

Pre-eradication assessment of feral cat density and population size across Kangaroo Island, South Australia

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Abstract

Context. Feral cats (*Felis catus*) are a significant threat to wildlife in Australia and globally. In Australia, densities of feral cats vary across the continent and also between the mainland and offshore islands. Densities on small islands may be at least an order of magnitude higher than those in adjacent mainland areas. To provide cat-free havens for biodiversity, cat-control and eradication programs are increasingly occurring on Australian offshore islands. However, planning such eradications is difficult, particularly on large islands where cat densities could vary considerably.

Aims. In the present study, we examined how feral cat densities vary among three habitats on Kangaroo Island, a large Australian offshore island for which feral cat eradication is planned.

Methods. Densities were compared among the following three broad habitat types: forest, forest–farmland boundaries and farmland. To detect cats, three remote-camera arrays were deployed in each habitat type, and density around each array was calculated using a spatially explicit capture–recapture framework.

Key results. The average feral cat density on Kangaroo Island ($0.37 \text{ cats km}^{-2}$) was slightly higher than that on the Australian mainland. Densities varied from 0.06 to $3.27 \text{ cats km}^{-2}$ and were inconsistent within broad habitat types. Densities were highest on farms that had a high availability of macropod and sheep carcasses. The relationship between cat density and the proportion of cleared land in the surrounding area was weak. The total feral cat population of Kangaroo Island was estimated at 1629 ± 661 (mean \pm s.e.) individuals.

Conclusions. Cat densities on Kangaroo Island are highly variable and may be locally affected by factors such as prey and carrion availability.

Implications. For cat eradication to be successful, resources must be sufficient to control at least the average cat density ($0.37 \text{ cats km}^{-2}$), with additional effort around areas of high carcass availability (where cats are likely to be at a higher density) potentially also being required.

Additional keywords: camera trapping, *Felis catus*, habitat use, invasive species, spatially explicit capture–recapture, threatened species.

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Introduction

Introduced vertebrate predators are one of the top threats to Australian wildlife (Evans *et al.* 2011) and are a key cause of

biodiversity loss globally (Doherty *et al.* 2016). Of the ~ 34 mammal species that have become extinct in Australia since colonisation, the feral cat (*Felis catus*) and red fox

(*Vulpes vulpes*) are listed as the main cause of extinction for ~22 species, and a contributing cause for many of the others (Woinarski *et al.* 2014). Cats are continuing to drive biodiversity declines across Australia (Woinarski *et al.* 2014, 2017) through predation, competition and disease transmission (Nishimura *et al.* 1999; Veitch 2001; Medway 2004; Phillips *et al.* 2007). As a result, cat-free islands are viewed as critical biodiversity havens (Burbidge and Morris 2002; Nogales *et al.* 2004; Commonwealth of Australia 2015). This is especially so given that eradicating feral cats from islands may provide long-term benefits, assuming adequate biosecurity, whereas comparable control programs on mainland areas are likely to provide only short-term benefits because of ongoing immigration from neighbouring areas.

For feral cat control and eradication projects to be successful, an understanding of variation in density across the target area is critical. Previous reviews have suggested that variation in feral cat habitat preferences and density can be difficult to predict (Doherty *et al.* 2014). Studies, in Australia and elsewhere, have suggested that feral cats may favour habitats with some level of low- to mid-storey vegetation structural complexity, such as shrublands and woodlands, avoiding mature pine forests or open grasslands (Horn *et al.* 2011; Bengsen *et al.* 2012). Other studies have reported that cats preferentially use habitat boundaries (Graham *et al.* 2012), or select for more open habitats, avoiding dense vegetation (McGregor *et al.* 2014) and topographically complex areas (Hohnen *et al.* 2016). Given the range of habitat preferences evident across such studies, site specific information on cat habitat use and density is required to inform effective cat control and eradication programs (Dickman *et al.* 2010; Doherty *et al.* 2015).

Kangaroo Island is one of five Australian islands currently targeted for feral cat eradication under the Threatened Species Strategy (Commonwealth of Australia 2015); the eradication program is supported by the local community, as well as the local, state and federal governments. At 4405 km², Kangaroo Island is Australia's third largest island after Tasmania and Melville Island. If the eradication program is successful, it would represent the world's largest island to have had cats eradicated (Campbell *et al.* 2011). The proposed cat eradication is supported for both economic and environmental reasons. Feral cats are contributing to the high incidence of toxoplasmosis and sarcosporidiosis in Kangaroo Island livestock, which significantly reduces their market value (O'Donoghue and Ford 1986; O'Donoghue *et al.* 1987; Taggart *et al.* 2019b). Kangaroo Island is also home to several threatened mammal species, including the southern brown bandicoot (*Isodon obesulus*) and the endemic Kangaroo Island dunnart (*Sminthopsis fuliginosus aitkeni*), that sit within the prey weight range of feral cats, and whose populations would be likely to significantly benefit from the eradication.

