

Factors influencing the activity ranges of feral pigs (*Sus scrofa*) across four sites in eastern Australia

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ABSTRACT

Context. Understanding the home-range size and the ecological drivers that influence the spatial distribution of feral pigs is of paramount importance for exotic-disease modelling and the improvement of pest management programs. **Aims.** To investigate various factors affecting home- and core-range size and test selection of habitat, to better inform disease modelling and pest management programs. **Methods.** In this study, 59 GPS-collared feral pigs were tracked over four sites in eastern Australia between 2017 and 2021. Using minimum convex polygon (MCP) and the nearest-neighbour–local convex hull (k-LoCoH) as home-range estimators and foliage projective cover (FPC) as an estimator of landscape-scale shelter, we investigated the influence of sex, site, season, year and body weight on range size and tested selection of habitat by using chi-squared and Jacob's index tests. **Key results.** Home-range sizes were highly variable, with k-LoCoH90 (home) ranges between 0.08 and 54.97 km² and k-LoCoH50 (core) ranges between 0.01 and 7.02 km². MCP90 ranged between 0.15 and 242.30 km², with MCP50 being between 0.07 and 60.61 km². Sex and site both significantly ($P < 0.001$) influenced home-range size, but season and year did not. Home-range size was shown to increase with body mass for both sexes ($P = 0.001$). Importantly, the data indicated that feral pigs prefer habitat within 20–40% FPC (woodland), whereas open forests (51–80% FPC) and closed forests (>80% FPC) were actively avoided. Typically, use of open vegetation (1–10% FPC) was also avoided, but this behaviour varied and was dependent on site. **Conclusion.** Feral pig ranges are influenced by sex, site and body mass but not by season and year. Broad-scale selection for shelter indicated that feral pigs prefer habitat between 20% and 40% FPC. **Implications.** Targeting or avoiding such areas respectively for control or monitoring tool placement may result in improved, efficient outcomes to monitor or manage feral pig populations. Feral pig distribution modelling may also find benefit in the consideration and further study of the above factors and the influence of food and water sources on the activity ranges and behaviour of feral pigs.

Keywords: activity range, African swine fever, core range, disease modelling, feral pig, foliage projective cover, habitat selection, home range, k-LoCoH, MCP, pest management.

Introduction

Feral pigs (*Sus scrofa*) are a significant vertebrate pest, both in Australia and around the world. Despite control efforts, the distribution of feral pigs in Australia continues to expand through either natural dispersal (Saunders and McLeod 1999; Hone 2002; Cowled *et al.* 2009) or through anthropogenic means (Spencer and Hampton 2005). Their habits and distribution translate to wide-ranging impacts to the environment, agricultural economy and to human health. Feral pigs can damage important ecosystems through the dispersal of invasive plants (Lynes and Campbell 2000; Setter *et al.* 2002), the destruction of wetland habitats and water quality (Mitchell 2010), the predation on and/or competition with native animals (Fordham *et al.* 2006) and through the disruption of native plant establishment and dispersal (Hone 2002; Mitchell *et al.* 2007; Webber *et al.* 2010; Taylor *et al.* 2011). Feral pigs have been demonstrated to predate

on young lambs (Pavlov *et al.* 1981; Choquenot *et al.* 1997) and selectively feed on crop species (Gentle *et al.* 2015), potentially resulting in significant economic impacts (Bradhurst *et al.* 2015). Feral pigs are also hosts for a variety of diseases, both zoonotic (Eales *et al.* 2010) and non-zoonotic (Ward *et al.* 2007; Chenais *et al.* 2019), which may result in human health concerns (Massey *et al.* 2011).

The recent outbreak of African swine fever (ASF) throughout Eurasia has resulted in severe economic losses (World Organisation for Animal Health 2021). An incursion of the disease in Australia could cost upwards of AUD\$2 billion (ACIL Allen Consulting 2019). Despite strong biosecurity legislation and stakeholder awareness, there remains a considerable risk of wild pig populations complicating disease eradications by acting as viral reservoirs and spreading disease through both direct and indirect contact with domestic populations (Guinat *et al.* 2016; Miller *et al.* 2017; Podgórski *et al.* 2018; VanderWaal and Deen 2018; VerCauteren *et al.* 2018; Bradhurst *et al.* 2021; Animal Health Australia 2022). As a result, it is imperative that government and industry gain an improved understanding of the feral pig-related aspects of ASF disease ecology in Australia to support ASF preparedness and response strategies.

Epidemiological modelling is a useful tool for understanding the influence of different factors on the dynamics of a pathogen, and the potential effect of various prevention or management interventions on transmission, infection patterns and persistence in animal populations (Garner and Beckett 2005; Garner *et al.* 2007; Harvey *et al.* 2007). This approach is particularly useful for formulating preparation and policy guidelines for rare or exotic diseases where field data are limited (Bradhurst *et al.* 2021). The Australian animal disease spread (AADIS) modelling framework simulates the spread and control of emergency animal diseases (EADs) such as ASF (Bradhurst *et al.* 2021) and incorporates aspects of and interactions between domestic and feral pig populations. The AADIS-ASF model has been adapted to local conditions considering key disease parameters from international ASF outbreaks and a range of ecological data from Australian and international wild pig populations. The current iteration uses measures based on the movement of female pigs (sounders), but separate parameters for modelling males may be required where substantially different. Understanding the geospatial and ecological drivers that influence feral pig populations is a critical factor in modelling disease spread (Cowled and Garner 2008) and model refinement using field-based data will improve the accuracy and precision of model output. These drivers incorporate the distribution, density, movement, social and age structure of feral pig populations as well as the productivity of suitable habitat, climatic effects and the presence of alternate hosts (Pech and McIlroy 1990; Caley 1993; Choquenot *et al.* 1996; Kern *et al.* 1999; McCallum *et al.* 2001; Morgan *et al.* 2006; Cowled and Garner 2008).

However, suitable distribution and movement data from Australian feral pig populations is currently limited. While there have been studies assessing movement ecology in Australian feral pig populations (Saunders and Kay 1991; Saunders and Kay 1996; Caley 1997; Dexter 1999; Mitchell *et al.* 2009), the more recent availability and improvements in GPS technology provide a far greater quantity of high-quality data. This technology provides the means to more accurately quantify ranging behaviour (e.g. daily and/or seasonal home range and movements across a range of environments) and examine the factors that may influence such movements. There is also very little data examining the fine-scale habitat use of feral pig distributions across Australia and the geospatial relationships between key habitat types and/or focal points (e.g. water sources) to assist modellers to better predict connectivity of pig populations (Cowled and Garner 2008).

