

Feral pig (*Sus scrofa*) activity and landscape feature revisitation across four sites in eastern Australia

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ABSTRACT

Quantifying feral pig movements and understanding the fine-scale ecological drivers of feral pig landscape use are important factors for optimising pest management programs. We tracked 59 GPS-collared feral pigs at four sites in eastern Australia between 2017 and 2021, for a mean of 375 ± 277 (s.d.) days. The mean number of successful GPS fixes was $15\,577 \pm 11\,833$ (s.d.) and these were recorded at 30-min intervals. We calculated mean hourly and daily distances travelled to determine feral pig activity and investigated the influence of sex, site, season and time of day on this activity. We also investigated the proximity of highly active sites to habitat covariates, along with intensity and frequency of site use. Male daily movement, 4.9 km (95% CI = 4.2, 5.6 km), was significantly greater than it was for females, 3.6 km (95% CI = 3.0, 4.1 km) and males maintained a high level of activity all night, while female activity was predominantly crepuscular. Study site was a significant determinant of daily movement, but season was not, across either sex or site. Highly-visited site selection was negatively associated with distance from creeks, dams, cultivation, open herbaceous vegetation and medium woody vegetation. Both medium woody vegetation and dam sites had the longest duration of use (3 and 2.7 h respectively) and the shortest time between visitations (14.5 and 13 h respectively). Quantifying feral pig activity and key habitat feature preference are important steps in improving management programs. Better prediction of feral pig movement and behaviour allows for more targeted placement of control tools, potentially increasing encounter rates.

Keywords: animal telemetry, discrete choice model, feral pig, habitat selection, movement, pest management, recurse analysis, site revisitation.

Introduction

The feral pig (*Sus scrofa*) is a well-recognised and long-established invasive animal in Australia that has been the focus of extensive ecological studies (Saunders and Kay 1991, 1996; Caley 1997; Mitchell *et al.* 2007b). Their widespread distribution and continued expansion across the country (Cowled *et al.* 2009), coupled with their environmental (Hone 2002; Mitchell 2010) and agricultural impacts (Choquenot *et al.* 1997; Gentle *et al.* 2015) and their potential to harbour and transmit diseases (Ward *et al.* 2007; Chenais *et al.* 2019), has meant that feral pigs and their impacts are often targeted by control programs.

Mitigating the negative impacts of feral pigs, as with other invasive species, ideally requires the implementation of a well-developed strategy specific to each situation which considers species-specific impacts and ecology, feasibility cost-effectiveness and cost versus benefit (Braysher 1993). However, mitigation programs are often undertaken reactively, with little consideration of the ecology or the behaviour of the species, and they consequently often have limited long-term success (Lapidge *et al.* 2012; Australian Pork Limited 2021). Wildlife management programs often rely on deploying devices or control tools into the environment to monitor or otherwise target the species, and these can be time and resource-consuming (Harriott *et al.* 2021). Ill-considered placement of control tools, either spatially (Saunders *et al.* 1993; Dexter 1995) or temporally

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(Mcilroy *et al.* 1993), as influenced by shelter, temperature, water and food availability (Choquenot and Dexter 1996; Fleming *et al.* 2000), could also result in poor encounter rates and therefore limited program success. Strategic placement of control devices to improve encounter rates is important for increasing capture rate and efficacy during management programs. For feral pigs, control tool encounter rates may be improved where foraging is widely dispersed and, consequently, movements are greater (i.e. in poor seasons; Dexter (1995)). Similarly, encounter rates could be improved by targeting environments demonstrated to be of high preference (Saunders and Kay 1991; Caley 1997). Information that identifies the periods or areas which yield increased encounter rates could increase the efficacy or efficiency of field programs, and this requires further attention.

Recent outbreaks of African swine fever (ASF) and foot and mouth disease (FMD) in south-east Asia, and the incursion of Japanese encephalitis (JE) in Australia have emphasised the importance of understanding feral pig ecology in an Australian context so as to inform emergency animal disease (EAD) preparedness and response strategies. Selective and strategic control of feral pigs is likely to be important in an EAD response (Ward *et al.* 2015). Disease modelling frameworks such as the Australian Animal Disease Spread (AADIS) have been developed to model the spread and management of EADs in Australia, in both domestic and feral pig populations (Bradhurst *et al.* 2021). These models require a sound knowledge of the host species' ecology (Cowled and Garner 2008), including movement patterns and habitat preferences, that may affect contact (Bradhurst *et al.* 2021). Where the availability of empirical data is limited, data from outside the study area, from other modelling studies, and from expert-derived values or assumptions are used instead. This limitation of data, drives a need to improve upon and validate the performance of such models. Information on feral pig habitat selection, movement, and seasonal influences may be of importance for the refinement of habitat suitability models which can be used to predict outcomes, assess risk and justify investments into prevention strategies (e.g. Froese *et al.* (2017)).

Despite the completion of several broad-scale habitat use assessments of feral pigs in Australia (Saunders and Kay 1991; Caley 1997; Dexter 1999), there is very little published data on the finer-scale selection of habitat features. Feral pig sign has been used as an indicator of habitat use. For example Mitchell *et al.* (2007b) found higher daily digging indices in swamps and creeks at three study sites. However, due to study limitations, it is unknown whether these sites were revisited frequently or just used intensely for short periods. Knowledge of focal activity points with high revisitations could provide a better understanding of feral pig behaviour, suggesting target areas for feral pig control programs (Mitchell and Mayer 1997) and informing habitat suitability assessments for epidemiological modelling (Cowled and Garner 2008).

