Swamp[A]	379	4690.6	128.2	204 452.3
Murray	1465	5287.9	2563.7	11508.3
Yarragil	1468	4389.4	2251.0	8607.5
Dwellingup	4267	5161.3	2860.2	9431.8

[A]Swamp vegetation complex under-represented on monitoring transects.

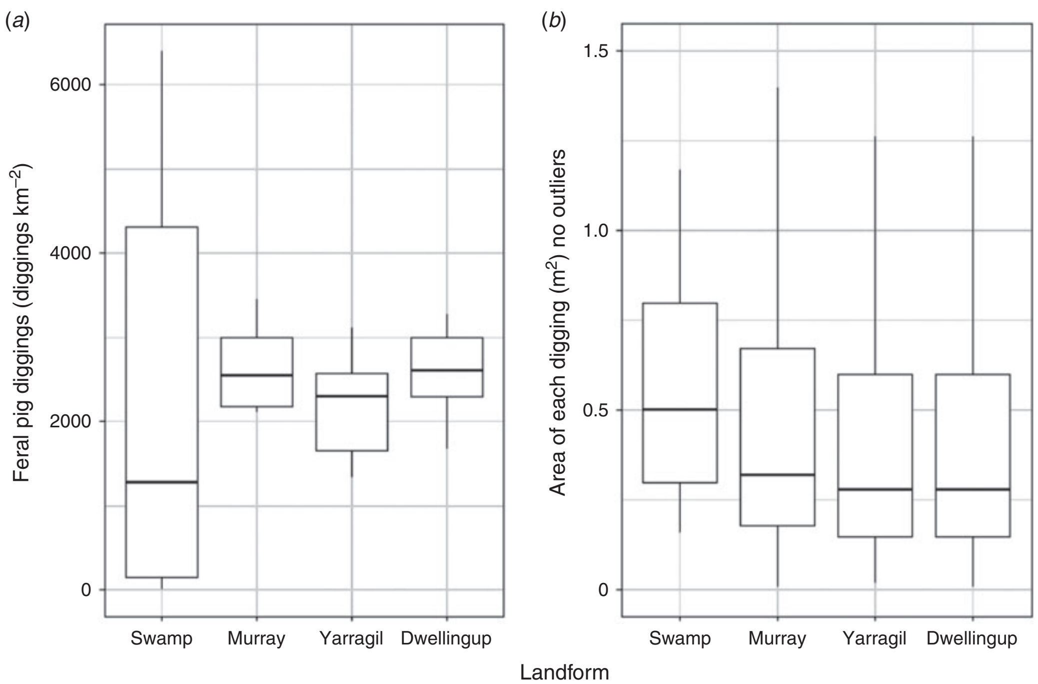

Fig. 5. Comparison of (*a*) density and (*b*) area of individual feral pig diggings across four vegetation complexes. Data are pooled across all three sample years and across all eight catchments.

Discussion

Feral pigs are abundant within drinking water catchments of the northern jarrah forest, Western Australia, where the soil disturbance associated with their rooting activities is substantial. Extrapolation of the feral pig density calculated from the present study – 1.127 feral pigs km^{-2} (95% CI: 0.899–1.412) across the entire northern jarrah forest (10 500 km^2; Havel 1975) – yields an estimated population of 11 837 feral pigs (95% CI: 9440–14 826). We found no evidence that current feral pig population management practices, which are seasonal, substantially reduce abundance of feral pigs, or have an impact on the density of their diggings. In hindsight this finding is not surprising, given the disproportionate scale of population management (feral pigs removed, $n = 393$, only 26 of which were removed from baited sites) in relation to estimated population size ($n \approx 9440$).

Management of feral pigs within water catchments of the northern jarrah forest aims to reduce their density in order to reduce their effects on water quality and the environment. Management programs aiming to reduce feral pig impacts over a broad area need to remove a large proportion of the population to prevent rapid recovery to pre-control densities (Bengsen *et al.* 2014). Clearly, this has not been achieved in the present study; however, these management actions have never been tested in the northern jarrah forest before and these results provide a valuable insight regarding the scale of effort required to achieve the intended objectives.