In addition to informing disease preparedness, spatial modelling data support wider feral pig management decision-making. Effective control of vertebrate pests to mitigate their impacts requires a strategic, integrated approach that considers the ecology of the targeted species. The refinement of pest management strategies through the application of ecological intelligence could significantly improve existing feral pig control methods (Nogueira *et al.* 2007), resulting in more efficient and effective mitigation of impacts. Maximising control tool encounter rates, by identifying and targeting focal sites with a high probability of pig use, may increase effectiveness but with concomitant reduction in effort and cost (Recio *et al.* 2017). Understanding how these focal sites are affected by various biological or environmental factors could enable even greater refinement of control strategies.

It is currently understood that the home range of female feral pigs is negatively correlated with landscape productivity (Dexter 1999; Clontz *et al.* 2022), whereas male pigs maintain ranges that maximise access to breeding females (Dexter 1999). As such, male ranges are typically larger than female ranges (Saunders and Kay 1991; Saunders and Kay 1996; Caley 1997; Dexter 1999; Mitchell 2002), although there are exceptions (e.g. Mitchell *et al.* (2009)). Home range of pigs may also be influenced by body weight (Saunders and McLeod 1999) and climatic conditions (Baber and Coblenz 1986; Hone 1987; Mitchell *et al.* 2009), with various environmental factors influencing behaviour. Garza *et al.* (2018) found that mammal species richness was positively correlated with feral pig home-range size, although this, in turn, may be linked to other environmental factors such as latitude and elevation (Garza *et al.* 2018) and may be more relevant to overseas environs.

Habitat selection has long been recognised as a useful tool in wildlife science (Neu *et al.* 1974). Feral pig habitat selection (preference/avoidance) in Australia has been examined using empirical field data (Saunders and Kay 1991; Caley 1997; Dexter 1999) and, more recently, Bayesian network

modelling of expert knowledge has been applied to identify habitat suitability for feral pigs (Froese *et al.* 2017). However, these approaches could be refined given their reliance on site-specific assessments or expert knowledge, which may not be transferable to other areas. Foliage projective cover (FPC) is a quantitative measure of canopy cover density that is correlated with protection from heat and possibly disturbance. Because pigs lack sweat glands, they are restricted to shadier habitats during hot weather (Dexter 1999); thus, habitats with higher FPC values may be preferred. FPC can be quantified in all habitat types, allowing for comparison across sites, reducing potential errors from variable classification and nomenclature of landscape types. The application of FPC as a proxy for habitat type and as a measure of landscape-based shelter may allow for a higher accuracy in determining habitat preference and may indicate areas of higher use within the landscape.

Quantifying key parameters for feral pig spatial ecology is critical for applications of spatial modelling, disease modelling or management, and to inform future research on both broad-scale and fine-scale habitat preference. A deeper understanding of the factors that influence feral pig ranging behaviour and activity levels may also allow for modellers or practitioners to tailor pig management strategies that consider temporal, environmental or biological factors. Using GPS location data, this research quantifies the site, and seasonal and annual home range of feral pigs across four study areas in eastern Australia. Key factors influencing home-range size, specifically sex, site, season, year, bodyweight and habitat selection, are examined and the implications for management and future research are discussed.

Methods

Data collection

Data were collected from 59 feral pigs collared at four sites in eastern Australia, namely, Arcadia Valley, Downfall Creek, Gebar Island (Queensland) and Palerang (New South Wales), between 2017 and 2021. Details of pigs across all sites is displayed in Supplementary material Table S1. Feral pigs were captured through a combination of box, panel or corral traps, with a pre-feeding period of approximately 7–10 days or until an asymptote of feed consumption was achieved. Wheat (dry or fermented) was used as a lure, with the occasional additive (molasses or carasweet). Captured pigs were sedated with an intramuscular injection of Zoletil (Virbac Australia Pty Ltd, Milperra, NSW, Australia) at a dosage rate of 1 mg kg⁻¹. Pigs were collared with Lotek Iridiumtrack Heavy Duty 3D collars (Lotek, Ontario, Canada), programmed to take a fix every 30 min and all data were remotely downloaded via their online portal. Animal ethics permits were approved by the University of New England (AEC 16-115 and AEC 20-023).

Study sites

Arcadia Valley is an ~15 km wide valley stretching between Carnarvon and Expedition National Parks, in the Central Highlands region of Queensland (Fig. 1). Land use is predominately free-range cattle grazing with scattered small-scale feedlots. Our study site extended over 960 km² of open grassland with small pockets of eucalyptus woodland. It has a subtropical climate (Bureau of Meteorology 2022a), with mean annual rainfall of 635.8 mm (Bureau of Meteorology 2022e).

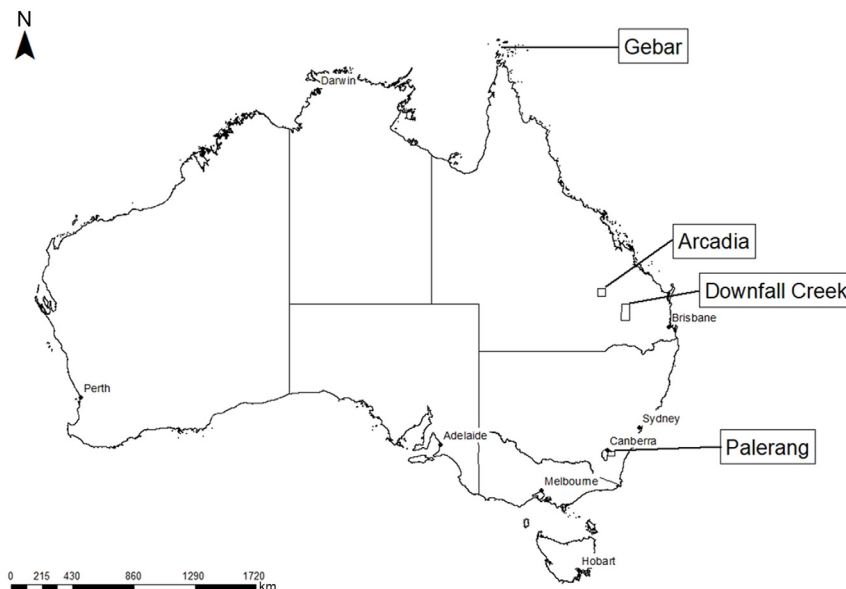


Fig. 1. Map of Australia identifying study sites.