Modern global positioning system (GPS) collars allow for significantly more data to be collected, yielding exceptionally refined analyses of range size, movement and habitat use. The recurse analysis, as demonstrated by Bracis *et al.* (2018), utilises this type of data to count revisitations of GPS-collared animals to exact locations within the environment, thereby allowing the identification of highly-revisited sites. Consequent habitat assessment at these sites may provide for a finer-scale analysis of feral pig habits in highly-used locations, potentially leading to improvements in control tool placement, encounter rates and therefore control program success.

Using GPS-equipped collars, we aimed to identify what factors influenced feral pig movements and we investigated how the proximity of highly-revisited sites to habitat covariates determined fine-scale habitat use across four study sites in eastern Australia. We discuss the importance and application of these data to the improvement of our understanding of ecological factors in feral pig management. Potential parameters for feral pig epidemiological modelling will also be discussed.

Methods

Data collection

All data used in this study were collected from 59 collared feral pigs at four sites in eastern Australia between 2017 and 2021. Three sites were located in Queensland: Arcadia Valley (Arcadia); Downfall Creek (Downfall); and Gebar Island (Gebar). Our fourth site (Palerang) was located at Palerang, New South Wales. A map of study sites is provided in Wilson *et al.* (2023). Details of individual pigs are displayed in Supplementary Table S1. A combination of corral, box and panel traps, pre-fed until an asymptote of consumption was achieved (~7–10 days), were used to capture pigs. Both dry and fermented wheat were utilised as lures. Captured pigs were sedated with an intramuscular injection of 1 mg/kg Zoletil (Virbac Australia Pty Ltd, Milperra, NSW, Australia), before collaring with Lotek Iridiumtrack Heavy Duty 3D collars (Lotek, Ontario, Canada). Collars were programmed to record a GPS fix at 30-min intervals. Animal ethic permits AEC 16–115 and AEC 20–023 were approved by the University of New England.

Study sites

Our Arcadia Valley study site consisted of ~960 km² of open grassland and eucalyptus woodland sandwiched between Carnarvon and Expedition National Parks, in the central highlands of Queensland. This area experiences a mean annual rainfall of 635.8 mm (Bureau of Meteorology 2022g) and is predominantly used for cattle grazing and small-scale feedlots. Collars were active at this site between May 2017 and January 2021, for an average duration of 289 days.

Downfall Creek covers an area of $\sim 1380 \text{ km}^2$ of eucalypt woodland and open grassland on the western downs of Queensland. This area, between Miles and Wandoan records a mean annual rainfall of 643.4 mm (Bureau of Meteorology 2022f) and is used for cattle grazing and natural gas extraction. Collars were active at this site between June 2017 and May 2020, for an average duration of 630 days.

Our third Queensland site (Gebar) was a small ($\sim 4.2 \text{ km}^2$) and uninhabited island in the Torres Strait. This site has a tropical climate and experiences a mean annual rainfall of 1441.7 mm (Bureau of Meteorology 2022d). The island is owned by the Gebaralgal (Torres Strait Islanders) Corporation (National Native Title Tribunal 2004). Collars were active at this site from October 2017 to August 2019, for an average duration of 569 days.

Our fourth site, Palerang, was located east of Queanbeyan, New South Wales. This $\sim 777 \text{ km}^2$ area is primarily open grassland and open eucalypt forests and experiences a mean annual rainfall of 624.4 mm (Bureau of Meteorology 2022e). The area is predominantly used for cattle production. Collars were active at this site from May 2020 to October 2021, for an average duration of 306 days.

Collar accuracy and data management

Using thirteen locations of deceased pigs (11 764 GPS points), we compared two methods of filtering data based on direct (Bjørneraas non-movement model; Bjørneraas *et al.* (2010)) and indirect (dilution of precision (DOP); following Fancourt *et al.* (2021)) quality indicators. From this comparison, we used $\text{DOP} \geq 5$ as an acceptable proxy of locational error, given previous assessment found it resulted in 99.75% accurate points ($< 20 \text{ m}$) for analysis. For further details, see Wilson *et al.* (2023).

Collar movement error

Following Theuerkauf *et al.* (2023), collar movement error was approximated using the pseudo-movement of consecutive fixes from known stationary collars. The collar error was estimated as the mean distance between consecutive fixes, calculated from the cleaned location data of the thirteen deceased pigs.

Activity estimations

Activity for each animal was represented by the distance travelled and estimated as the sum of the distance between consecutive fixes. The distance of each consecutive fix from the last recorded fix was calculated using the Euclidean distance formula, minus the collar movement error. We utilised a linear regression model to estimate a correction factor for differing time intervals between consecutive fixes. This correction factor was added or subtracted from the estimated distance between points if the time interval differed from the standard 30 min. Where the correction factor

was greater than the measured distance between two points, resulting in a movement of negative distance (i.e. biologically impossible), we inferred that the pig was stationary, and the distance moved was recorded as zero. The coordinates were converted from degrees, minutes, seconds to Universal Transverse Mercator (UTM) for the desired metric output.