An unexpected finding of the present study was that we recorded increases in feral pig population estimates for catchments where the greatest level of population management had been carried out (i.e. trapping). Large ungulate population models propose that when a species' density is reduced from the local environmental carrying capacity, compensatory population growth is likely to occur due to a resultant increase in fecundity and juvenile survival and/or recruitment (Caughley 1977). Previous studies of feral pig population growth across a range of environments in Australia have demonstrated the potential for high annual reproductive rates (Bengsen *et al.* 2014). As such, it is quite likely that the removal of 367 feral pigs from these three catchments over the duration of this study ultimately resulted in increased breeding and survival of the population. In comparison, the low number of feral pigs removed from baited catchments ($n = 26$) is unlikely to have influenced the population. Indeed, the decrease in feral pig digging density detected in the two baited catchments is almost certainly a result of external or seasonal influence in feral pig activity.

Estimates of feral pig dig density varied markedly across each of the eight catchments in this study. Feral pigs readily switch foods, feeding behaviours and feeding locations when the availability of food resources changes (Choquenot *et al.* 1996), and variability in digging activity recorded among catchments likely reflects the relative availability of food resources in each catchment. This variability in abundance and digging impacts, and the lack of correlation between feral pig density estimates and records of their digging impacts, would further reduce the power of statistical comparisons, despite the large scale of the current monitoring program.

We recorded a decrease in feral pig density estimates over the 3 years of monitoring. This decrease is unlikely a reflection of population management practices because the reduction in feral pig density was noted across all water catchments. It is therefore likely a result of extrinsic factor(s) influencing the entire study area. In 2010, following the commencement of monitoring in December 2009, the northern jarrah forest experienced one of the driest winters on record (Bureau of Meteorology 2011), followed by a period of extreme drought and heat conditions in summer 2010–2011 (Matusick *et al.* 2013). Drought conditions typically cause declines in feral pig abundance in Australia (Caley 1993; Choquenot 1998), due to decreased food availability and a resultant increase in juvenile mortality. Additionally, Fernández-Llario and Carranza (2000) observed only 16.9% of wild sows to be breeding during 'poor' conditions in Spain, and Massei *et al.* (1996) similarly described a decrease in lactating sows from 90% in 1992 to 20% in 1993 in Italy, attributed to a lack of food availability. These findings support the anecdotal reports from staff operating in the northern jarrah forest at this time that feral pigs were in markedly poorer condition than previous years, and that sows were producing fewer or no young. Our data highlight potential susceptibility of feral pigs to unfavourable weather conditions that affect food resources and availability in this temperate forest habitat.

Other studies have reported that ground disturbance or digging caused by feral pigs is related to their abundance (Hone 2012), but we found no significant correlation between feral pig density estimates and their digging impacts. Therefore, digging is not a reflection of population density in the northern jarrah forest at the densities estimated in the present study; instead it may be a reflection of landscape heterogeneity and localised food abundance. Because digging estimates were calculated as the overall density across vegetation type for each season, there were few data in this dataset for analysis and there was no statistical difference in digging density among vegetation types. However, diggings were significantly larger in area in Swamp vegetation compared with the other three dominant vegetation types. The four vegetation complexes covered by these transects represent ~72% of the northern jarrah forest, but there are an additional 11 vegetation complexes recognised within the eastern margin of the northern jarrah forest (Mattiske and Havel 1998), highlighting the landscape variability. Confounding factors, such as soil composition and proximity of agriculture or mining activities within these catchments also cannot be ignored. Open-cut bauxite mining has been undertaken by Alcoa Inc. within these catchments since 1976, resulting in the clearing, mining and rehabilitation of ~450 ha of open forest annually (Nichols *et al.* 1985; Koch *et al.* 1996). These activities may potentially have the effect of 'concentrating' feral pigs in areas of remnant forest and riparian zones, thus resulting in a higher concentration of diggings within the vicinity of monitoring transects in these catchments. By contrast, agricultural land use may provide increased opportunities for feral pigs.