Downfall Creek was our study site in the Western Downs region of Queensland, covering an area of ~1380 km² from Wandoan to Miles, bordering the Barakula State Forest. This study site is used for natural gas extraction and cattle production. Downfall Creek consists of mostly eucalypt medium woodland or open grassland, experiences a subtropical climate (Bureau of Meteorology 2022a) and a mean annual rainfall of 643.4 mm (Bureau of Meteorology 2022d).

Gebar Island is a small (~4.2 km²) uninhabited island in the Torres Strait, Queensland, that is owned by the Gebaralgal (Torres Strait Islanders) Corporation (National Native Title Tribunal 2004). It is a tropical island with an equatorial climate (Bureau of Meteorology 2022a), with the nearby Coconut Island receiving a mean annual rainfall of 1441.7 mm (Bureau of Meteorology 2022b).

Palerang is a locality in southern New South Wales, east of Canberra. Our study site (~777 km²) consisted mostly of open grassland interspersed with open eucalypt forests and the site is mostly used for livestock production. This area of Australia experiences a temperate climate (Bureau of Meteorology 2022a) and a mean annual rainfall of 624.4 mm (Canberra) (Bureau of Meteorology 2022c).

Collar-accuracy test

To determine a protocol for identifying and removing inaccurate points, 13 locations of deceased pigs were investigated. These locations were typified by large clusters of points in close proximity to one another because of variations in recorded locations prior to the collar being retrieved. The mean location across all points at each site was considered as the 'true' location of each deceased pig. We defined all points less than or equal to 20 m away from this location as being accurate, because this distance is unlikely to change the habitat type where the pig is present at, at that time. All points greater than 20 m away were investigated for their potential cause of error. A comparison of filtering on direct quality indicators [i.e. Bjørneraas non-movement model; Bjørneraas *et al.* (2010)] and indirect quality indicators [i.e. dilution of precision (DOP) values following Fancourt *et al.* (2021)] was investigated. Where the Bjørneraas model identifies and removes unrealistic 'spikes' in the data (Bjørneraas *et al.* 2010), the DOP value is the measure of satellite configuration relative to the GPS collar at the time of location fix (D'eon and Delparte 2005) and is often used as an indicator of accuracy (owing to the ease of obtaining a value) with varying success (Ironsides *et al.* 2017). As supporting parameters of the Bjørneraas model (i.e. speed and turning angles) were not available for feral pigs, we used the 90th percentile threshold as a substitute, as recommended by Gupte *et al.* (2022). By comparing the Bjørneraas model and various DOP values to the points generated from the stationary pigs in this project, we determined a procedure for cleansing data of inaccurate

points (>20 m), beyond which datapoint accuracy was unreliable for the purposes of our research questions.

Data cleaning

To ensure acclimatisation of animals to the collars, only locations recorded after 2 days following collar attachment were examined further. To clean the dataset of inaccurate points, all failed points (those with a zero in latitude or longitude) were deleted. All points considered 'inaccurate' through the collar-accuracy test were also deleted. Finally, a visual inspection of the remaining points on ArcMap[®] was conducted to identify and remove points that were erroneous or obvious outliers (e.g. 3 km out to sea), or not biologically plausible (e.g. 28 km movement outside their range between successive points in 30 min).

Home/core range

To represent the home range, or area utilised by each animal for normal foraging activities (Burt 1943), two methods were chosen, the minimum convex polygon (MCP) and the nearest-neighbour-local convex hull (k-LoCoH). The MCP method is a simple and practical method but has poor resolution to the true home range of the targeted species (Burgman and Fox 2003; Getz and Wilmers 2004; Wilson 2020). However, its wide usage allows for uniformity in comparisons with other studies. The nearest-neighbour local convex hull (k-LoCoH) is a more refined estimator than are other methods (Getz and Wilmers 2004) and has been shown to demonstrate low error rates with high conformity to utilised landscape features (Wilson 2020). The 90% isopleth was chosen to represent the home range, because of an increase in bias in higher isopleths (Börger *et al.* 2006). Similarly, because accuracy declines below the 50% isopleth (Börger *et al.* 2006), this value was chosen to represent the core range. The core range represents the highest density of points within the smallest area, thereby highlighting key areas of high activity (Edwards *et al.* 2001; Wilson 2020). Pigs were excluded from the analysis if they had less than 160 observations (four fixes/day over 40 days), so as to ensure sufficient sampling for convergence with the true extent of the home range (Leo *et al.* 2016). For seasonal range changes, only animals that had more than 28 observations (four fixes/day over 7 days) were used to present an indication of range size over that period.

Minimum convex polygon

MCP areas for each pig were estimated for the 50% and 90% isopleths by using the adehabitatHR package (Calenge 2006) in R (v. 4.0.5; see <https://cran.r-project.org/>). Four fixes per day (0200; 0800; 1400; 2000) were used in home range and core ranges analyses to avoid the influence of spatial autocorrelation. This temporal range of fixes allows a regular

array of locations spanning night, morning, afternoon and evening. Home ranges were estimated for the entire monitored period (overall), each year (annual) and each season (autumn, winter, spring or summer). Calculated MCP values are displayed with pig details in Table S1.

Nearest-neighbour-local convex hull

The nearest-neighbour-local convex hull (k-LoCoH) areas for each pig were estimated for the 50% and 90% isopleths by using the `adehabitatHR` package (Calenge 2006) in R (v. 4.0.5). As with the MCP, only four fixes per day were used and ranges were estimated overall, annually and seasonally to test for changes. The default parameter of the square root of the number of points was used, but where polygon errors (e.g. orphaned holes, etc.) caused the script to fail, a value of at least five was added to the parameter value (k). This parameter influences the number of neighbouring locations each point is associated with for the creation of hulls (Getz and Wilmers 2004). Adjusting the k -value is akin to the 'minimum spurious hole covering' rule in Getz and Wilmers (2004). The utilised k -value was recorded with the estimated area and is displayed with pig details in Table S1.

Home- and core-range statistics

All range estimations were log-transformed (\log_{10}) to conform to normality prior to analysis. A Student's unpaired t -test was conducted in R (v. 4.0.5) to compare overall range sizes between male and female pigs (Zar 2014). An ANOVA was conducted to determine whether range size varied by study site, season and year (Zar 2014). A linear regression model was used to determine the significance of body mass in influencing the activity range of feral pigs (Zar 2014). Both the dependent (activity range) and independent variables (mass) were log-transformed to conform to normality. All statistical tests were calculated through the 'stats' package (R Core Team 2021) or 'car' package (Fox and Weisberg 2019) in R (R Core Team 2021).