Daily and seasonal activity

For daily activity estimations, the calculated distance (m) between each consecutive point (corrected for errors) was summed per pig, according to date. To investigate seasonal differences, daily distance was averaged per season. Shapiro–Wilk tests indicated that mean daily movement per pig met the assumptions of a normal distribution without data transformations. ANOVAs were used to test for significance between sexes, sites and seasons. Variation between individuals is represented as standard error.

Activity relative to solar transitions

To investigate whether feral pig activity varied according to the time of day, activity (movement per hour) was measured relative to sunrise and sunset times (referred to here as solar transitions). As these times change according to both latitude and day of year, we used a geodetic calculator (Geoscience Australia 2020) to measure the difference in hours from each point to the closest solar transition. Fixes were then arranged into hourly increments according to their closest solar transition. Each reported hourly interval represents a time period beginning 59 min prior to the reported hour and ending at the reported hour. For example, 7 h before sunrise refers to all fixes recorded > 6 and ≤ 7 h before sunrise. Where a fix was recorded exactly at the time of a solar transition, the fix was recorded as being between 0 and 1 h after the phenomenon. Hourly movements relative to solar transitions were then estimated for all pigs. Shapiro–Wilk tests indicated that this hourly movement data and subsequent data transformations did not satisfy normality assumptions. A Kruskal–Wallis test was therefore used to determine significance between periods relative to solar transitions, sexes and sites and interactions between these groups. Variation between individuals is represented as standard error.

Fine-scale habitat use and site revisitation

The recurse analysis tool (Bracis *et al.* 2018) in R (version 4.0.5) (R Core Team 2021) was used to investigate habitat use and site revisitation. This tool records visitations to certain areas and aims to identify highly-visited points within the environment (Bracis *et al.* 2018). To align our analysis with Bracis *et al.* (2018), we restricted our collar interval data to hourly. To avoid erroneous movements, we specified a recurse radius of 50 m (i.e. to encompass an area greater than GPS error ($\pm 20 \text{ m}$) plus median step distance ($\pm 21 \text{ m}$) (Bracis *et al.* 2018)). Highly revisited sites are

classified as the upper 35% of revisited trajectory locations (Bracis et al. 2018). However, following assessment of four percentiles: 35; 25; 15; and 5%, we determined that 15% was appropriately refined for feral pigs, enabling key features to be highlighted whilst not including extreme amounts of data for analysis. These high visitation sites were then grouped into clusters according to their proximity to one another. A 50 m radius polygon was plotted over each recurse point in the dataset and overlapping polygons were merged through 'sf::st_union' (Pebesma 2018). For merged polygons, a cluster centroid point was generated and revisitations were recalculated using 'recurse::getRecursionsAtLocations' (Bracis et al. 2018). The resultant data on highly-revisited sites were then analysed for distance to habitat covariates using discrete choice modelling (Cooper and Millsaugh 1999).

Habitat covariates were downloaded from multiple sources. Vegetation layers were classed into woody (closed, medium, open, sparse), herbaceous (open, sparse), very sparse vegetation, and cultivation using Digital Earth Australia's Land Cover (Landsat) dataset (25 m raster) (Geoscience Australia 2021). Supplementary Table S2 provides a description of vegetative layers used in this study. Road and farm track layers were downloaded through Department of Resources (2021a) (Queensland) and Spatial Services (2020a) (New South Wales). Water spatial layers were accessed through Department of Environment and Science (2022) (Queensland) and Spatial Services (2020b) (New South Wales). In this study, watercourses are defined as creeks and rivers, while waterbodies are any large reservoir of water (e.g. dams, lakes). Finally, urban and rural residential blocks were accessed through land use datasets (Department of Resources 2021b) (Queensland) and (Department of Planning and Environment 2022) (New South Wales). Spatial layers for the Gebar Island site were not available, hence this site was excluded from analysis in this section.

Assuming the pigs had *a priori* knowledge of habitat types, five randomised points were generated per actual recurse point to generate 453 choice sets. To determine the spatial width of each choice set, we estimated the minimum time the pig could have possibly completed the corresponding count of revisitations for each actual point and multiplied the result by the average hourly distance of all pigs in the study (184 m/h). To avoid biologically implausible extreme spatial widths calculated from exceptionally high revisitation counts, we capped the maximum choice set radius as half the square root of the median (by site) 100% minimum convex polygon. Habitat covariates (identified above) were attributed to the data through an automated proximity analysis using the 'rgeos:gDistance' tool (Bivand and Rundel 2020) in R. The resultant data determined a calculated distance to each habitat covariate for each point (both actual and random). Using these proximity data as continuous independent variables, conditional logistic regressions were calculated through 'survival::clogit' in R (R Core Team 2021).

Intensity and frequency of site use

Frequency and intensity of site use were calculated through an assessment of entrance and exit times generated through the recurse analysis. Individual sites were associated with the habitat variable that they were principally within. Due to the nature of the watercourse data type (ESRI polyline feature), these data were excluded from this part of the analysis. Median length of use (intensity) and median time between visitations (frequency) were calculated.

Results

Data collection

Across all sites, pigs were collared for a mean of 375 ± 277 days (s.d.) and demonstrated a mean of $15\,577 \pm 11\,833$ (s.d.) successful GPS fixes. Details on individual pigs, including sex, weight, days collared, raw and successful GPS fixes and mean daily distance is available in Supplementary Table S1. The mean distance between consecutive fixes (used as a proxy for collar error rate) for thirteen stationary (deceased pigs) collars was 3.3 m (s.e. = 0.04 m).