Cat eradication commenced on the eastern side of the island (the Dudley Peninsula) in June 2019 (Natural Resources Kangaroo Island 2015). However, the large size of Kangaroo Island and the lack of information on variation in cat density across the island make planning and future resource allocation difficult. An estimate of feral cat density, 0.7 cats km⁻², is available for one site (Dudley Peninsula) on Kangaroo Island, derived by Bengsen *et al.* (2011), but given environmental and

land-use variability across the island, this may be unrepresentative of other parts of the island. A recent study found that, compared with the mainland, relative abundance of cats on Kangaroo Island was 10 times higher (Taggart *et al.* 2019a).

Feral cat density can vary considerably with long-term and recent rainfall, habitat type, land use, and also between the mainland and islands (McGregor *et al.* 2015; Legge *et al.* 2017; Hohnen *et al.* 2019). Legge *et al.* (2017) estimated that, across Australia, there are, on average, 0.27 feral cats km⁻². On Australian islands, there is a negative relationship between cat density and island area, with highest densities (sometimes over an order of magnitude higher than the average mainland estimates) being found on smaller islands (Legge *et al.* 2017). This is likely to be driven by the high availability of food on small islands, such as seabird colonies and shoreline debris, and the absence of at least some other predators.

Given the long-term goal of eradicating cats from Kangaroo Island, more information is required about how cat density varies among habitats across the island. Accurate estimates of density in different habitats could help managers control cats more efficiently, such as, for example, by indicating the appropriate densities of baits or traps, and to measure cat density reduction as eradication is undertaken. Here, we assess variation in feral cat density across the three most prevalent habitat types on Kangaroo Island, and provide the first estimate of total population size.

Materials and methods

Study area

The present study was conducted on Kangaroo Island (4405 km²), South Australia (Fig. 1), in farmland, conservation reserves (Flinders Chase National Park, Ravine des Casoars Wilderness Protected Area, Kelly Hill Conservation Park, Simpson's Conservation Area) and crown land. The climate on the island is temperate with warm dry summers and cool wet winters and there is a notable rainfall gradient from the east (500 mm annual rainfall) to the west (700 mm annual rainfall; Bureau of Meteorology 2019). The vegetation of western Kangaroo Island is dominated by an overstorey of Kangaroo Island mallee-ash (*Eucalyptus remota*), brown stringybark (*E. baxteri*) or coastal white mallee (*E. diversifolia*; Ball and Carruthers 1998). In contrast, much of the east of the island is cleared farmland and much of the on-farm remnant vegetation is dominated by an overstorey of Kangaroo Island narrow-leaved mallee (*Eucalyptus cneorifolia*).

Unlike most of mainland Australia (where the red fox, *Vulpes vulpes*, is widespread), the feral cat is the only introduced predator on Kangaroo Island, which also does not have populations of dingoes or wild dogs. Hence, population size, density and habitat use of cats on Kangaroo Island will be unaffected by any influence from these potential competitors and predators.

Camera trapping

Between September 2017 and December 2018, we placed nine arrays of between 14 and 44 motion-sensor cameras across the study area, including three arrays each in the three main landscape types, namely, forest, farmland and the forest-farmland boundary (see Table 1 for deployment dates). The camera arrays

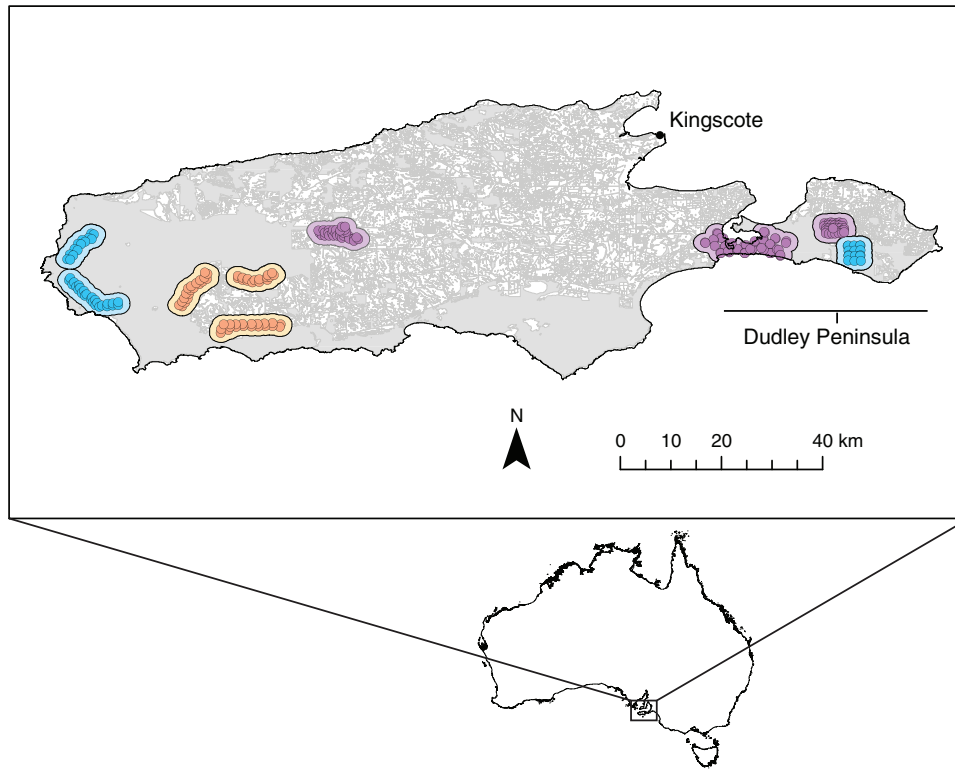


Fig. 1. The locations of motion-sensor camera arrays (including a 2.18-km-diameter buffer) deployed during the present study. Blue shading indicates arrays located primarily in forest, yellow indicates those located on forest–farmland borders, and purple those in farmland. Grey shading indicates forested areas, and white indicates cleared farmland and, less commonly, natural grassland.