Habitat preference

Foliage projective cover data were chosen to represent landscape-scale shelter for feral pigs. For the three Queensland sites, FPC data (raster with 30 m resolution) was downloaded from the Long Paddock website (The State of Queensland 2021). For Palerang (New South Wales), FPC data (raster with 25 m resolution) was accessed through the Department of Planning, Industry and Environment (NSW Government 2021). To calculate the habitat available to each pig, the MCP100 was calculated for each pig to encompass the entire landscape used. The original FPC raster layer was cropped to the MCP100 range for each pig and converted to an ESRI shapefile by using R packages 'raster' (Hijmans 2021), 'rgdal' (Bivand *et al.* 2021), 'sp' (Pebesma and Bivand 2005) and 'sf'

(Pebesma 2018). According to their percentage foliage cover, individual attributes were grouped into FPC ranges with increments of 10% and the total area within each FPC group was calculated to provide a proportion of each FPC group within the pig's home range. These proportions were then used to estimate the expected proportion of GPS points per FPC group. Observed points per group were calculated through an intersection tool ('`sp::over`') in R (Pebesma and Bivand 2005). Points that fell within an area of 'no data' (i.e. in an area of no recorded data or a waterbody) were removed from the analysis. Following McDonald (2014), FPC ranges with an expected value of less than five were also removed from the analysis.

To investigate preference, proportional use or avoidance of habitat, the observed and expected proportions of points within each FPC range were compared through the chi-squared goodness-of-fit (GOF) test (following Saunders and Kay (1991) and Fernanda Cuevas *et al.* (2013) and the Jacob's index (Jacobs 1974; as per Moseby *et al.* 2021). Using a Dunn-Sidak corrected α -value of 0.00087, a chi-squared test was estimated using the '`stats::chisq.test`' function in R (R Core Team 2021). The median residual per FPC range was used to avoid the skewing of averages by extreme values and each residual was inspected for preferential use. Any residual greater than two was considered as 'preference', less than negative two as 'avoidance' and between two and negative two as 'proportional'. All pigs that demonstrated an insignificance in the chi-squared test were also removed from the Jacob's index test and for further uniformity, the median Jacob's index (JI) per FPC range was also calculated. To distinguish among strong, normal and weak selection, the JI output was classified as being 'strong preference' (≥ 0.75), 'preference' (≥ 0.45 and < 0.75), 'weak preference' (≥ 0.15 and < 0.45), 'used in proportion' (> -0.15 and < 0.15), 'weak avoidance' (≤ -0.15 and > -0.45), 'avoidance' (≤ -0.45 and > -0.75) and 'strong avoidance' (≤ -0.75). Pigs may demonstrate preferential selection or avoidance for more than one FPC range.

Results

Collar-accuracy test

The Bjørneraas non-movement model (Bjørneraas *et al.* 2010) and DOP values (D'eon and Delparte 2005) were investigated as potential means of cleaning data of inaccurate points. Using the 90th percentile threshold for speed and turning angle (Gupte *et al.* 2022), the Bjørneraas model removed fewer accurate points than did $DOP \geq 5$, but removed just 8.6% of inaccurate points (compared to 51.7% of inaccurate points by $DOP \geq 5$), resulting in a dataset with a lower proportion of accurate points (see Table 1). Higher removal of inaccurate points was possible with a lower DOP value but with the corresponding sacrifice of too many accurate

Table 1. Results of the collar-accuracy test from 13 collars.

Parameter	Inaccurate points remaining (n)	Accurate points remaining (n)	Total points remaining (n)	Proportion of inaccurate points (%)	Proportion of accurate points (%)
HDOP ≥ 2	2	3053	3055	0.07	99.93
HDOP ≥ 3	12	8225	8237	0.15	99.85
HDOP ≥ 4	21	10 177	10 198	0.21	99.79
HDOP ≥ 5	28	11 009	11 037	0.25	99.75
HDOP ≥ 6	45	11 377	11 422	0.39	99.61
HDOP ≥ 7	47	11 537	11 584	0.41	99.59
HDOP ≥ 8	52	11 624	11 676	0.45	99.55
HDOP ≥ 9	55	11 665	11 720	0.47	99.53
Bjørneraas	53	11 612	11 665	0.45	99.55
Total points	58	11 706	11 764	0.49	99.51

Inaccurate points were defined as those >20 m from the centre point of the cluster. Accurate points were those points ≤ 20 m from the centre point.

points (DOP ≥ 5 retained 94% of accurate points). We thus used the DOP ≥ 5 as an acceptable proxy of locational error, resulting in a final dataset that contained 99.75% accurate points.

Home range size

The mean male and female home- and core ranges are displayed in Table 2.

The mean Arcadia home ranges for both sexes (pooled) were $>17\%$ larger than in any other site, while their core ranges were marginally smaller than those at Downfall Creek. Feral pigs at the Palerang site had considerably smaller home and core ranges than did pigs at located at both Arcadia or Downfall Creek. Pigs on Gebar Island had by far the smallest home and core ranges. Study site was the most important factor affecting home- and core-range sizes (all methods: $P = <0.001$). We also found a statistically significant difference in range size between sexes (MCP90, MCP50, k-LoCoH90: $P = <0.001$), with the exception of k-LoCoH50

($P = 0.07$), although the interaction between the study site and sex was not significant for either method or isopleth ($P = >0.05$). The large standard errors also indicate a large variation in the size of the ranges across the sample.

Home ranges by body mass (kg)

Linear regressions of log-transformed mass to log-transformed activity range (Fig. 2) for both 90% and 50% range isopleths showed a positive association. The most significant relationship was demonstrated by the MCP90 ($n = 25$, $r^2 = 0.36$, $P = 0.001$) for female pigs and ($n = 34$, $r^2 = 0.25$, $P = 0.001$) for male pigs. The least significant relationship was demonstrated by k-LoCoH50, which demonstrated gentler slopes and weaker r^2 -values. The k-LoCoH50 demonstrated $y = -6.06 + 3.17x$ ($n = 25$, $r^2 = 0.18$, $P = 0.02$) for female pigs and $y = -3.11 + 1.52x$ ($n = 34$, $r^2 = 0.10$, $P = 0.04$) for male pigs. Both methods and isopleths indicated a critical point where regression lines of male and female pigs intersect. Inverse logarithms of these points indicated a

Table 2. Mean home-range (90%) and core-range (50%) estimations \pm standard error (s.e.) across all pigs and sites.

