

Contents lists available at [ScienceDirect](https://www.sciencedirect.com)

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Feral cats use fine scale prey cues and microhabitat patches of dense vegetation when hunting prey in arid Australia

K.E. Moseby^{a,*}, H.M. McGregor^{b,c}^a School of Biological, Earth and Environmental Sciences, University of New South Wales, Kensington, Sydney 2052, Australia^b National Environmental Science Program Threatened Species Recovery Hub, Centre for Biodiversity and Conservation Science, University of Queensland, St Lucia, QLD 4075, Australia^c School of Natural Sciences, University of Tasmania, Private Bag 55, Hobart, TAS 7001, Australia

ARTICLE INFO

Keywords:

Feral cat
Hunting
Predation
Australia
Movement
Kill sites

ABSTRACT

Introduced predators are one of the leading causes of decline in island vertebrates. Understanding how they hunt and kill threatened prey can help improve management activities. Although broadscale features are known to influence predator movement patterns, factors influencing fine scale movement are often overlooked. In particular, the influence of prey cues and microhabitat features has received little attention despite predators spending considerable time hunting prey using a range of visual, olfactory and auditory cues. Using feral cats as a case study, we utilised video and GPS collars combined with ground-truthing to determine if predators use fine-scale prey cues or microhabitat features to hunt in an arid environment.

Feral cat activity was comprised of continuous traverses interspersed with periods of stationary activity (GPS clusters) generally less than 40 min in duration. Video collars confirmed that these clusters included the majority of stalk and pounce hunting bouts. Stationary activity was significantly focussed on prominent prey cues such as burrows, foraging digs or warrens of mammalian prey including both exotic (rabbits) and threatened native species (rodents, bilbies and bettongs). Evidence of prey kills was higher at cluster sites. Cats spent significantly more time at microsites with high vegetation cover including single shrubs and trees, suggesting that they use prominent prey cues and patches of thick cover to increase their probability of encountering prey and/or to conceal themselves during hunting or feeding activity. Results suggest prey species with conspicuous cues are at higher risk of predation and this vulnerability could increase over time as resident cats learn to identify the location of prey cues within their home range. Conversely, removing resident knowledgeable predators may reduce predation rates if immigrating predators take time to learn to locate prey cues in their new environment. We urge researchers to investigate fine-scale drivers of movement patterns as this information is likely to be critical for long term management of predator species.

1. Introduction

Introduced predators are a leading cause of population decline in native species particularly in insular environments (Courchamp et al., 2003). Ground nesting birds and Australian marsupials are particularly affected (Medina et al., 2011; Doherty et al., 2016).

* Corresponding author.

E-mail address: k.moseby@unsw.edu.au (K.E. Moseby).

<https://doi.org/10.1016/j.gecco.2022.e02093>

Received 22 November 2021; Received in revised form 14 February 2022; Accepted 13 March 2022

Available online 19 March 2022

2351-9894/© 2022 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Understanding the predatory behaviour of these species is a key step towards developing ways to reduce their impact on native prey. Predators do not move through their environment randomly (e.g. Fryxell et al., 2008; Austin et al., 2004) and prey distribution and abundance remains one of the most important determinants of predator movement patterns (Hayward et al., 2008; Stevens and Krebs, 1986). Predator movement patterns can also vary according to intrinsic factors such as breeding status (Heupel and Simpfendorfer, 2015), sex (Austin et al., 2004) and age (Elliot et al., 2014), and extrinsic factors such as landscape features (topography, elevation), anthropogenic development (Wang et al., 2017; Nisi et al., 2021), roads (Whittington et al., 2005; Dickson et al., 2005) and habitat type (Phillips et al., 2004). Understanding how introduced predators use their environment at both broad and fine scales can assist with developing more targeted control methods for the protection of threatened prey species including guiding the placement of traps or other control devices (Courchamp et al., 2003; Recio et al., 2017).