Daily and seasonal activity

The mean daily activity for male and female feral pigs at each site are shown in Table 1. Excluding Gebar, male pigs travelled greater distances per day than females and the disparity of mean daily distance between sexes varied between 28.6% (Downfall) and 38.3% (Palerang). Across all sites there was a significant difference between sexes ($F_{1,57} = 7.84$, $P = 0.007$) for average daily distance travelled: females 3.6 km; males 4.9 km. Overall, there was a demonstrated significant difference between sites ($F_{3,55} = 9.84$, $P = <0.001$). The greatest daily distance travelled by any pig was by a 49 kg sow at Downfall, who travelled 33.6 km in a single 24-h period. For all sites combined, there was no significant difference ($F_{3,193} = 0.13$, $P = 0.94$) in the average daily distance travelled between different seasons. Neither sex demonstrated a significant interaction between site and season for the mean daily distance travelled (male - $F_{9,91} = 0.22$, $P = 0.991$ and female - $F_{9,74} = 0.34$, $P = 0.958$).

Activity relative to solar transitions

Over all sites and sexes combined, there was a significant difference ($\chi^2 = 754.5$, d.f. = 30, $P = <0.001$) in the distance travelled at different times of day, and with the exception of Gebar pigs, fewer movements observed during daylight hours and greater movements during the night, with a rapid increase immediately after sunset. There were some differences in activity between study sites (Fig. 1), with Arcadia and Palerang pigs demonstrating a distinct increase in activity immediately after sunset, with a daily

Table 1. Mean fixes per pig, mean days collared per pig and mean daily distances per pig (km) travelled for male and female pigs in each study site.

Site	Sex, sample size (n)	Mean fixes per pig (s.e.)	Mean days collared per pig (s.e.)	Mean daily distance (km) per pig (s.e.)
Arcadia	F (14)	17 990 (4010)	402 (89)	3.8 (0.3)
	M (17)	8909 (1734)	197 (38)	5.5 (0.3)
Downfall	F (5)	32 810 (5118)	774 (109)	4.4 (0.6)
	M (6)	21 424 (4881)	511 (118)	6.1 (1.0)
Gebar	F (1)	17 337	641	1.1
	M (3)	9456 (3016)	545 (124)	0.8 (0.1)
Palerang	F (5)	18 163 (1556)	404 (37)	2.6 (0.3)
	M (8)	10 824 (2381)	244 (53)	4.2 (0.5)
All sites	F (25)	20 962 (2701)	486 (62)	3.6 (0.3)
	M (34)	11 616 (1530)	294 (39)	4.9 (0.4)

Standard error (s.e.) is provided in parentheses.