Site	Sex, sample size (n)	Mean MCP90 \pm s.e. (km ²)	Mean MCP50 \pm s.e. (km ²)	Mean k-LoCoH90 \pm s.e. (km ²)	Mean k-LoCoH50 \pm s.e. (km ²)
Arcadia	Male (17)	77.43 \pm 16.35	21.73 \pm 4.43	19.82 \pm 3.8	1.47 \pm 0.43
	Female (14)	25.92 \pm 5.13	7.09 \pm 1.30	9.45 \pm 2.31	1.01 \pm 0.34
Downfall Creek	Male (6)	59.71 \pm 24.89	20.95 \pm 7.05	14.95 \pm 2.85	1.25 \pm 0.33
	Female (5)	24.40 \pm 6.11	9.02 \pm 2.53	9.47 \pm 2.92	1.32 \pm 0.42
Gebar	Male (3)	0.96 \pm 0.45	0.66 \pm 0.49	0.19 \pm 0.01	0.024 \pm 0.002
	Female (1)	0.15	0.07	0.08	0.01
Palerang	Male (8)	22.98 \pm 6.11	8.84 \pm 2.77	5.64 \pm 1.92	0.53 \pm 0.22
	Female (5)	3.32 \pm 0.80	0.81 \pm 0.26	1.42 \pm 0.28	0.091 \pm 0.02
Two-way ANOVA		$F_{3,51} = 0.57$, $P = 0.64$	$F_{3,51} = 0.69$, $P = 0.56$	$F_{3,51} = 0.13$, $P = 0.94$	$F_{3,51} = 0.38$, $P = 0.77$

Two-way ANOVA indicate no significant interaction between sex and site on range size.

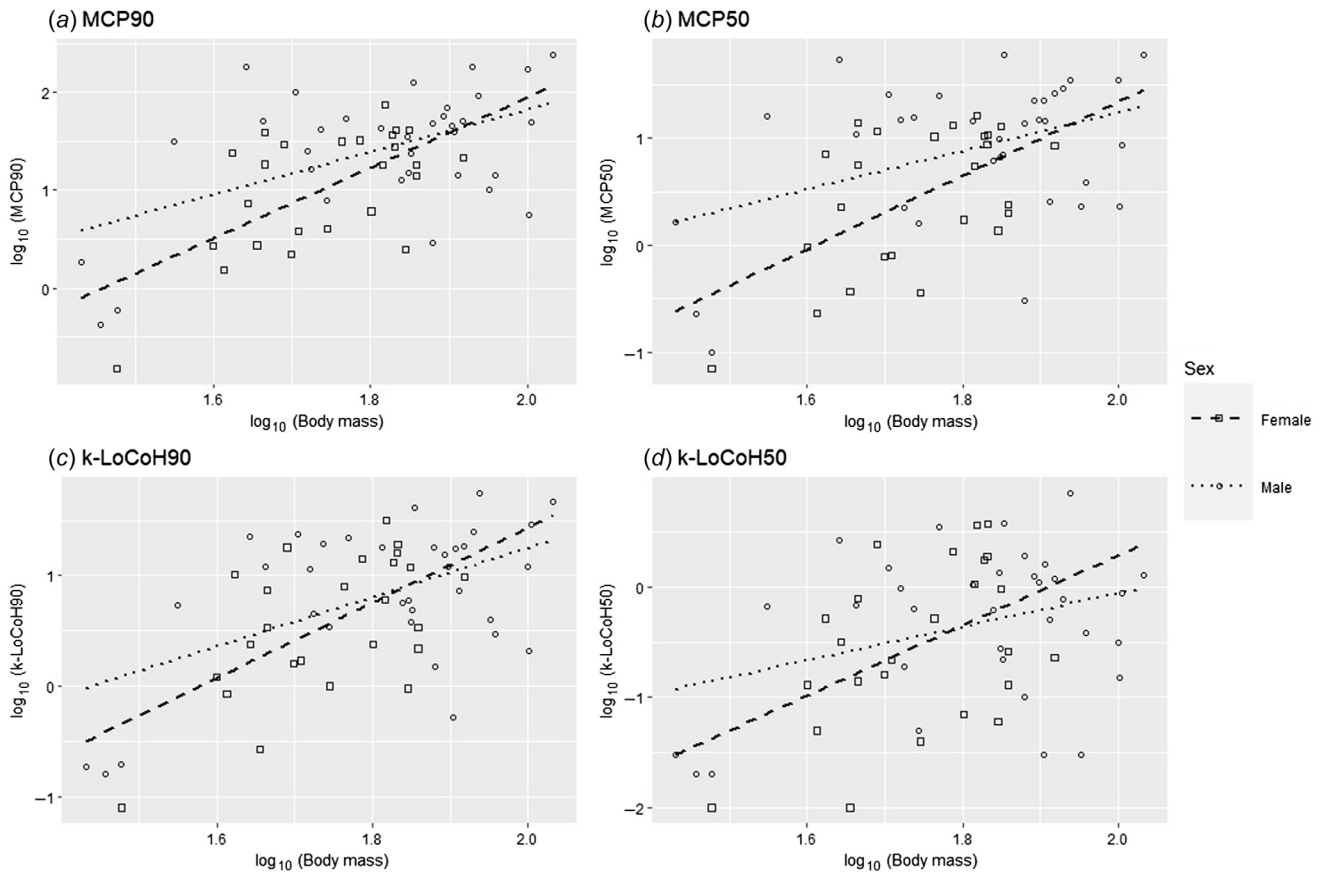


Fig. 2. Linear regressions of \log_{10} -transformed activity range to \log_{10} -transformed mass for (a) MCP90, (b) MCP50, (c) k-LoCoH90 and (d) k-LoCoH50 methods and isopleths (respectively) used in this study.

body mass of between 69 and 82 kg for home ranges and 62 and 87 kg for core ranges where female pig ranges will surpass that of similarly sized males. Multiple linear regressions examining interactions between body mass and site found no significant interactions ($P = >0.05$) across either method, isopleth or sex. When split into weight categories of 25 kg increments, male pigs >100 kg demonstrated significantly larger k-LoCoH90 ranges ($F_{3,30} = 3.07$, $P = 0.04$) than did all smaller pigs. However, there was no significant difference between the sizes of the core range (k-LoCoH50) ($F_{3,30} = 1.17$, $P = 0.34$).