Most predator movement studies use GPS or VHF collars (Getz and Saltz, 2008; Criffield et al., 2018) and compare temporal or spatial movement patterns with broad habitat features using remote sensing satellite images and mapping tools (McKenzie et al., 2012; Wang et al., 2017; Morato et al., 2018). Recent advances in the resolution of satellite data has enabled spatial movement to be compared with some habitat features such as projected vegetation cover at fine scales (Recio et al., 2013, 2014). Other studies use direct observations of large predators such as lions and cheetahs and compare movement patterns with prey presence or abundance (Funston et al., 2001). However, the influence of prey cues on predator movement patterns has received little attention despite the fact that predators use olfactory, visual and auditory cues to detect prey. Many mammalian predators use olfaction to detect bird or mammalian prey (Lawson et al., 2019; Price et al., 2020) and predators are attracted to areas where prey scent mark (Hughes et al., 2010) or where mammals have permanent nesting sites (Bolton and Moseby, 2004). Other microhabitat variables might significantly influence fine scale predator movement patterns. For example, in hot arid climates, predators can also shelter in underground burrows constructed by prey species (Jones and Coman, 1982), and predators that stalk, such as most felines, may use areas of dense vegetation cover to stalk prey more effectively.

Searching, encountering and detecting prey are three key steps in the predation cycle (Saul and Jeschke, 2015). Thus, targeting prey cues such as burrows and nests during hunting could improve the encounter rate of predators and prey. Subtle prey cues such as latrines, shelter sites and prey foraging digs may also be important hunting sites, particularly for predator species that hunt in habitats where prey are cryptic or in low abundance. The paucity of research on the use of prey cues may be exacerbated by two factors. Firstly, large GPS datasets lend themselves to desktop spatial assessments and modelling. Although broad habitat features such as roads, broad vegetation types and elevation are easy to map using satellite images or GIS software, prey cues are not. Secondly, even if sites are ground-truthed, subtle prey cues are often not easy to identify in the field and require researchers to have experience in the natural history of prey species. This combination means research into spatial movement patterns of predators is often missing the “why?” and instead concentrating on the “what?”. Exacerbating this issue is that predator movement studies on large mammalian predators are often naturally skewed towards focussing on locations where predators spend longer time periods. Long periods of inactivity are likely to involve resting, breeding or feeding at large carcass sites, thus missing shorter hunting bouts, searches for prey or kills of smaller prey. This can lead to bias, particularly in dietary studies that rely on GPS clusters to identify kill sites (Tambling et al., 2010). Understanding the reasons why predators move in certain ways or spend varying amounts of time in different places is critical to understanding predator prey interactions and can assist with predator management (Alterio et al., 1998). For example, manipulating prey cues could help reduce problem predators (Price et al., 2020) or protecting key microhabitat features used by endangered predators could assist their conservation.

We chose the feral domestic cat (*Felis catus*) as a case study to determine the importance of prey cues and microhabitat features in structuring the spatial and temporal movement patterns in predators. Feral cats are adept at hunting and killing a range of prey species including birds, reptiles and mammals (Woolley et al., 2019; Read and Bowen, 2001; Doherty et al., 2015). Their hunting efficacy has made them one of the most lethal predators of island seabird colonies, native Australian mammals and New Zealand birds. Feral cat predation is a leading cause of extinction and decline in island vertebrates (Medina et al., 2011) and cats are listed as one of the worst global invasive species (IUCN/SSC Invasive Species Specialist Group (ISSG)). Cats hunt prey generally using an ambush, stalk and pounce hunting strategy and locate prey using primarily visual and auditory cues (Bradshaw et al., 2012). Some studies suggest that certain prey species are more vulnerable to cat predation than others possibly due to differences in life history, body size, shelter site, foraging behaviour or aggression (Woolley et al., 2019). We suggest that prey with obvious visual cues, i.e. burrow systems or latrines, may be more vulnerable to cat predation because cats could learn to associate these structures with preferred prey species. Seabird nesting colonies are one example of prey with obvious static cues that are repeatedly visited by feral cats on islands (Keitt et al., 2002; Faulquier et al., 2009). Understanding how feral cats use particular habitat features and prey cues within the landscape is vital for improving control and understanding why predation impacts vary between prey species.