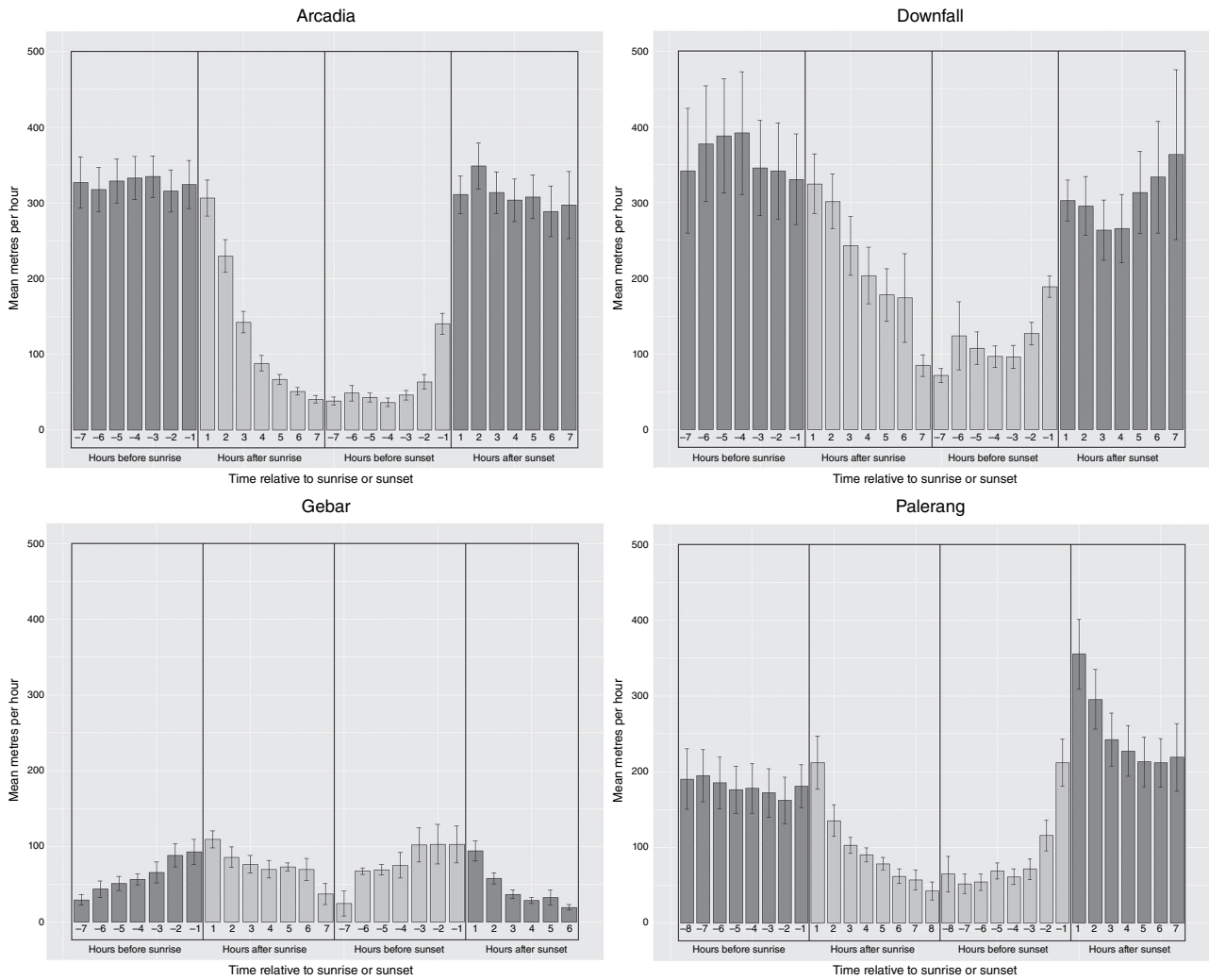


Fig. 1. Average distance (error bars = s.e.) travelled per hour relative to solar transitions (i.e. sunrise and sunset) according to study site. Note Gebar results are from one female pig.

peak occurring within 1–2 h after sunset before declining slightly and plateauing out for the remainder of the night. Arcadia pigs demonstrated the greatest increase in activity in relation to sunset, evidenced by an increase from a mean of 64 m/h at 2 h before sunset to 349 m/h at 2 h after sunset. Downfall pigs also exhibited a distinct increase in activity immediately after sunset, but activity continued to incline steadily, eventually peaking at 4 h prior to sunrise. Daylight activity at Downfall also declined more steadily than at Arcadia and Palerang. Gebar pigs appeared to demonstrate more crepuscular activity than other sites, with peaks at sunrise and sunset and activity declining to approximately midnight and midday, before increasing gradually again to the next solar transition. Pigs at Gebar were considerably less active than other sites, and demonstrated a different distribution of activity, with the lowest activity recorded at night (Fig. 1). Overall, there was a significant interaction between site and solar period on mean hourly distance ($\chi^2 = 1023.6$, d.f. = 113, $P = <0.001$). Female pigs exhibited a distinct peak in activity within 1 h after sunset, followed by a slight decline for 2 h and then little variation ($\chi^2 = 12.66$, d.f. = 15, $P = 0.629$) from 3 h after sunset to 3 h after sunrise (Fig. 2). There was, however, a slight increase in activity within 2 h post sunrise. Male pigs also displayed a rapid increase in activity immediately after sunset, but activity did not decline after this dusk period. Little variation ($\chi^2 = 5.93$, d.f. = 13, $P = 0.949$) in movement per hour was recorded between sunset and sunrise, despite a peak of activity appearing to occur 7 h post sunset and a dip in activity immediately after, at 8 h prior to sunrise. Male activity also declined rapidly after just 1 h following sunrise (Fig. 2). Across all pigs and times of day, the average hourly distance moved was 184 m/h.

Fine-scale habitat use and site revisitation

Conditional logistic regression statistics for individual sites and all sites combined can be found in Supplementary Tables S3–S6. Significant-only results by site can be seen in Table 2. Across all sites (combined), the distance to watercourse, waterbody, cultivation, open herbaceous vegetation and medium woody vegetation habitat variables were all negatively correlated with highly-revisited sites. Watercourses were the only habitat variable to maintain significant selection and negative coefficients across all three study sites (Tables 2), and 50.8% of all highly-revisited sites were located within 150 m of a watercourse. Cultivation demonstrated significant selection at Arcadia and Palerang but not at Downfall. Habitat with proximity to open herbaceous vegetation was selected by pigs at Arcadia and Downfall but not at Palerang. Across all highly-revisited sites, 89% of all points within any woody vegetation class were within 150 m of herbaceous vegetation. Conversely, less than half (46%) of all points within herbaceous vegetation are within 150 m of woody vegetation. Habitat with proximity to

waterbodies (e.g. dams) was only selected for at Arcadia. Habitat selection with proximity to road/tracks was significant at Downfall but demonstrated positive coefficients, indicating increasing use with increased distance (i.e. avoidance). Female pigs selected habitat with proximity to cultivation (coef. = -0.0005 , $P = 0.007$), while males did not ($P = 0.3$). No other habitat covariate tested in this study demonstrated a significant difference between sexes.

Frequency and intensity of site use

Overall, medium woody vegetation had the longest time period of use per visit (median = 3.03 h), followed by waterbodies (median = 2.65 h). Correspondingly, both these habitat types also had the shortest time between visitations (median values for medium woody vegetation and waterbodies, were 14.54 and 12.97 h, respectively). Neither habitat type showed significant differences between sites (Table 3). Very sparse vegetation (median = 1.02 h) and closed woody vegetation (median = 1.14 h) had the shortest length of use across all features. Very sparse vegetation also had the second longest time (20.99 h) between visitations. Closed woody vegetation also had a longer time (20.7 h) between visitations than most other habitat features and demonstrated a significant difference in length of use between sites ($P = 0.02$). Sparse herbaceous vegetation demonstrated a difference ($P = 0.02$) between sites for the median time between visitations.