Home ranges by season and year

There was considerable variation in the seasonal home-range size among different sites and sexes. Using the k-LoCoH90 home-range size, mean feral pig ranges appear to be marginally larger in autumn for male pigs at Arcadia and Downfall Creek and larger in summer at Gebar and winter at Palerang. For female pigs, autumn displayed larger ranges at all sites except Palerang (winter). Summer at Arcadia and Palerang represented considerably smaller ranges for male pigs, whereas for the other two sites, spring represented the smallest ranges. Winter (Downfall Creek and Gebar), spring

(Arcadia) and summer (Palerang) displayed the smallest ranges for female pigs. Despite these seasonal changes, k-LoCoH90 did not demonstrate a significance in home range-size change through interactions between season and site ($F_{9,149} = 0.45$, $P = 0.91$), nor between season and sex ($F_{3,157} = 0.37$, $P = 0.77$). No method or isopleth indicated a significant change in range size through these interactions. There was also no significant difference indicated among years, nor any interaction among sex, site and year on activity-range size (MCP90; $F_{4,68} = 1.42$, $P = 0.23$).

Habitat preference

Through the chi-squared test, 58 of the 59 pigs in this study demonstrated a significance in habitat selection. Residual medians of both the chi-squared test and Jacob's index for all pigs, male and female, are presented in Table 3.

Across all pigs, both methods indicated a preferential selection of habitat between 21% and 40% FPC, whereas the ranges immediately below (11–20% FPC) and above (41–50% FPC) were used in proportion to their availability. All other FPC ranges indicated avoidance, with the JI demonstrating a strong avoidance for habitat, with an FPC value of $>70\%$. Overall, 91% (chi-squared) and 81% (JI) of

Table 3. Residual medians of the chi-squared test and Jacob's index (JI) test, with selection (preference, avoidance, proportional).

Sex	FPC range (% cover)	Median chi-squared residual	Chi-squared selection	Median JI	JI selection	n
All pigs (male and female)	1–10	–3.57	Avoidance	–0.19	Weak avoidance	58
	11–20	0.94	Proportional	0.05	Proportional	53
	21–30	5.95	Preference	0.22	Weak preference	58
	31–40	8.22	Preference	0.18	Weak preference	58
	41–50	0.89	Proportional	0.04	Proportional	57
	51–60	–3.23	Avoidance	–0.23	Weak avoidance	45
	61–70	–2.79	Avoidance	–0.41	Weak avoidance	29
	71–80	–4.63	Avoidance	–0.83	Strong avoidance	7
	81–90	–8.83	Avoidance	–1.00	Strong avoidance	1
	91–100	–10.20	Avoidance	–0.98	Strong avoidance	2
Male	1–10	–2.57	Avoidance	–0.19	Weak avoidance	33
	11–20	0.94	Proportional	0.04	Proportional	29
	21–30	3.89	Preference	0.10	Proportional	33
	31–40	8.46	Preference	0.20	Weak preference	33
	41–50	0.73	Proportional	0.04	Proportional	32
	51–60	–5.40	Avoidance	–0.33	Weak avoidance	25
	61–70	–4.60	Avoidance	–0.40	Weak avoidance	17
	71–80	–5.78	Avoidance	–0.83	Strong avoidance	5
	81–90	–8.83	Avoidance	–1.00	Strong avoidance	1
	91–100	–10.20	Avoidance	–0.98	Strong avoidance	2
Female	1–10	–5.80	Avoidance	–0.17	Weak avoidance	25
	11–20	5.48	Preference	–0.05	Proportional	24
	21–30	9.83	Preference	0.23	Weak preference	25
	31–40	5.82	Preference	0.07	Proportional	25
	41–50	3.79	Preference	0.13	Proportional	25
	51–60	–0.96	Proportional	0.02	Proportional	20
	61–70	–2.30	Avoidance	–0.46	Weak avoidance	12
	71–80	–2.21	Avoidance	–0.85	Strong avoidance	2

The JI test further separated the selection into weak, strong or proportional. Sample size (*n*) is also presented.

pigs demonstrated a preference for one or more FPC groups within the range of 11–50% FPC. Both methods indicated that female pigs have a marginally wider range of proportional or preferential use (11–60% FPC) than do males. Although males potentially have a wider range of habitat available because of their greater home-range size, they are slightly more selective, either preferring or using habitat in proportion to its availability between 11% and 50% FPC. There were some slight differences among sites, with the vast majority of pigs at Arcadia (97%), Palerang (92%), Downfall Creek (82%) and Gebar (75%) demonstrating a preference for habitat within 11–50% FPC. Across all pigs, 57% (chi-squared) and 47% (JI) demonstrated an avoidance of very open habitat (1–10% FPC), with no statistical difference between the sexes ($P = 0.72$ (chi-squared), $P = 0.75$ (JI)]. However, there was a

greater disparity among sites for the use of open habitat ($F_{5,55} = 4.25$, $P = 0.002$), with 68% pigs at Arcadia and 50% at Palerang demonstrating avoidance, whereas at Downfall and Gebar, 55% and 75% (respectively) demonstrated a preference for this habitat type. Almost half (43%, chi-squared, and 46%, JI) of all pigs actively avoided habitat containing the highest FPC density that is available to them. In all circumstances, the resultant JI was more conservative in determining preference than was the chi-squared test, but where the JI indicated the strongest preference (in this case, weak), the corresponding chi-squared residual median was the highest or second-highest presented (Table 3). ANOVA tests indicated that there was no significant difference ($P = >0.05$) between the proportions of retained and deleted points (removed during our cleaning process) for all FPC values, except

for 51–60% FPC ($P = 0.016$), where a slightly higher proportion was deleted than retained.

Discussion

Feral pig range sizes were highly variable, with both home and core ranges being significantly affected by study site and bodyweight, but not by season or year. Sex significantly influenced MCP90, k-LoCoH90 and MCP50 ranges but did not significantly influence k-LoCoH50 ranges. Across all sites, feral pigs preferentially used habitat with 20–40% FPC (woodland), proportionally used habitats of 11–20% FPC and 41–50% FPC and tended to avoid habitats with all other FPC ranges. Identifying the critical factors affecting feral pig home-range size and habitat preference are informative for monitoring, management, and modelling of feral pig populations, and to guide future research.