The density of feral pigs estimated in the present study for the northern jarrah forest is comparable to those for feral pigs in forested habitats elsewhere in Australia (Douglas Daly National Park, NT: 0.8 pigs km^{-2} (Caley 1993); Namadgi National Park, ACT: 1.7 pigs km^{-2} (Hone 2002); Kosciusko National Park, NSW: 1.6 pigs km^{-2} (Saunders 1993)). We calculated that feral pigs are responsible for creating 4580 digs km^{-2} year^{-1} across these four vegetation complexes in the northern jarrah forest, with only 6.98% of these diggings occurring in previously disturbed soil. The area of soil disturbed by feral pig diggings in this study varied considerably (1.06 m^2 ± 2.61 s.d., range 0.01 to >20 m^2); however, the distribution of dig size was strongly skewed to smaller dig areas, similar to that observed in other studies (Kotanen 1995; Welander 2000; Hone 2002). The estimated volume of soil displaced by pig digging varied less so (0.36 $m^3 \pm 0.24$ s.d., range 0.1–1 m^3), suggesting two different types of digging behaviours: (1) indirect or exploratory foraging, resulting in larger but relatively shallow soil disturbance; or (2) targeted foraging, resulting in smaller but deeper soil disturbance. The more consistent volume of soil disturbed by pigs during their digging behaviours may also indicate a giving-up density relating to energetic cost and/or accessibility of food resources (Nolet *et al.* 2006).

Based on median values for area and volume of soil disturbed by feral pig digging, feral pigs disturb ~0.2% (15.2 km^2) of the forest landscape represented by the four main vegetation complexes (i.e. Yarragil, Murray, Dwellingup and Swamp). This equates to ~12.89 million tonnes of soil (5.07, 37.46; 95% CI) in the northern jarrah forest every year (based on an average weight of 1.25 tonnes m^{-3} of gravel and loam soil). With an estimated feral pig abundance of 8541 in the four main vegetation complexes of the northern jarrah forest, an 'average' feral pig is calculated to be responsible for disturbing 1207.1 m^3 (1508.9 tonnes) of soil every 12 months. This equates to 52.7 tonnes of soil per kilogram of body mass (based on an average pig weight of 28.6 ± 18.4 kg for juvenile and adult feral pigs >10 kg trapped in northern jarrah forest ($n = 266$); P. J. Adams, unpubl. data). This is >2.5 times more soil disturbed per kilogram of bodyweight than that reported for northern hairy-nosed wombat (*Lasiorhinus krefftii*; Löffler and Margules 1980), or greater bilbies (*Macrotis lagotis*) and boodies (*Bettongia lesueur*) (Newell 2008), which create foraging pits and extensive burrow complexes, and are regarded as the most accomplished native mammal biopedturbators in Australia (Fleming *et al.* 2014). Indeed, the estimated annual feral pig soil disturbance in the northern jarrah forest (12.89 million tonnes) is more directly comparable to the annual output, in tonnes of ore processed, of a commercial open-cut bauxite mining operation in the same region (Geoscience Australia 2014).

Conclusion

In Australia, where the soils are amongst some of the most nutrient-poor in the world, the role of native digging species contributing to soil productivity, water infiltration and nutrient cycling is extremely important (Fleming *et al.* 2014). These diggings typically increase landscape heterogeneity (Davidson and Lightfoot 2008), by affecting soil texture, structure, bulk density, mixing, erosion and surface runoff (Whitford and Kay 1999). Digging mammals also manipulate the surface and subsurface soil, which affects resource availability and ecosystem health, and contributes to both soil and water quality (Martin 2003). However, the characteristics of feral pig diggings are typically divergent from those of smaller foraging mammals (Kotanen 1995; Welander 2000), and it is unknown, though highly unlikely, whether they are capable of replicating or replacing these bioengineering functions. Numerous studies investigating the impact of feral pig digging activities in forest habitats have reported extensive damage to ecosystem processes and invariably a resultant decrease in native vegetation, as well as an increase in exotic plants and weed colonisation (see Campbell and Long 2009 for a review of feral pig digging impacts). Additionally, digging and soil disturbance by feral pigs can also increase soil erosion, leading to elevated water turbidity (Doupé *et al.* 2009), as well as increased leaching of soil nutrients from leaf litter and upper soil horizons (Singer *et al.* 1984). As such, the substantial level of soil disturbance caused by feral pig digging in the northern jarrah forest is likely to have a significant impact on sustainable ecosystem function and biodiversity conservation.