We used fine scale GPS collars combined with intensive site visits to determine how feral cats moved and hunted in arid Australia. We used GPS fix clusters to identify areas where cats paused for periods of more than 5 min. GPS cluster analysis has been successfully used to identify carcass kill sites of large carnivores such as lions (*Panthera leo*) (Tambling et al., 2010) and cougars (*Puma concolor*) (Anderson and Lindzey, 2003) by visiting sites of successive fixes in close proximity. We used video collars on other cats in the same location to record stationary hunting bouts and used the duration of these bouts to inform which GPS clusters to use for hunting analysis. We examined the factors associated with the location and duration of clusters including microhabitat variables and prey cues such as burrows, scats and diggings of a variety of mammalian prey species. Due to the low productivity and high aridity of arid sites we hypothesised that feral cat hunting behaviour would be strongly influenced by prey cues in order to increase the chances of prey detection at low densities.

2. Methods

2.1. Study sites

Feral cats were studied at two study sites in South Australia, the Arid Recovery Reserve and the Ikara-Flinders Ranges National Park (I-FRNP, Fig. 1). The Arid Recovery Reserve is located 20 km north of Roxby Downs in South Australia (SA) and incorporates 123 km² of arid land surrounded by a predator-proof fence (Moseby et al., 2011). The reserve includes two experimental paddocks (26 km² Red Lake Paddock and an adjacent 37 km² North Paddock) both of which contained free living feral cats. Mammal species present in the Red Lake Paddock included feral cats, rabbits (*Oryctolagus cuniculus*), native rodents (spinifex hopping mice, *Notomys alexis*, and plains mice, *Pseudomys australis*), reintroduced burrowing bettongs (*Bettongia lesueur*) and bilbies (*Macrotis lagotis*). All of these mammal species have been recorded in the diet of feral cats (Read and Bowen, 2001; Moseby et al., 2011; Bannister et al., 2021). The North Paddock contained native rodents and rabbits and both paddocks supported a wide variety of reptile and bird species (Read et al., 2015). Both paddocks contained similar habitats, comprising longitudinal orange dunes supporting *Acacia* and *Dodonaea* shrubland separated by interdunal clay swales vegetated with chenopods (*Maireana* spp. and *Atriplex* spp.). The climate is arid with hot dry summers and mild winters and the long-term average annual rainfall is 166 mm (Bureau of Meteorology, <http://www.BOM.gov.au>). Rainfall recorded during the study period was 121 mm in 2017 and only 51 mm in 2018.

The Ikara-Flinders Ranges National Park (IFRNP) is a 93,812 ha arid zone conservation reserve situated within an area of continuous semi-arid habitat in northern SA. The national park supports a variety of habitats including rocky ranges and gorges, *Triodia* hummock grasslands, chenopod shrublands, and *Callitris* and mallee *Eucalyptus* woodlands. The park supports introduced cats and mammalian prey such as rabbits and reintroduced western quolls (*Dasyurus geoffroii*) and brushtail possums (*Trichosurus vulpecula*). During the study period the annual rainfall recorded at the nearest weather station with records (Edeowie Station) was below average in 2017, 2018 and 2019 (153, 123, 109 mm respectively <http://www.bom.gov.au/climate/data/stations>).

2.2. Radiocollaring and GPS fixes

Feral cats were captured in wire mesh cage traps, leghold traps or hand nets and fitted with remote download GPS VHF collars (Telemetry Solutions, USA). Collars weighed 110 g and were only fitted to cats weighing at least 2.75 kg to ensure they weighed less than 4% of body mass. Cats were captured at Arid Recovery between August 2017 and June 2018 (n = 9, 6 males and 3 females) and in the Flinders Ranges between March and May 2019 (n = 8, 5 males and 3 females). Captured cats were sedated using a mixture of alfaxin and medetomidine administered intramuscularly and then given a reversal drug (Antisedan- Atipamezole Hydrochloride). In later sessions some cats were fitted with collars using manual restraint and no anaesthesia as this resulted in faster recovery time and meant cats could be released immediately. All cats were released at point of capture within 12 h of capture.