Table 1. Number of cats identified on each array during the period of camera deployment

Array	Transect	Cat passes	Identifiable cat passes	Number of individuals	Trap-nights	Year	Time period
Border 1	1	41	31	7	900	2017	Oct.–Dec.
Border 2	2	50	36	10	900	2017	Oct.–Dec.
Border 3 ^A	3	23	17	7	720	2017	Oct.–Dec.
Forest 1	1	127	95	11	1246	2017	Dec.–Feb.
Forest 2	2	92	76	18	2314	2017	Dec.–Feb.
Forest 3	3	29	24	7	1168	2018/19	Nov.–Jan.
Farm 1	1	70	51	12	1612	2018	Sep.–Nov.
Farm 2	2	148	117	26	2304	2017	Dec.–Feb.
Farm 3	3	149	105	30	2196	2018/19	Dec.–Feb.

^ADensity was not calculated for one border array because of insufficient recaptures of individuals on multiple cameras.

varied in their design (Table S1, available as Supplementary material to this paper), but all consisted of two to three parallel transects of cameras (forming a thin rectangular grid), sometimes being constricted by landscape features such as a narrow coastal isthmus, or farmland boundary. Parallel transects were used (rather than square grids), because some habitats such as forest–farmland boundaries, and the farms we used, tended to be long and linear in shape, and a square grid would not have fitted. Also, a previous study found that parallel transects were a reliable means of assessing variation in cat density across the landscape (McGregor *et al.* 2015). Most cameras were spaced

~700 m apart; however, where the terrain constrained camera placement (e.g. steep ravine, or a change in habitat type), they were placed slightly closer or further away (0.5–1 km). The spacing was chosen on the basis of GPS tracking of 33 feral cats on the Dudley Peninsula, which suggested that cats have an average home range of 3.72 km² (P. Hodgens, unpubl. data). The diameter of a 3.72-km² circle is 2180 m; therefore, with cameras spaced at an average distance of 700 m, a cat would have access to multiple cameras within its home range. Although the design differed among arrays, there was unlikely to be any bias or systematic differences in the estimates derived from these

methodological variations. At the time of the study, there had been minimal cat control around most arrays, apart from the array on the Dudley Peninsula isthmus. At this array, 12 feral cats were culled while camera deployment was taking place (P. Hodgens, unpubl. data).

We used Reconyx® (Holmen, WI, USA) Hyperfire HC600 or PC800 cameras with infrared flash and a shutter speed of 0.2 s. Cameras were programmed to take three images per trigger, 1 s apart, with there being no minimum time delay between triggers. Unbaited cameras were attached to trees or stakes 30–40 cm from the ground and all obstructions within 1.5 m of the front of the camera were removed. Cameras were placed in open areas or along animal trackways, because tracking of cats elsewhere in Australia has indicated that although cats do not show strong preferences for tracks, they will move along them for short distances if they are encountered (McGregor *et al.* 2015). Cameras were deployed for 6–12 weeks.

Each pass of a cat in front of a camera was examined and the pelage markings, particularly on the lower legs and tail, were noted. Individual identification of cats on the basis of these pelage markings was performed using the methods outlined in McGregor *et al.* (2015), where markings of each animal are used to identify individuals on subsequent passes. Once all cats from an array had been identified, the set of photos was re-examined twice for any inconsistencies in identification. The images of cats were then re-examined by volunteers, using the same methods, and the identification of individuals compared between the two processes. Some cats were unidentifiable from the camera images either because they had no unique pelage or body markings (such as black cats) and these were included in the models as ‘unmarked’ individuals. Other images could not be identified to individual cats because the cats in the image were orientated towards the camera at an angle where critical identifying features such as the shoulder and rump were not visible. These individuals were included in the models as ‘uncertain’.

Statistical analyses

The cat-encounter history was divided across each 6–12-week period into nights, and cats were recorded if present at a given detector on a given night. Density was estimated using a spatially explicit mark–resight approach in the package ‘secr’ ver. 3.2.1 in the program R (Efford 2019). This approach requires the estimation of a buffer, which is the maximum distance from the home-range centre of a given animal, where the probability of detection approaches zero. We chose a buffer of 2180 m, which is the diameter of a circle with an area of 3.72 km², which is the average home range of feral cats on eastern Kangaroo Island on the basis of a study of 33 cats (P. Hodgens, unpubl. data). Three arrays (Border arrays 1 and 2, and Farm array 1) appeared to have cats with large home ranges and, therefore, required a larger buffer size (Fig. S1, available as Supplementary Material to this paper). For these arrays, we used the buffer width produced by the ‘suggest.buffer’ function in the ‘secr’ package. In all models, we used the half-normal detection function (HN). We then created a set of models with variables that influence the estimated probability of detecting an individual at the centre of its activity range (g0), including the following: ‘b’, a learned

response to cameras; ‘t’, variation in detection with time; and ‘v1’, variation in detection between cameras on roads and those on trackways. We also modelled a set of variables that might affect sigma (the shoulder of the detection function), including the following: ‘t’, variation in home range through time; and ‘h2’, variation in home-range size among individuals. All models were compared using Akaike information criterion (AIC) scores; the model with the lowest AIC value was used to predict cat density.