The present study has demonstrated the resilience of feral pig populations to current population management practices. These findings demonstrate the importance of understanding the relative abundance and impact(s) of a target species when attempting to implement control or management programs. Monitoring before and after the implementation of feral pig population management is required to derive any conclusions about the efficacy of such practices. In the present study, we determined that current practice was insufficient to cause a measurable decrease in feral pig population density at the landscape level. In addition, the influence of environmental conditions on feral pig densities, particularly increased temperatures and reduced rainfall (a scenario in the northern jarrah forest that is predicted to increase in frequency with climate change (Matusick *et al.* 2013)), may present opportunities for increasing the efficacy of feral pig management actions.

Conflicts of interest

The authors declare no conflicts of interest.

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References

Akaike, H. (1973). Information theory as an extension of the maximum likelihood principle. In 'Second International Symposium on Information Theory, Tsahkadsor, Armenia, USSR, 2–8 September 1971'. (Eds B. N. Petrov and F. Csaki.) pp. 267–281. (Akademiai Kiado: Budapest, Hungary.)

Bengsen, A. J., Gentle, M. N., Mitchell, J. L., Pearson, H. E., and Saunders, G. R. (2014). Impacts and management of wild pigs *Sus scrofa* in Australia. *Mammal Review* **44**, 135–147. doi:10.1111/mam.12011

Bowman, D., and McDonough, L. (1991). Feral pig (*Sus scrofa*) rooting in a monsoon forest-wetland transition, northern Australia. *Wildlife Research* **18**, 761–765. doi:10.1071/WR9910761

Bowman, D., and Panton, W. (1991). Sign and habitat impact of banteng (*Bos javanicus*) and pig (*Sus scrofa*), Cobourg Peninsula, northern Australia. *Australian Journal of Ecology* **16**, 15–17. doi:10.1111/j.1442-9993.1991.tb01477.x

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., and Thomas, L. (2001). 'Introduction to Distance Sampling: Estimating Abundance of Biological Populations.' (Oxford University Press: New York.)

Bureau of Meteorology (2011). Perth in 2010: one of the hottest and driest years on record. In 'Annual Climate Summary for Perth'. (Bureau of Meteorology: Canberra.) Available at http://www.bom.gov.au/climate/current/annual/wa/archive/2010.perth.shtml

Burnham, K. P., and Anderson, D. R. (1998). 'Model Selection and Inference, a Practical Information-theoretic Approach.' (Springer-Verlag: New York.)

Caley, P. (1993). Population dynamics of feral pigs (*Sus scrofa*) in a tropical riverine habitat complex. *Wildlife Research* **20**, 625–636. doi:10.1071/WR9930625

Campbell, T. A., and Long, D. B. (2009). Feral swine damage and damage management in forested ecosystems. *Forest Ecology and Management* **257**, 2319–2326. doi:10.1016/j.foreco.2009.03.036

Caughley, G. (1977). 'Analysis of Vertebrate Populations.' (Wiley: London.)

Choquenot, D. (1998). Testing the relative influence of instrinsic and extrinsic variation in food availability on feral pig populations in Australia's rangelands. *Journal of Animal Ecology* **67**, 887–907. doi:10.1046/j.1365-2656.1998.6760887.x

Choquenot, D., McIlroy, J. C., and Korn, T. (1996). 'Managing Vertebrate Pests: Feral Pigs.' (Australian Government Publishing Service: Canberra.)

Davidson, A. D., and Lightfoot, D. C. (2008). Burrowing rodents increase landscape heterogeneity in a desert grassland. *Journal of Arid Environments* **72**, 1133–1145. doi:10.1016/j.jaridenv.2007.12.015

Doupé, R. G., Mitchell, J., Knott, M. J., Davis, A. M., and Lymbery, A. J. (2009). Efficacy of exclusion fencing to protect ephemeral floodplain lagoon habitats from feral pigs (*Sus scrofa*). *Wetlands Ecology and Management* **18**, 69–78.