The findings indicated study site as the most significant factor in determining feral pig home- and core-range sizes. These results support the hypothesis that the considerable variation demonstrated both herein and across previous Australian studies (Saunders and Kay 1991; Saunders and Kay 1996; Caley 1997; Dexter 1999; Mitchell *et al.* 2009) reflects differences in landscape productivity (Singer *et al.* 1981; Dexter 1999; Bengsen *et al.* 2016; Clontz *et al.* 2022). Female range size is believed to be negatively scaled to landscape productivity (Singer *et al.* 1981; Bengsen *et al.* 2016), whereas male ranges are scaled positively to the range size of coexisting females (Dexter 1999). The limitation of island size and the more compact resources in tropical island biomes such as Gebar Island (this study) and Hawaiian Islands (Salbosa and Lepczyk 2009) are likely to influence more compact range sizes. In contrast, the likely lower productive areas of Downfall Creek and Arcadia coincide with considerably larger ranges in the feral pigs studied. Paradoxically, previous home-range estimates from pigs in semi-arid regions of New South Wales (NSW; Dexter 1999) have shown considerably smaller ranges than our study sites (excluding Gebar), although this difference is likely to be due to differences in data-collection quantity and quality (i.e. radio-telemetry vs GPS technology). Similarly, there are disparities between our Palerang site and other studies in similar sites in southern NSW, with both sexes in Saunders and Kay (1996) and female pigs in Saunders and Kay (1991) demonstrating considerably larger home ranges (MCP) than in our study. Even though both site and sex have significant effects on home-range size, the lack of significant interaction between site and sex supports the theory that relationships between the sexes is not different per site. Because home-range size is highly site-specific, generalising or using mean values generated across vastly different areas may not be appropriate where more accurate estimates are critical,

such as in disease-spread modelling. Alternatively, feral pig distribution modelling may benefit from factoring in landscape productivity, through the use of a metric of vegetative vigour such as in Campbell *et al.* (2021) or through more complicated Bayesian networks (Froese *et al.* 2017).

With the exception of Mitchell *et al.* (2009), all other published Australian feral pig-range studies have demonstrated a significant range-size difference between sexes (Saunders and Kay 1991, 1996; Caley 1997; Dexter 1999). The larger ranges demonstrated by males in this study ($P = <0.001$) and others are likely to be related to their biological desire to actively seek out breeding females. Regardless, this suggests that focussing distribution models exclusively on sounder behaviour may lead to the model underestimating true feral pig movements and home-range sizes. Although females are more gregarious (Choquenot *et al.* 1996), the typically larger ranges of males may mean greater distribution and, therefore, greater inter-sounder connectivity than for females. Dexter (1996) also suggested that exotic-disease spread may result from a combination of simple diffusion and through long-distance animal movements. Our analysis, across both range methods and isopleths, indicated that range size increases as a function of body mass. This may be related to the greater energetic requirement of larger animals (Harestad and Bunnell 1979) and supports the findings of Saunders and McLeod (1999) and Mitchell *et al.* (2009). However, the high standard errors and a less robust r^2 -value observed in this study than in that of Saunders and McLeod (1999) suggests that there may be other, more influential, factors affecting range size at the four study sites. Differences in range size as a function of the interaction between study site and body mass yielded no significant interaction across either sex, method or isopleth. This suggests that while body mass and study site individually influence range size, the effect of body mass on range size is not different per site. Differences in range size per site are likely to be influenced by extrinsic factors such as landscape composition and productivity rather than body mass. The demonstration that large male pigs (>100 kg) have significantly larger home (k-LoCoH90) ranges while having core (k-LoCoH50) ranges similar-sized to those of smaller males, suggests that resources within the core range support basic needs (food, water, shelter), whereas an extended home range is influenced by other factors such as higher sexual motivation (Singer *et al.* 1981; Caley 1997; Dexter 1999). Linear regressions across both methods and isopleths indicated that both the home- and core-range sizes of female feral pigs with a body mass of greater than 62 kg will surpass that of similarly sized males, suggesting that larger females may require larger range sizes, and hence, resources to meet their needs. However, this result may have been affected by the higher number of males ($n = 30$) than females ($n = 17$) greater than 62 kg in this dataset rather than a biological feature; therefore, further investigation to confirm the findings is recommended for future study.