We evaluated the correlation between cat density and the proportion of the surrounding area that was either cleared or naturally open (i.e. farmland and unfarmed grassland). This was calculated over a buffered distance of 2180 m surrounding each array (Fig. 1). We then modelled the relationship between cat density and the proportion of farmland in the surrounding area by using simple linear regression. Farmland is defined here as open grassland, including areas such as roadside verges that have been cleared but are not actively farmed.

Results

Individual cats were detected at a minimum of one and a maximum of eight cameras, and, on average, were detected on 2.3 cameras. The mean distance between detection locations averaged across all arrays was 956 m (Table S1). In total, there were 706 cat passes, and 121 individuals were identifiable on 535 of those occasions, from a total of 12 640 camera trap-nights (Table 1). Almost all unidentifiable cat photos were due to poor image quality, such as when the animal was moving quickly, so that the image was blurred. These passes were classified and included in the models as ‘uncertain’ (Table S1). Only one site included individuals that were classified as ‘unmarked’ where no distinct pelage markings were visible (Table S1). Eight of the nine camera arrays deployed across Kangaroo Island had sufficient recaptures of feral cats to compute density estimates (three in forest, three in farmland, and two on the forest–farmland border); Array 3 in the farmland–forest border habitat had insufficient recaptures to derive a density estimate.

Density estimates across the eight arrays varied between 0.06 and 3.27 cats km⁻² (Table 2). For two arrays (Farm 1 and Border 2), the best-fitting model included the g0 variable ‘V1’, which describes a change in detection probability between cameras placed on roads and those placed on trackways (Tables 2, S2). For three other arrays (Forest 1, Forest 2 and Farm 2), the best-fitting model included the sigma variable ‘H2’, which describes variation in home-range size among individuals. For the final farmland array (Farm 3), the best-fitting model included the sigma variable ‘T’, which describes change in home range through time.

Three density estimates were problematic for various reasons. There was an estimated 3.27 cats km⁻² at the third farmland array (Farm 3) on the Dudley Peninsula, being four times higher than the island average. During camera deployment, a farm carcass dump was present on the property, and culling of kangaroos took place on the boundary, with both factors potentially increasing carrion availability and, therefore, cat density. The farmland array on the Dudley Peninsula isthmus displayed a density of 0.59 cats km⁻²; however, 2 weeks before

Table 2. Density estimates for all arrays deployed on Kangaroo Island between September 2017 and December 2018 in farmland, forest and on forest–farmland borders

Variables that influence the estimated probability of detecting an individual at the centre of its activity range (g_0) include: 'b', a learned response to cameras; 't', variation in detection with time; 'l', variation in detection between cameras on roads and those on trackways; and 'n' when g_0 is held constant (~ 1). Variables that influence sigma include: 't', variation in home range though time; 'h2', variation in home-range size among individuals; and 'n' when sigma is held constant (~ 1)

Array	% farmland	Transect	Year	Time period	Cats per km ²	Density s.e.	Lower confidence interval	Upper confidence interval	g_0	g_0 value	s.e.	Sigma	Sigma value	s.e.
Border 1	37	1	2017	Oct.–Dec.	0.06	0.03	0.02	0.17	n	0.05	0.02	n	1548.39	338.61
Border 2	34	2	2017	Oct.–Dec.	0.27	0.10	0.13	0.56	v1	0.05	0.01	n	845.88	129.76
Forest 1	0	1	2017	Dec.–Feb.	0.30	0.11	0.15	0.59	n	0.02	0.00	h2	558.66	82.63
Forest 2	0	2	2017	Dec.–Feb.	0.87	0.36	0.40	1.91	n	0.01	0.00	h2	366.33	88.51
Forest 3	16	3	2018/19	Nov.–Jan.	0.53	0.22	0.24	1.15	n	0.05	0.02	n	328.87	54.98
Farm 1	78	1	2018	Sep.–Nov.	0.19	0.06	0.10	0.35	v1	0.02	0.01	n	1442.81	139.80
Farm 2	50	2	2017	Dec.–Feb.	0.59	0.15	0.36	0.96	n	0.01	0.00	h2	480.78	59.45
Farm 3	68	3	2018/19	Dec.–Feb.	3.27	0.13	3.02	3.54	n	0.09	0.02	t	237.45	14.97

camera deployment, 12 feral cats were removed from the area (P. Hodgens, unpubl. data). Therefore, potentially, this density estimate represents a post-control level that is atypically low. The final problematic array was the third array on the forest–farmland border (Border 3). Although seven cats were detected on this array, four of those individuals were detected only on a single camera, which meant that there were insufficient recaptures to produce a density estimate.