Discussion

Analysis of GPS-tracked feral pigs across four sites in eastern Australia found that the average daily distance travelled by feral pigs was significantly affected by sex, site and time of day, but not season. Male pigs typically travelled further than females and both sexes indicated immediate increases in activity post-sunset. For highly-revisited sites, site selection was negatively related to distance from watercourses, waterbodies, cultivation, open herbaceous vegetation and medium woody vegetation, thereby demonstrating a preference for sites closer to these features. Conversely, there was an indicated avoidance of roads and tracks at Downfall. Waterbodies and medium woody vegetation were also used more frequently and for longer periods than any other covariate tested in this study, while features like cultivation and open herbaceous vegetation were used for shorter periods and less frequently.

The average daily distance travelled (Table 1) was likely to be negatively related to landscape productivity and for males, distance between sounders. Smaller daily distances were observed at Gebar (high rainfall), while the drier sites (Arcadia and Downfall) demonstrated much larger daily distances, suggesting an increase in movement at sites with lower productivity. However, the small size of Gebar Island

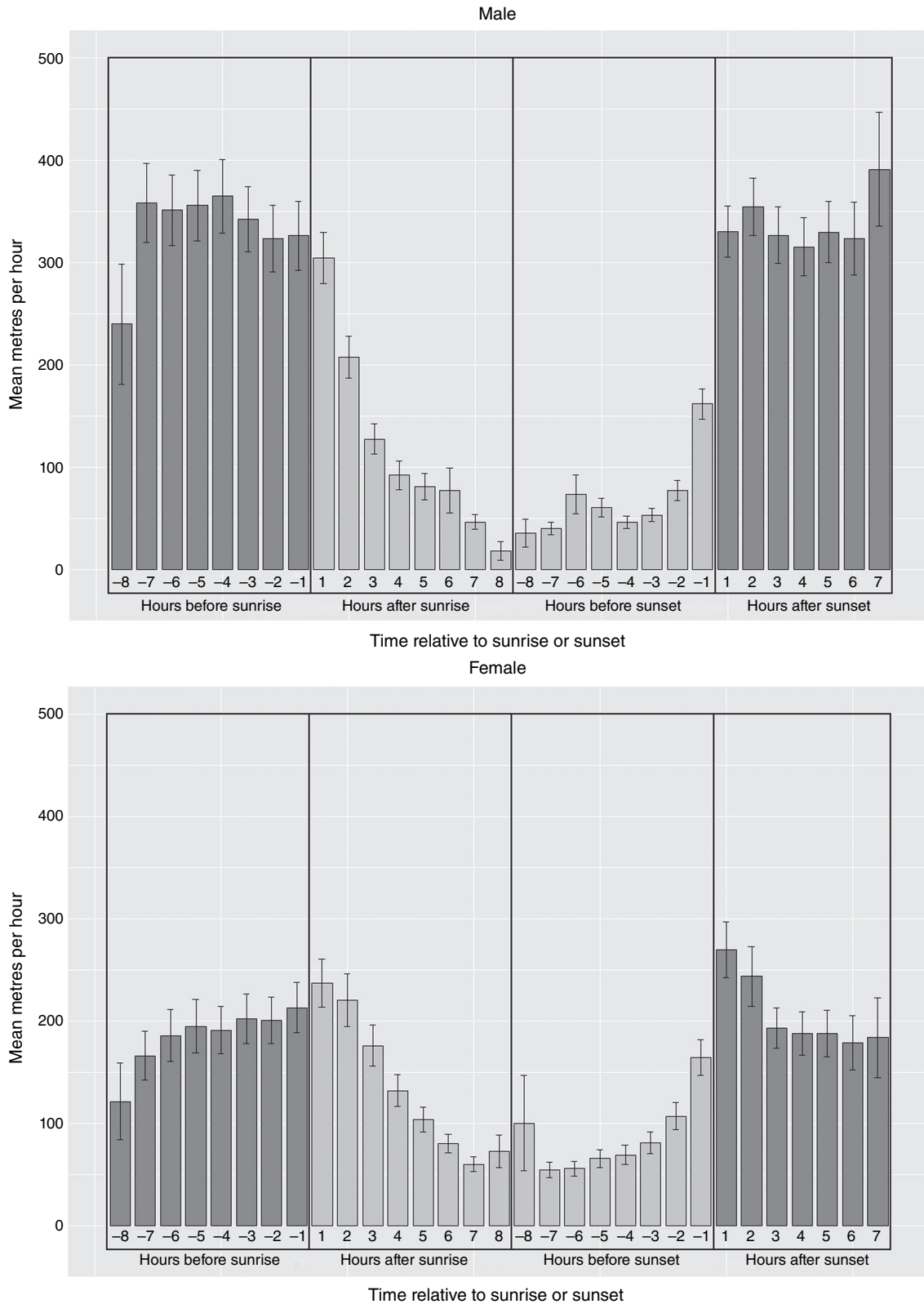


Fig. 2. Average distance (error bars = s.e.) travelled per hour relative to solar transitions (i.e. sunrise and sunset) according to sex.

Table 2. Site significant variables of conditional logistic regressions of feral pig high-use site proximity to habitat variable.