Collars were programmed to not start recording GPS fixes until at least a week after capture to enable cats to recover from any stress related to capture and handling. Collars were then programmed to take GPS fixes every 5 min between 4 pm and 8 am for two to five days. Fixes were not recorded between 8 am and 4 pm to save battery life and because previous research in the area found most cat activity was crepuscular or nocturnal (HM, KM unpublished data). An attempt was made to remotely download GPS fixes after 2 days and again after 4 days in order to collect fresh fixes from the previous two night's movement. For each individual cat, fixes were plotted using ArcGIS to identify fix clusters where two or more consecutive fixes (ie more than 5 min) were spent within 10 m of the first point (based on 4200 fixes taken from three stationary GPS units, where 95% of fixes were within 5 m of the actual location). All fix clusters for the two to five days of movement were identified and visited on the ground within a few days of downloading. In addition, up to 40 single fix sites (randomly chosen) and an addition 40 random fixes were visited. This number was based on the fact that most cats used around 40 cluster sites over the 2–5 days of GPS fixes. Random fixes were identified by selecting a random direction and distance between 10 and 200 m of a single or cluster site and were all located within the home range of each cat but not known to be visited during the study.

2.3. Habitat and prey variables

At each random, single or cluster site we recorded the following attributes within a 10 m x 10 m quadrat centred around each fix. This quadrat area is based on the error value taken from 4200 fixes from three stationary GPS units at the study site where 95% of fixes were within 5 m of the actual location. The open habitat at our arid study site and absence of thick canopy cover assisted in achieving fine scale accuracy of GPS fixes. For cluster fixes, the centre point was determined as the most central location of all fixes recorded.

2.3.1. Animal sign

We recorded presence of scat, foraging diggings or obvious cleared runways for the following mammal species; bilby, rabbit, bettong, rodent or kangaroo (*Macropus* spp.). Despite being too large to be a prey item for cats, kangaroos were included because they create obvious runways that may be used by cats and the addition of a non-prey item allows for improved interpretation of association of cluster sites with prey cues. Foraging diggings and scats were distinguished between species by their size and shape (Moseby et al., 2009a). Kangaroo runways were wider and deeper than runways of rodents or rabbits. Bilbies and bettongs did not create runways that were independent of warrens. The presence of scat, foraging diggings and/or runways were combined to form a category of presence/absence of any sign for each species.

2.3.2. Animal burrow

The presence of any burrows (single entrance) or warrens (multiple entrances) within 10 m metres of the fix site was recorded, along with the number of active entrances. At Arid Recovery where both bettongs and rabbits were present, they often shared large warrens and in these cases, rabbit and bettong warrens were combined for analysis. An entrance was categorised as active if it had no obstruction from soil, vegetation or spiderwebs for at least a depth of 1 m and had disturbed soil or animal tracks at the entrance. Rodent burrows comprised mostly plains mice burrows identified by their location in clay swale habitat, the shallow angle of the burrow, size of entrance and scats. Bilby burrows were typically single entranced in sandy soils with obvious bilby tracks.

2.3.3. Prey remains

We recorded if any fresh or old remains were present at each site including carcasses, bones or feathers of rabbit, bettong, bilby, rodent, reptile and birds. Cats were the only mammalian predator present at the Arid Recovery site and the dominant mammalian predator at IFRNP as aerial baiting for foxes and dingoes had been in place for over 10 years.

2.3.4. Landform

The landform at each site was categorically recorded as either creekline, dune, dune edge, swale, open plain, ridgetop or undulating hill, based on the dominate landform at each site. Creeklines supported the tallest vegetation including *Eucalyptus camaldulensis* or *Acacia* spp., dunes supported *Dodonaea viscosa* and *Acacia ligulata* mixed shrubland, swales were gibber interdunal areas with chenopod shrublands, plains were stony with open grassland, ridgetops supported native pine, *Callitris* spp. and mixed shrubs, and undulating hills were vegetated with native pine and *E. intertexta*.

2.3.5. Vegetation cover

At each 10 m x 10 m quadrat we visually estimated the percentage projected cover of vegetation in three height categories. Low (<50 cm) included grass and forb cover, medium (50 cm-1.5 m) included perennial shrubs and tall (>1.5 m) included trees and tall shrubs. Trees and tall shrubs included bullock bush, *Alectryon oleaefolius*, needlewood, *Hakea leucoptera*, emu bush, *Eremophila longifolia*, mulga, *Acacia aneura*, native pine, *Callitris glaucophylla*, rough-barked coolibah, *E. intertexta*, river red gum *E. camaldulensis*, wattle, *Acacia ligulata*, hopbush, *Dodonaea viscosa*, dead finish, *A.tetragonaphylla* and native apricot, *Pittosporum augustifolium*.