When considering all eight arrays (including the three problematic arrays), the average density (mean \pm s.e.) of feral cats was $0.76 \text{ cats km}^{-2} \pm 0.15$. There was a positive relationship between the density of cats and the amount of farmland in the buffered area surrounding each camera ($R^2 = 0.21$), but the relationship was not significant ($F = 1.61$, d.f. = 6, $P = 0.25$); however, this value is strongly influenced by the high density estimate from the third farmland array. Excluding the three problematic arrays, the average density (mean \pm s.e.) of cats on Kangaroo Island was $0.37 \pm 0.15 \text{ cats km}^{-2}$ and there was a weak negative relationship between the density of cats and the percentage farmland ($R^2 = 0.35$), but this relationship was also not significant ($F = 2.18$, d.f. = 4, $P = 0.21$).

Estimates of detection probability (g_0) did not vary considerably among the arrays (Table 2). Detection probability was highest for the third farmland array (0.09), but values for all other arrays were between 0.09 and 0.01. Because there was no association between habitat type and density, the total number of cats on Kangaroo Island was estimated by multiplying the island area by the predicted average density of feral cats (excluding erroneous estimates). The total number of feral cats on Kangaroo Island (using an average density estimate of $0.37 \text{ cats km}^{-2}$) was predicted to be 1629 ± 661 (mean \pm s.e.).

Discussion

Feral cat densities on Kangaroo Island varied at least three-fold among sites, and not consistently among habitat types. We found that densities could vary considerably within all sampled habitats, suggesting that factors other than broad habitat type may influence cat density. These results also suggest that using estimates from only one or two arrays to generalise and direct

cat-management effort could lead to an under- or over-allocation of effort in some areas. Like on other Australian offshore islands, the average density of cats on Kangaroo Island ($0.37 \text{ cats km}^{-2}$ excluding problematic arrays) was higher than the average density of cats on the mainland ($0.27 \text{ cats km}^{-2}$), but broadly similar to what was predicted for the adjacent mainland ($0.25\text{--}0.4 \text{ cats km}^{-2}$; Legge *et al.* 2017).

A weak negative relationship was detected between the percentage of farmland in the study area and cat density, when the density estimates from arrays in unusual circumstances were excluded. Overall, this suggests that factors other than habitat type may influence cat density across Kangaroo Island. Elsewhere in Australia, feral cat densities vary with some landscape features, but not with others. In north-western Australia, cat densities did not vary considerably with the extent of livestock grazing (McGregor *et al.* 2015), but feral cat site occupancy did vary with topographic complexity (Hohnen *et al.* 2016). Potentially, feral cat densities reflect multiple factors, including prey density and accessibility, cat control, management regimes and intensity, and possibly competition with other predators (Legge *et al.* 2017).

In Australia, there is a relationship between island size and cat density, in that smaller islands tend to have the higher cat densities (e.g. Great Dog Island 0.35 km^2 , density = 57 cats km^{-2} ; Hayde 1992), and larger islands have lower densities (e.g. French Island 173 km^2 , density = $0.75 \text{ cats km}^{-2}$; McTier 2000). This is thought to be driven largely by the high density of prey species (such as seabirds) that small islands often support (Legge *et al.* 2017). The data described here for Kangaroo Island fit with this general trend (Fig. 2), where the island has higher than average mainland densities, but lower densities than smaller islands. A recent study found that the relative abundance of cats on Kangaroo Island was 10 times higher than that on the adjacent mainland (Taggart *et al.* 2019a). Relative abundance (based on an occupancy framework) has a strong positive relationship with density in some situations (Linden *et al.* 2017), but is misleading in others (Carbone *et al.* 2002; Jennelle *et al.* 2002; Sollmann *et al.* 2013). Therefore, although it is likely that density of feral cats on the adjacent mainland is extremely low, deployment of a camera array appropriate for density analysis is required to clarify this discrepancy.

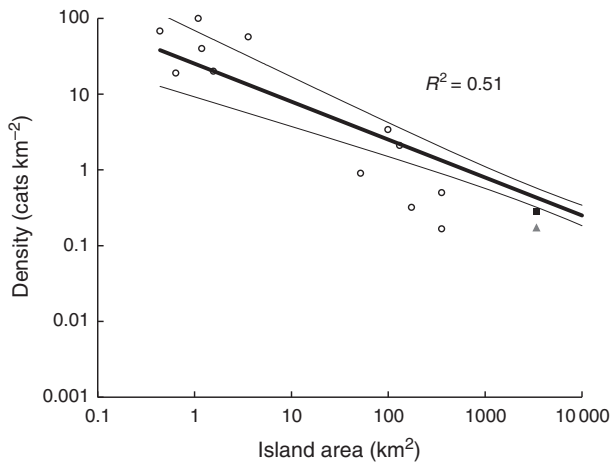


Fig. 2. This figure is adapted from Legge *et al.* (2017) and shows the relationship between island size and density of cats for Australian offshore islands (hollow circles). The values from the current study for Kangaroo Island of 0.76 cats km⁻² (including all arrays) is indicated with the black square and 0.37 cats km⁻² (including just a subset of the arrays) is indicated with a grey triangle.