Site	Habitat variable	Coefficient	Odds ratio	s.e.	Z	P
Arcadia	Watercourse	-0.0007	0.9993	0.0003	-2.72	0.006
	Waterbody	-0.0003	0.9997	0.0001	-2.06	0.039
	Cultivation	-0.0004	0.9996	0.0002	-2.38	0.017
	Open herbaceous vegetation	-0.0084	0.9917	0.003	-3.18	0.001
Downfall	Watercourse	-0.0022	0.9978	0.0004	-5.05	<0.001
	Road and track	0.0004	1	0.0002	2.00	0.047
	Open herbaceous vegetation	-0.0057	0.9943	0.002	-2.36	0.018
Palerang	Watercourse	-0.0079	0.9921	0.002	-3.34	<0.001
	Cultivation	-0.0034	0.9966	0.002	-2.02	0.044
	Medium woody vegetation	-0.0116	0.9885	0.005	-2.40	0.017

Negative coefficients indicate that increasing distance from the habitat variable is negatively associated with habitat revisitation. Positive coefficients (see Downfall: Road and track) indicate greater habitat selection with increasing distance from this variable.

Table 3. Median period of use and time between visitations (both in hours) for highly revisited points in different habitat types and study sites.

Habitat feature	Site	Median period of use (h)	P	Median time between visits (h)	P	No. pigs	Sample size
Cultivation	Arcadia	2.63	0.203	26.12	0.256	4	85
	Palerang	1.24		16.64		8	896
Closed woody	Arcadia	4.95	0.024*	22.76	0.548	1	24
	Palerang	1.13		20.72		7	661
Medium woody	Arcadia	3.29	0.511	12.82	0.606	16	1082
	Downfall	3.13		18.00		9	1964
	Palerang	2.75		13.29		11	1512
Open herb	Arcadia	1.83	0.169	14.86	0.127	29	5542
	Downfall	1.14		22.98		10	2269
	Palerang	1.35		23.23		2	143
Open woody	Arcadia	3.17	0.265	17.08	0.497	10	378
	Downfall	1.74		20.04		7	921
	Palerang	9.71		8.23		2	138
Sparse herb	Arcadia	1.76	0.456	14.78	0.020*	6	149
	Downfall	1.10		23.70		2	236
Very sparse vegetation	Arcadia	0.74	0.625	25.40	0.509	4	103
	Downfall	4.78		8.78		1	43
Waterbody	Arcadia	3.06	0.669	13.94	0.904	13	593
	Downfall	2.14		11.36		2	261

Significance is a measure of variation between study sites. Significant variables are indicated with an asterisk (*).

(~4.2 km²) may have physically limited movements. The observation of greater daily travel distances of males relative to females is consistent with results from other movement studies (Saunders and Kay 1991; Caley 1997; Kay et al. 2017) and is perhaps indicative of individual-level factors such as sexual motivation or higher metabolic

rates (Caley 1997), or a combination of the two. The greater daily distance travelled by male pigs suggests that boars may be more predisposed to encounter control tools and may have higher inter-sounder connectivity than females, thereby potentially resulting in a higher disease spread risk (Saunders and Kay 1991; Dexter 1999).

We detected no significant difference in the daily distance travelled by pigs between seasons. A concurrent study (Wilson *et al.* 2023), also found no significant difference in home range size between seasons. It is possible that resource availability per season may not have differed enough during the study period to influence movements and, as feral pigs can breed all year where resources are available (Caley 1993), the influence of seasonal breeding on daily distance travelled is not observed as it is in other species such as deer (Amos *et al.* 2014). Tracking movements in response to other climatic variables like rainfall (Mitchell and Mayer 1997; Brivio *et al.* 2017), air temperature (Kay *et al.* 2017), pressure (Kay *et al.* 2017) and humidity (Brivio *et al.* 2017) or other lagged meteorological conditions (Kay *et al.* 2017) may improve detections of fine-scale changes in daily movement, and these are worth examining in future studies.

Time of day significantly influenced the activity of feral pigs, with results influenced by sex and site. Female pigs appeared to demonstrate a preference for crepuscular periods and although both sexes indicated a rapid incline of activity post-sunset, male pigs maintained a higher level of activity throughout the night and activity declined more rapidly than females after sunrise. The greater nightly movements of males to females supports the findings of Caley (1997) and, as postulated by Kay *et al.* (2017), is likely to be due to a combination of individual, geographical, landscape, meteorological and temporal factors such as foraging and pursuit of breeding opportunities. The demonstrated peak of male activity 7 h post sunset was influenced by the extreme movements of a particular male at this time period (1191 m/h) and the dip in activity 8 h prior to sunrise is due to a lower sample size at this time ($n = 7$) to others (mean $n = 30$). The lower relative nightly activity of pigs on Gebar compared to all other sites, was probably due to lower hunting pressure on the island. Pigs may change their habits according to hunting pressure (Saunders and Kay 1991; Gaston *et al.* 2008; Thurfjell *et al.* 2013), even at the cost of increasing the distance to resources (Saïd *et al.* 2012). Nevertheless, a change in peak activity time, regardless of the cause, may lower encounter rates and susceptibility to control during such periods (Gaston *et al.* 2008; Keuling *et al.* 2008; Ohashi *et al.* 2013).