Elledge, A. E., McAlpine, C. A., Murray, P. J., and Gordon, I. J. (2013). Modelling habitat preferences of feral pigs for rooting in lowland rainforest. *Biological Invasions* **15**, 1523–1535. doi:10.1007/s10530-012-0387-6

Fernández-Llario, P., and Carranza, J. (2000). Reproductive performance of the wild boar in a Mediterranean ecosystem under drought conditions. *Ethology Ecology and Evolution* **12**, 335–343. doi:10.1080/08927014.2000.9522791

Fleming, P. A., Anderson, H., Prendergast, A. S., Bretz, M. R., Valentine, L. E., and Hardy, G. E. S. (2014). Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function? *Mammal Review* **44**, 94–108. doi:10.1111/mam.12014

Fordham, D., Georges, A., Corey, B., and Brook, B. W. (2006). Feral pig predation threatens the indigenous harvest and local persistence of snake-necked turtles in northern Australia. *Biological Conservation* **133**, 379–388. doi:10.1016/j.biocon.2006.07.001

Geoscience Australia (2014). 'Australia's Identified Mineral Resources 2013.' (Geoscience Australia: Canberra.)

Gong, W., Sinden, J., Braysher, M., and Jones, R. (2009). 'The Economic Impacts of Vertebrate Pests in Australia.' (Invasive Animals Cooperative Research Centre: Canberra.)

Hampton, J., Spencer, P., Elliot, A., and Thompson, R. C. (2006). Prevalence of zoonotic pathogens from feral pigs in major public drinking water catchments in Western Australia. *EcoHealth* **3**, 103–108. doi:10.1007/s10393-006-0018-8

Havel, J. J. (1975). 'Site-vegetation Mapping in the Northern Jarrah Forest (Darling Range) 1. Definition of Site-vegetation Types.' (Western Australian Forests Department: Perth.)

Hone, J. (1988). Evaluation of methods for ground survey of feral pigs and their sign. *Acta Theriologica* **33**, 451–465. doi:10.4098/AT.arch.88-38

Hone, J. (2002). Feral pigs in Namadgi National Park, Australia: dynamics, impacts and management. *Biological Conservation* **105**, 231–242. doi:10.1016/S0006-3207(01)00185-9

Hone, J. (2012). 'Applied Population and Community Ecology: The Case of Feral Pigs in Australia.' (Wiley-Blackwell: West Sussex.)

Hone, J., and Martin, W. (1998). A study of dung decay and plot size for surveying feral pigs using dung counts. *Wildlife Research* **25**, 255–260. doi:10.1071/WR97024

Irwin, M. J., Massey, P. D., Walker, B., and Durrheim, D. N. (2009). Feral pig hunting: a risk factor for human brucellosis in north-west NSW? *NSW Public Health Bulletin* **20**, 192–194. doi:10.1071/NB09023

Jay, M. T., Cooley, M., Carychao, D., Wiscomb, G. W., Sweitzer, R. A., Crawford-Miksza, L., Farrar, J. A., Lau, D. K., O'Connell, J., Millington, A., Asmundson, R. V., Atwill, E. R., and Mandrell, R. E. (2007). *Escherichia coli* O157:H7 in feral swine near spinach fields and cattle, Central California Coast. *Emerging Infectious Diseases* **13**, 1908–1911. doi:10.3201/eid1312.070763

Koch, J. M., Ward, S. C., Grant, C. D., and Ainsworth, G. L. (1996). Effects of bauxite mine restoration operations on topsoil seed reserves in the jarrah forest of Western Australia. *Restoration Ecology* **4**, 368–376. doi:10.1111/j.1526-100X.1996.tb00189.x

Kotanen, P. M. (1995). Responses of vegetation to a changing regime of disturbance: effects of feral pigs in a Californian coastal prairie. *Ecography* **18**, 190–199. doi:10.1111/j.1600-0587.1995.tb00340.x