During the current study, 12 feral cats were removed from the farmland array on the isthmus of Dudley Peninsula while camera deployment was taking place (P. Hodgins, unpubl. data). Our estimate for this site of 0.59 cats km⁻² was slightly higher than a previous post-control estimate. Prior to that previous episode of cat control, Bengsen *et al.* (2011) estimated a density of 0.7 cats km⁻² in the area. Therefore, potentially, the density estimate calculated during the present study represents a post-control level that is slightly lower than what has been naturally maintained in the past. This site is also unusual because it is situated on a narrow isthmus connecting the eastern and western portions of the island. Compared with density estimates from other parts of the island, the estimate of cats on the Dudley Peninsula was reasonably high. The isthmus may act as a land bridge between the eastern and western sides of the island, and, therefore, as a bottleneck for cats that are moving between those areas, potentially maintaining higher densities than in other parts of the island.

A much higher density was estimated in nearby farmland on the Dudley Peninsula (3.27 cats km⁻²); this was over four times the island-wide average. Many of the cats detected on this array were detected on cameras close to a carcass dump also on the southern boundary of the property. During camera deployment at this site, some culling of kangaroos took place on a nearby boundary, with carcasses left on the ground, potentially also attracting cats. Rubbish dumps and areas of unnaturally high food availability are known to boost cat densities (Denny 2005). At small sites with unnaturally high food supply (such as rubbish dumps, or farm carcass sites), cats can transition from solitary behaviour to forming colonies (MacDonald *et al.* 1987; Short *et al.* 2013). Cats in the colony form a matriarchal social hierarchy and have smaller home ranges (centred around the food source) than do their solitary counterparts (Rees 1981). Because of the high densities of cats at rubbish or carcass dumps, the distribution of these sites across the landscape would need to

be taken into account when allocating cat control effort, and they may be critical sites to serve as a particular focus for such efforts.

For two arrays (one on farmland and one on the forest–farmland border), the best-fitting model included the g_0 variable that described a change in detection probability between cameras placed on roads and those on trackways. Previous studies have also shown that cats can preferentially use linear features such as roads, vegetation edges or creek lines (Gehring and Swihart 2003; Graham *et al.* 2012; Doherty *et al.* 2014). However, in the present study, strong variation in detectability between cameras on and off roads was not consistent within habitat types (such as forest–farmland borders). For three other arrays (two in forest and one in farmland), the best-fitting model included the variable that described variation in home-range size among individuals. Male cats often exhibit larger home ranges than do females, particularly during the breeding season (Biró *et al.* 2004; McGregor *et al.* 2015; Bengsen *et al.* 2016). Selection for these variables illustrates that multiple factors, including camera placement and home-range size, can strongly influence density estimates and are important variables to consider during analysis.

Overall, feral cat densities appear to vary considerably across Kangaroo Island and inconsistently among the main habitat types of the island. Cat densities varied between slightly lower than average mainland estimates to 10 times as high, indicating that approaches to cat control on Kangaroo Island should be flexible. For example, extra control effort around rubbish dumps and areas of high carcass availability (where cats are likely to be at locally high density), coupled with allocating resources sufficient to control at least the average cat density (0.37 cats km⁻²) in other areas, could be appropriate. The total estimated number of 1629 feral cats on Kangaroo Island provides some indication of the magnitude of the eradication challenge, but, of course, given the time taken to control cats and their high reproductive potential, many more than this will need to be removed before eradication is achieved.

Conflicts of interest

Sarah Legge is an associate editor for *Wildlife Research* and was the guest Editor-in-Chief for this special edition. Other co-authors of this paper (John Woinarski, Chris Dickman and Brett Murphy) are also guest Associate Editors of this edition. Notwithstanding this relationship, none of the co-authors, at any stage, had editor-level access to this manuscript while in peer review. Such exclusion is the standard practice when handling manuscripts submitted by an editor to this journal. *Wildlife Research* encourages its editors to publish in the journal and they are kept totally separate from the decision-making process for their manuscripts. The authors have no further conflicts of interest to declare.