The significant use of watercourses across all three sites in this study suggests a consistently strong selection for this habitat variable. In fact, 51% of all highly-revisited sites are located within 150 m of a watercourse (i.e. creek), and negative coefficients indicate that increasing distance to water reduces the probability of site selection. This corresponds with previous Australian research (Saunders and Kay 1991; Dexter 1996; Caley 1997; Mitchell *et al.* 2007b). Despite waterbodies demonstrating significance overall, individually, Arcadia was the only site where feral pigs showed significant selection for this habitat variable. This may be an artefact of sample size, with 56.4% of pigs in this

study from this site. The lack of significant selection for waterbodies at Downfall and Palerang may reflect differing requirements for water for pigs at these sites in comparison to Arcadia. The study periods at Arcadia and Downfall demonstrated below average rainfall (Bureau of Meteorology 2022b, 2022c), while Palerang demonstrated well above average rainfall (Bureau of Meteorology 2022a), possibly because it provides access to ephemeral water that is not captured by spatial layers. Future epidemiological modelling projects and habitat suitability assessments should consider the positive influence that preferred habitats, watercourses and, in drier periods and locations, waterbodies can have on contact rates and model accuracy. Similarly, pest management programs should consider how these factors influence device encounter rates for monitoring and control programs.

Landscape composition (i.e. proportions of vegetation type) differed across all three study sites, likely influencing site-specific habitat selection as seen in Table 2. Cultivation was selected for at Arcadia but not Downfall, despite representing similar proportions of the landscape (0.83 and 0.90%, respectively). However, the crop type and status (e.g. fallow, planted) of these cultivated areas is unknown. Although targeting of such relatively small and defined areas could be useful for improving efficiencies in pest control programs, actual use may depend on other factors (i.e. crop type and status) that could not be accounted for here. Our finding that 89% of highly-revisited sites in woody vegetation are within 150 m of the interface between woody and herbaceous vegetation corresponds with the findings of other studies. Caley (1997), Saunders and Kay (1991) and Thurfjell *et al.* (2009) all reported high usage of landscape at the interface of open and dense vegetation, citing both shelter and foraging opportunities. This suggests that disease spread modelling and feral pig control programs should consider the effect of ecotones to refine results or improve efficacy.

Shelter-related recurse points (i.e. medium woody vegetation and waterbodies) were also typically utilised for longer periods and more frequently than others (Table 3) with hot weather likely to emphasise their importance (Dexter 1999). It is also possible that denser vegetation provides for some foraging behaviour (Mitchell and Mayer 1997; Vernes *et al.* 2001; Mitchell *et al.* 2007a) and potentially some water-driven behaviour. It is possible that control tool encounter rates could be improved by targeting such areas, but more research is required to confirm this. The positive relationship between site selection and distance from roads and tracks at Downfall (Supplementary Table S4), suggests that pigs at this site avoid habitat in close proximity to these landscape features, supporting Johann *et al.* (2020). Our results show that there is no advantage to be gained from placing control (track baiting, traps) and monitoring (cameras or road-based track counts) tools in areas close to tracks or roads to increase the encounter rate. But given the significant site differences in this study, local knowledge of landscapes, environmental conditions and pig behaviour is of

extreme importance for effective localised pest control programs.

It is a limitation of this study that the recurse method only assesses the top 15% of highly-revisited points. It is possible that pigs utilise a habitat frequently, but not the same geographical location (i.e. < 50 m, as per the recurse method), thus misrepresenting the habitat utilisation. Given the exclusion of watercourses from the frequency and intensity analysis, it is possible that the high use of locations where wooded vegetation adjoins watercourses (i.e. vegetated creek lines), corresponding with significant selection for habitat with proximity to watercourses, increases the apparent use of woody vegetation. However, such habitat likely provides convenient access to shelter, water and possibly food and is therefore very important for targeting feral pigs. Through satellite imagery, we also visually identified refuse tips, feedlots, water troughs, tanks and landscape drainage lines as highly-revisited sites (Wilson unpubl. data). But as our data layers do not adequately capture these features, it is difficult to consistently identify and quantify them, thus their influence on revisitation could not be assessed in this study.

This research has quantified and discussed influences on the movements and site revisitations of feral pigs across four study sites in eastern Australia. The strong preference of habitat in close proximity to watercourses and to vegetative ecotones, indicates that the refinement of control programs may be achieved by targeting such areas to increase encounter rates with control tools. Similarly, the significantly higher crepuscular and nocturnal movements of feral pigs may mean that late-afternoon baiting could result in higher encounter rates with more attractive, palatable and lethal baits. Maximising control tool encounter rates by targeting focal areas at key times may increase effectiveness with a concomitant reduction in cost and effort (Recio et al. 2017). Similarly, these areas of high activity may also provide a focal point of contact, interactions or connectivity between sounders of feral pigs (i.e. a higher risk disease transfer site) and may be applicable in disease spread models. Accounting for the movements of male pigs should also be considered in disease modelling, due to their higher movements and possibly higher inter-sounder connectivity. Understanding and applying fine-scale movements and habitat use of feral pigs is critical for improving efficiencies in both pest management and in epidemiological modelling of emergency animal diseases such as ASF and FMD (Cowled and Garner 2008).

Supplementary material

Supplementary material is available [online](#).

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Data availability. The data that support this study were obtained from Southern Queensland Landscapes by permission. Data will be shared upon reasonable request to the corresponding author with permission from Southern Queensland Landscapes.

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