Krull, C., Choquenot, D., Burns, B., and Stanley, M. (2013). Feral pigs in a temperate rainforest ecosystem: disturbance and ecological impacts. *Biological Invasions* **15**, 2193–2204. doi:10.1007/s10530-013-0444-9

Laing, S. E., Buckland, S. T., Burn, R. W., Lambie, D., and Amphlett, A. (2003). Dung and nest surveys: estimating decay rates. *Journal of Applied Ecology* **40**, 1102–1111. doi:10.1111/j.1365-2664.2003.00861.x

Laurance, W. F., and Harrington, G. N. (1997). Ecological associations of feeding sites of feral pigs in the Queensland wet tropics. *Wildlife Research* **24**, 579–590. doi:10.1071/WR96029

Li, A. Y., Williams, N., Fenwick, S. G., Hardy, G. E. S. J., and Adams, P. J. (2013). Potential for dissemination of *Phytophthora cinnamomi* by feral pigs via ingestion of infected plant material. *Biological Invasions* **16**, 765–774.

Löffler, E., and Margules, C. (1980). Wombats detected from space. *Remote Sensing of Environment* **9**, 47–56. doi:10.1016/0034-4257(80)90046-2

Lynes, B. C., and Campbell, S. D. (2000). Germination and viability of mesquite (*Prosopis pallida*) seed following ingestion and excretion by feral pigs (*Sus scrofa*). *Tropical Grasslands* **34**, 125–128.

Marques, F. F. C., Buckland, S. T., Goffin, D., Dixon, C. E., Borchers, D. L., Mayle, B. A., and Peace, A. J. (2001). Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. *Journal of Applied Ecology* **38**, 349–363. doi:10.1046/j.1365-2664.2001.00584.x

Martin, G. (2003). The role of small ground-foraging mammals in topsoil health and biodiversity: implications to management and restoration. *Ecological Management & Restoration* **4**, 114–119. doi:10.1046/j.1442-8903.2003.00145.x

Massei, G., Genov, P. V., and Staines, B. W. (1996). Diet, food availability and reproduction of wild boar in a Mediterranean coastal area. *Acta Theriologica* **41**, 307–320. doi:10.4098/AT.arch.96-29

Mattiske, E. M., and Havel, J. J. (1998). Regional Forest Agreement, vegetation complexes – Perth, Pinjarra, Collie, Busselton/Augusta, Pemberton, Mt Barker – Western Australia 1:250,000 maps. Department of Conservation and Land Management Western Australia, Perth, Western Australia, Australia.

Matusick, G., Ruthrof, K., Brouwers, N., Dell, B., and Hardy, G. J. (2013). Sudden forest canopy collapse corresponding with extreme drought and heat in a mediterranean-type eucalypt forest in southwestern Australia. *European Journal of Forest Research* **132**, 497–510. doi:10.1007/s10342-013-0690-5

Melzer, R. I., Twyford, K. L., Rowston, C., and Augusteyn, J. D. (2009). Pest arrest in central Queensland: conserving biodiversity through pest management. *Australasian Journal of Environmental Management* **16**, 227–235. doi:10.1080/14486563.2009.9725238

Mitchell, J., and Mayer, R. (1997). Diggings by feral pigs within the Wet Tropics World Heritage Area of north Queensland. *Wildlife Research* **24**, 591–601. doi:10.1071/WR96041

Mitchell, J., Dorney, W., Mayer, R., and McIlroy, J. (2007). Spatial and temporal patterns of feral pig diggings in rainforests of north Queensland. *Wildlife Research* **34**, 597–602. doi:10.1071/WR06064

Newell, J. (2008). The role of reintroduction of greater bilbies (*Macrotis lagotis*) and burrowing bettongs (*Bettongia lesueur*) in the ecological restoration of an arid ecosystem: foraging diggings, diet, and soil seed banks. PhD Thesis, University of Adelaide, Adelaide.