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References

- Ball, D., and Carruthers, S. (1998). 'Kangaroo Island Vegetation Mapping.' (South Australian Department for Transport, Urban Planning and the Arts: Adelaide, SA, Australia.)
- Bengsen, A., Butler, J., and Masters, P. (2011). Estimating and indexing feral cat population abundances using camera traps. *Wildlife Research* **38**, 732–739. doi:10.1071/WR11134
- Bengsen, A. J., Butler, J. A., and Masters, P. (2012). Applying home-range and landscape-use data to design effective feral-cat control programs. *Wildlife Research* **39**, 258–265. doi:10.1071/WR11097
- Bengsen, A., Algar, D., Ballard, G., Buckmaster, T., Comer, S., Fleming, P. J., Friend, J., Johnston, M., McGregor, H., and Moseby, K. (2016). Feral cat home-range size varies predictably with landscape productivity and population density. *Journal of Zoology* **298**, 112–120. doi:10.1111/jzo.12290
- Biró, Z., Szemethy, L., and Heltai, M. (2004). Home range sizes of wildcats (*Felis silvestris*) and feral domestic cats (*Felis silvestris f. catus*) in a hilly region of Hungary. *Mammalian Biology* **69**, 302–310. doi:10.1078/1616-5047-00149
- Burbidge, A., and Morris, K. (2002). Introduced mammal eradications for nature conservation on Western Australian islands: a review. In 'Turning the Tide: the Eradication of Invasive Species'. (Eds C. R. Veitch, and M. N. Clout.) pp. 64–70. (IUCN SSC Invasive Species Specialist Group: Gland, Switzerland.)
- Bureau of Meteorology (2019). Climate data online. Commonwealth of Australia, Bureau of Meteorology. Available at <http://www.bom.gov.au/climate/data/?ref=fr>. [Verified 2 February 2019]
- Campbell, K., Harper, G., Algar, D., Hanson, C., Keitt, B., and Robinson, S. (2011). Review of feral cat eradications on islands. In 'Island Invasives: Eradication and Management'. (Eds C. Veitch, M. Clout, and D. Towns.) pp. 37–46. (IUCN: Gland, Switzerland.)
- Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J., Griffiths, M., Holden, J., Kinnaird, M., and Laidlaw, R. (2002). The use of photographic rates to estimate densities of cryptic mammals: response to Jennelle *et al.* *Animal Conservation* **5**, 121–123. doi:10.1017/S1367943002002172
- Commonwealth of Australia (2015). 'Threatened Species Strategy.' (Department of Environment and Energy: Canberra, ACT, Australia.)
- Denny, E. A. (2005). Ecology of free-living cats exploiting waste disposal sites: diets, morphometrics, population dynamics and population genetics. Ph.D. Thesis, University of Sydney, Sydney, NSW, Australia.
- Dickman, C. R., Denny, E., and Buckmaster, T. (2010). Identification of sites of high conservation priority impacted by feral cats. Report to the Department of Environment, Water, Heritage and the Arts, Canberra, ACT, Australia.
- Doherty, T. S., Bengsen, A. J., and Davis, R. A. (2014). A critical review of habitat use by feral cats and key directions for future research and management. *Wildlife Research* **41**, 435–446. doi:10.1071/WR14159
- Doherty, T. S., Davis, R. A., Etten, E. J., Algar, D., Collier, N., Dickman, C. R., Edwards, G., Masters, P., Palmer, R., and Robinson, S. (2015). A continental scale analysis of feral cat diet in Australia. *Journal of Biogeography* **42**, 964–975. doi:10.1111/jbi.12469
- Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G., and Dickman, C. R. (2016). Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences of the United States of America* **113**, 11261–11265. doi:10.1073/pnas.1602480113
- Efford, M. G. (2019). 'secr: Spatially Explicit Capture–recapture Models.' Available at <https://cran.r-project.org/web/packages/secr/index.html> [verified 7 December 2019].
- Evans, M. C., Watson, J. E., Fuller, R. A., Venter, O., Bennett, S. C., Marsack, P. R., and Possingham, H. P. (2011). The spatial distribution of threats to species in Australia. *Bioscience* **61**, 281–289. doi:10.1525/bio.2011.61.4.8
- Gehring, T. M., and Swihart, R. K. (2003). Body size, niche breadth, and ecologically scaled responses to habitat fragmentation: mammalian predators in an agricultural landscape. *Biological Conservation* **109**, 283–295. doi:10.1016/S0006-3207(02)00156-8
- Graham, C. A., Maron, M., and McAlpine, C. A. (2012). Influence of landscape structure on invasive predators: feral cats and red foxes in the brigalow landscapes, Queensland, Australia. *Wildlife Research* **39**, 661–676. doi:10.1071/WR12008
- Hayde, K. A. (1992). Ecology of the feral cat *Felis catus* on Great Dog Island. B.Sc.(Hons) Thesis, University of Tasmania, Hobart, Tas., Australia.
- Hohnen, R., Tuft, K., McGregor, H., Legge, S., Radford, I., and Johnson, C. N. (2016). Occupancy of the invasive feral cat varies with habitat complexity. *PLoS One* **11**, e0152520. doi:10.1371/journal.pone.0152520
- Hohnen, R., Murphy, B. P., Gates, J. A., Legge, S., Dickman, C. R., and Woinarski, J. C. Z. (2019). Detecting and protecting the threatened Kangaroo Island dunnart (*Sminthopsis fuliginosus aitkeni*). *Conservation Science and Practice* **1**, e4.
- Horn, J. A., Mateus-Pinilla, N., Warner, R. E., and Heske, E. J. (2011). Home range, habitat use, and activity patterns of free-roaming domestic cats. *The Journal of Wildlife Management* **75**, 1177–1185. doi:10.1002/jwmg.145
- Jennelle, C. S., Runge, M. C., and MacKenzie, D. I. (2002). The use of photographic rates to estimate densities of tigers and other cryptic mammals: a comment on misleading conclusions. *Animal Conservation* **5**, 119–120. doi:10.1017/S1367943002002160
- Legge, S., Murphy, B., McGregor, H., Woinarski, J., Augusteyn, J., Ballard, G., Baseler, M., Buckmaster, T., Dickman, C., and Doherty, T. (2017). Enumerating a continental-scale threat: how many feral cats are in Australia? *Biological Conservation* **206**, 293–303. doi:10.1016/j.biocon.2016.11.032
- Linden, D. W., Fuller, A. K., Royle, J. A., and Hare, M. P. (2017). Examining the occupancy–density relationship for a low-density carnivore. *Journal of Applied Ecology* **54**, 2043–2052. doi:10.1111/1365-2664.12883
- MacDonald, D. W., Apps, P., Carr, G., and Kerby, G. (1987). Social dynamics, nursing coalitions and infanticide among farm cats, *Felis catus*. *Ethology* **28**, 1–66.
- McGregor, H. W., Legge, S., Jones, M. E., and Johnson, C. N. (2014). Landscape management of fire and grazing regimes alters the fine-scale habitat utilisation by feral cats. *PLoS One* **9**, e109097. doi:10.1371/journal.pone.0109097
- McGregor, H., Legge, S., Potts, J., Jones, M. E., and Johnson, C. N. (2015). Density and home range of feral cats in north-western Australia. *Wildlife Research* **42**, 223–231. doi:10.1071/WR14180
- McTier, M. (2000). The home range and habitat selection in a population of feral cats (*Felis catus*) on French Island. B.Sc.(Hons) Thesis, Monash University, Melbourne, Vic., Australia.
- Medway, D. G. (2004). The land bird fauna of Stephens Island, New Zealand in the early 1890s, and the cause of its demise. *Notornis* **51**, 201–211.
- Natural Resources Kangaroo Island (2015). 'Feral Cat Eradication on Kangaroo Island 2015–2030.' (South Australian Department of Environment and Water: Kingscote, SA, Australia.)
- Nishimura, Y., Goto, Y., Yoneda, K., Endo, Y., Mizuno, T., Hamachi, M., Maruyama, H., Kinoshita, H., Koga, S., and Komori, M. (1999). Interspecies transmission of feline immunodeficiency virus from the domestic cat to the Tsushima cat (*Felis bengalensis eupitlura*) in the