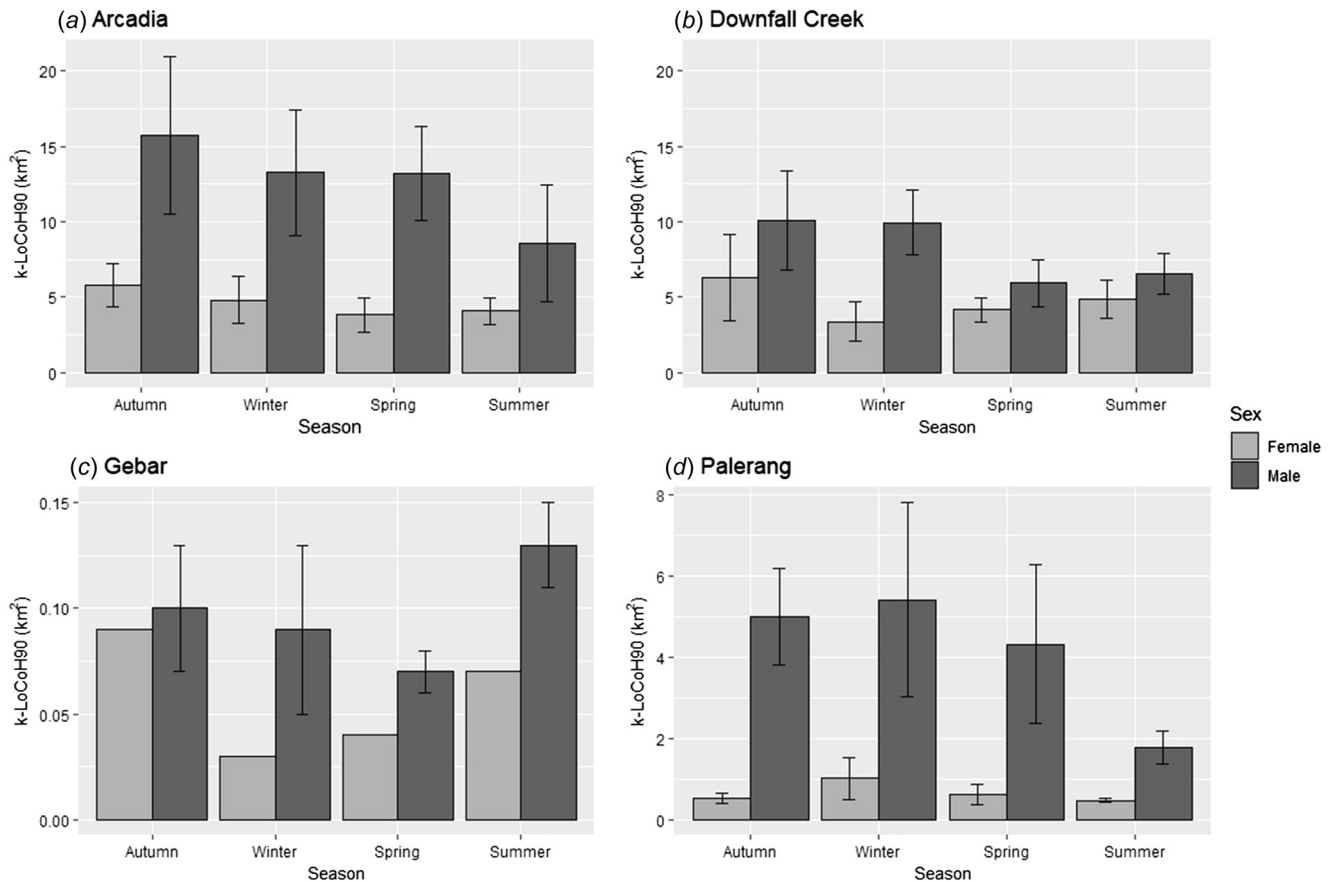


Fig. 3. Mean seasonal k-LoCoH90 home ranges and standard error for male and female pigs across the four study sites (a–d) and all years combined. Note the difference of scale on the y-axis.

Seasonal range fluctuations across all pigs were evident, yet statistically insignificant in this study (Fig. 3). Variations in home-range size among seasons appear to be site-dependent. Larger winter ranges were evident at Palerang and in Saunders and Kay (1991) and Dexter (1999), which is indicative of greater spatial distribution in cooler seasons, owing to lower requirements for water and protection from heat (Dexter 1999). Saunders and Kay (1991) suggested that management programs are ‘best implemented in the winter when movement within the population is greatest’. However, this also means that they are more widely distributed, which may influence control tool encounter rates, if control tool volume and spatial distribution are not increased in proportion to the relative home-range size. In our study, autumn typically produced larger ranges, corresponding with the results of Caley (1997), Massei et al. (1997) and Dexter (1999). There was no uniform season where ranges were condensed, neither in our study nor others (Saunders and Kay 1991; Caley 1997; Massei et al. 1997; Dexter 1999; Mitchell et al. 2009), suggesting that variations in seasonal ranges across different sites and studies is influenced by other factors. Varying climatic conditions (e.g. unpredictable rainfall, ambient air temperatures, abundance of and distance

to food, water and shelter) are more likely to influence range size than is a particular month or season (Heitman and Hughes 1949; Dexter 1999; Kay et al. 2017). In periods of unseasonal weather, using averaged seasonal predictors may affect the outcome. In this situation, lagged meteorological conditions may be a more appropriate variable than is month or season (Kay et al. 2017). However, the application of site-specific abiotic factors (e.g. rainfall, food abundance) may prove challenging for broad-scale modelling. Similarly, the changes seen among years appear to be highly individualistic and not a factor of sex or site, and are probably a result of factors not investigated here (e.g. breeding, sexual competition, food availability, hunting or other disturbances).

Habitat selection based on FPC should be considered as a covariate in future modelling of habitat assessments, and to assist in determining strategies for feral pig control. We found a significant preference for habitat with 21–40% FPC and a proportional usage of habitat with 11–20% and 41–50% FPC. In Australia, closed forests are classified as those where tree canopies (FPC) cover more than 80% of the land area, open forest as 51–80%, woodland forest as 20–50% and non-forest carrying other woody vegetation <20% (ABARES 2013). Feral pigs in this study indicated

a preferential use of woodland forest, whereas actively avoiding open forests and closed forests. This finding contradicts other Australian studies on habitat use, which found that pigs avoid open woodland and woodland areas but show a preference for open and closed forests (Saunders and Kay 1991; Caley 1997). This discrepancy may result from the small sample size and high error rate associated with radio-tracking in previous studies compared with the significantly larger dataset and highly accurate GPS locations in this study. Caley (1997) noted that the radio-tracking error rate is close to the width of some habitats and therefore use may be underestimated. However, more recent modelling studies have also predicted woodlands to be unsuitable habitat for breeding (in dry seasons) for feral pigs (Froese *et al.* 2017). However, this is likely to be site-dependent and, with fewer parameters examined, this study was limited to shelter only. Saunders and Kay (1991) also suggested that concentration of effort at the interface between heavy vegetation and open pasture may improve control/monitoring tool encounter rates. Further research into ecotone use and finer-scale habitat use, using large, fine-resolution datasets across sites, is required. It is unlikely that the disproportionate removal of high DOP-value points from specific FPC categories during our cleaning process affected the habitat preference results, because all but one FPC range (51–60%) indicated an insignificant ($P = >0.05$) difference between the proportion of retained and deleted points within each FPC range.

Site-specific differences in habitat use may be related to the distribution of resources at each site, which was not accounted for in this study. For example, at Gebar, pigs appear to forage for food in inter-tidal zones, hence demonstrating a higher preference for open habitat, owing to this site-specific food availability. This study clearly indicated that feral pigs avoid open forest and avoid (chi-squared) or strongly avoid (JI) closed forests. It is possible that habitats with higher density canopies do not provide significantly greater shelter than do lower FPC-range habitats, while also yielding lower food and water availability. This may not be the case in some habitats (e.g. wet tropical rainforests) and future work may be required to understand this better. The use of FPC is appropriate for examining landscape-based shelter for feral pigs but does not account for other components of the landscape that may affect how an animal uses the landscape. Future work to identify and determine the influence of detailed food- and water-source availability on habitat preference will enable refinement of feral pig landscape-use data to better inform modelling and control programs.

This research has quantified feral pig home ranges across four sites in eastern Australia, and assessed the influence of site, sex, season and bodyweight on home-range size. The preference for habitat with 20–40% FPC indicated that targeting such areas may result in improved feral pig control or monitoring at significantly reduced cost.

Both home-range and habitat-use analyses provide insights into factors that influence feral pig activity ranges for further consideration in distribution modelling and refining control strategies. It is also evident from this study and others that feral pig home range is highly variable and likely to be dependent on a multitude of factors, limiting the appropriateness of a ‘one-size-fits-all’ approach to home-range analyses. Understanding the ecological drivers and using this intelligence will allow us to tailor our approaches according to biotic and abiotic predictors. Further studies to understand these factors and how they influence feral pig behaviour is critical to both appropriately model disease spread (Cowled and Garner 2008) and to inform feral pig control programs.

Supplementary material

Supplementary material is available [online](#).

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