Nichols, O. G., Carbon, B. A., Colquhoun, I. J., Croton, J. T., and Murray, N. J. (1985). Rehabilitation after bauxite mining in south-western Australia. *Landscape Planning* **12**, 75–92. doi:10.1016/0304-3924(85)90071-1

Nolet, B. A., Fuld, V. N., and Van Rijswijk, M. E. (2006). Foraging costs and accessibility as determinants of giving-up densities in a swan–pondweed system. *Oikos* **112**, 353–362. doi:10.1111/j.0030-1299.2006.13463.x

Rivero, K., Rumiz, D. I., and Taber, A. B. (2004). Estimating brocket deer (*Mazama gouazoubira* and *M. americana*) abundance by dung pellet counts and other indices in seasonal Chiquitano forest habitats of Santa Cruz, Bolivia. *European Journal of Wildlife Research* **50**, 161–167. doi:10.1007/s10344-004-0064-x

Ruggiero, R. G. (1992). Seasonal forage utilization by elephants in central Africa. *African Journal of Ecology* **30**, 137–148. doi:10.1111/j.1365-2028.1992.tb00487.x

Saunders, G. (1993). The demography of feral pigs (*Sus scrofa*) in Kosciusko National Park, New South Wales. *Wildlife Research* **20**, 559–569. doi:10.1071/WR9930559

Schaffer, J., Doupé, R. G., and Lawler, I. R. (2009). What for the future of the Jardine River Painted Turtle? *Pacific Conservation Biology* **15**, 92–95. doi:10.1071/PC090092

Singer, F. J., Swank, W. T., and Clebsch, E. C. (1984). Effects of wild pig rooting in a deciduous forest. *The Journal of Wildlife Management* **48**, 464–473. doi:10.2307/3801179

Spencer, P. B. S., and Hampton, J. O. (2005). Illegal translocation and genetic structure of feral pigs in Western Australia. *The Journal of Wildlife Management* **69**, 377–384. doi:10.2193/0022-541X(2005)069<0377:ITAGSO>2.0.CO;2

Todd, A. F., Kuehl, H. S., Cipolletta, C., and Walsh, P. D. (2008). Using dung to estimate gorilla density: modeling dung production rate. *International Journal of Primatology* **29**, 549–563. doi:10.1007/s10764-008-9247-8

Waithman, J. D., Sweitzer, R. A., Vuren, D. V., Drew, J. D., Brinkhaus, A. J., Gardner, I. A., and Boyce, W. M. (1999). Range expansion, population sizes, and management of wild pigs in California. *The Journal of Wildlife Management* **63**, 298–308. doi:10.2307/3802513

Walsh, P. D., White, L. J. T., Mbina, C., Idiata, D., Mihindou, Y., Maisels, F., and Thibault, M. (2001). Estimates of forest elephant abundance: projecting the relationship between precision and effort. *Journal of Applied Ecology* **38**, 217–228. doi:10.1046/j.1365-2664.2001.00578.x

Webber, B. L., Norton, B. A., and Woodrow, I. E. (2010). Disturbance affects spatial patterning and stand structure of a tropical rainforest tree. *Austral Ecology* **35**, 423–434. doi:10.1111/j.1442-9993.2009.02054.x

Welander, J. (2000). Spatial and temporal dynamics of wild boar (*Sus scrofa*) rooting in a mosaic landscape. *Journal of Zoology* **252**, 263–271. doi:10.1111/j.1469-7998.2000.tb00621.x

White, L. J. T. (1995). Factors affecting the duration of elephant dung piles in rain forest in the Lopé Reserve, Gabon. *African Journal of Ecology* **33**, 142–150. doi:10.1111/j.1365-2028.1995.tb00789.x

Whitford, W. G., and Kay, F. R. (1999). Biopedturbation by mammals in deserts: a review. *Journal of Arid Environments* **41**, 203–230. doi:10.1006/jare.1998.0482

Whytlaw, P. A., Edwards, W., and Congdon, B. C. (2013). Marine turtle nest depredation by feral pigs (*Sus scrofa*) on the Western Cape York Peninsula, Australia: implications for management. *Wildlife Research* **40**, 377–384. doi:10.1071/WR12198