- wild. *Journal of Virology* **73**, 7916–7921. doi:10.1128/JVI.73.9.7916-7921.1999
- Nogales, M., Martin, A., Tershy, B. R., Donlan, C., Veitch, D., Puerta, N., Wood, B., and Alonso, J. (2004). A review of feral cat eradication on islands. *Conservation Biology* **18**, 310–319. doi:10.1111/j.1523-1739.2004.00442.x
- O'Donoghue, P., and Ford, G. (1986). The prevalence and intensity of *Sarcocystis* spp infections in sheep. *Australian Veterinary Journal* **63**, 273–278. doi:10.1111/j.1751-0813.1986.tb08065.x
- O'Donoghue, P., Riley, M., and Clarke, J. (1987). Serological survey for *Toxoplasma* infections in sheep. *Australian Veterinary Journal* **64**, 40–45. doi:10.1111/j.1751-0813.1987.tb16126.x
- Phillips, R. B., Winchell, C. S., and Schmidt, R. H. (2007). Dietary overlap of an alien and native carnivore on San Clemente Island, California. *Journal of Mammalogy* **88**, 173–180. doi:10.1644/06-MAMM-A-015R2.1
- Rees, P. (1981). 'The Ecological Distribution of Feral Cats and the Effects of Neutering a Hospital Colony.' Ph.D. Thesis, University of Bradford, Bradford, Yorkshire, UK.
- Short, J., Rakai, L., and Ingram, J. (2013). Control of feral cats at Shire rubbish tips to assist with the protection of the red-tailed phascogale. Project #SUS2.ECO.03.010. Final report to South West Catchments Council, Bunbury, June 2013.
- Sollmann, R., Mohamed, A., Samejima, H., and Wilting, A. (2013). Risky business or simple solution: relative abundance indices from camera-trapping. *Biological Conservation* **159**, 405–412. doi:10.1016/j.biocon.2012.12.025
- Taggart, P., Fancourt, B., Bengsen, A., Peacock, D., Hodgens, P., Read, J., McAllister, M., and Caraguel, C. (2019a). Evidence of significantly higher island feral cat abundance compared to the adjacent mainland. *Wildlife Research* **46**, 378–385. doi:10.1071/WR18118
- Taggart, P., Stevenson, M., Firestone, S., McAllister, M., and Caraguel, C. (2019b). Spatial analysis of a cat-borne disease reveals that soil pH and clay content are risk factors for sarcocystosis in sheep. *Frontiers in Veterinary Science* **6**, 127–132. doi:10.3389/fvets.2019.00127
- Veitch, C. (2001). The eradication of feral cats (*Felis catus*) from Little Barrier Island, New Zealand. *New Zealand Journal of Zoology* **28**, 1–12. doi:10.1080/03014223.2001.9518252
- Woinarski, J., Burbidge, A., and Harrison, P. (2014). 'The Action Plan for Australian Mammals 2012.' (CSIRO Publishing: Melbourne, Vic., Australia.)
- Woinarski, J. C. Z., Garnett, S. T., Legge, S. M., and Lindenmayer, D. B. (2017). The contribution of policy, law, management, research, and advocacy failings to the recent extinctions of three Australian vertebrate species. *Conservation Biology* **31**, 13–23. doi:10.1111/cobi.12852

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