2.4. Video collars

Video radiocollars were placed on 18 feral cats (11 males, 7 females) between August 2016 and May 2017 less than 10 km north of the Arid Recovery Reserve to verify behaviours assigned from GPS collars (see [McGregor et al., 2019](#) for full methods). Feral cats fitted with video collars were different individuals to those fitted with VHF collars due to the combined weight of both devices being above the ethical weight threshold (5% of body weight). Collars weighed between 80 g and 180 g (depending on number of batteries), and were only fitted to cats where the collar weighed less than 4% of body weight (e.g. a 180 g collar was only placed on cats weighing 4.5 kg or more). We used this lower weight threshold of 4% to reduce the chance of collars influencing hunting behaviour. Video collars were fitted to cats in a similar sex ratio to those fitted with GPS collars and in the same habitat type to enable comparisons. Videos were watched, and all stationary behaviour (movement of less than 10 m for 5 min or longer, which was equivalent to the temporal resolution of GPS collars used in the present study) was categorised as either hunting (alert head up behaviours such as slow stalk, wait, pounce and consumption of food components), sleeping (lying down and stationary) or other (awake, not moving and not actively hunting e.g. grooming, head down). From these stationary bouts, we ran a single binomial generalised linear model of duration log-transformed (the independent variable) against whether the bout was a hunting event (dependent variable). These results were used to determine the cluster periods most likely to represent hunting behaviour which were used in the following analyses.

2.5. Analysis of cat interest at sites

We investigated whether landform, prey cues or vegetation cover affected the time cats spent at each of the cluster sites. We only used clusters that were most likely to constitute hunting events (less than 60 min in duration as determined by the videocollar data – see results). We used the time spent at each location as the response variable (hereafter ‘duration’). For comparison, we included random sites, which were classed as zero duration (ie not visited), and single fix sites, which were included as 5 min duration. Cluster site duration was the total number of fixes in the cluster (minimum of 2 fixes within 10 m of the first fix) multiplied by the fix frequency (5 min). We log-transformed duration to minimise the skew caused by less common, longer clusters over 30 min. To model factors affecting the duration cats spend at locations, we used mixed-effects linear models using the ‘lmer’ library ([Bates et al., 2015](#)) in R v3.6.1 ([R Development Core Team, 2020](#)). The random effect was each individual cat. Fixed effect variables used included different animal sign (bilby, rabbit, bettong, rodent, kangaroo, each as binary presence/absence variable), animal burrow (bilby, rodent, or large warren (rabbit/bettong combined), each as binary presence/absence variable), number of warren entrances (continuous), landform (creekline, dune, dune edge, grassland, gibber/stony plain, ridgeline, pine woodland; as categorical variable), and percent vegetation cover (<0.5 m, 0.5–1/5 m and > 1.5 m height classes, each continuous). Multiple models containing different sets of these fixed variables were compared using Akaike’s Information Criterion corrected for small sample size (AICc) ([Grueber et al., 2011](#); [Symonds and Moussalli, 2011](#)), as although our ultimate sample size was large, once divided by the number of independent (17) and fixed variables (19) the ratio of variables to samples was low (i.e <40). We compared models with different combinations of variables to determine the most parsimonious. Models compared included a model with only animal variables (sign and burrows), only

landform, only vegetation structure, all combinations of these, and a null model. We thus compared eight models. We considered models within four $\Delta AICc$ of the top model to be well supported (AICcmodavg Mazerolle, 2017).

To evaluate whether inferences of site-level factors at cluster sites were likely associated with predation events, we conducted a second analysis including only cluster sites where prey remains were found. We utilised the same multiple-model inference, variables, and random-effect (individual cat) as the fore-mentioned analysis, but considered the dependent variable to be binary (prey found or not).

3. Results

3.1. Cat video collars

We collected 104 h of animal-borne video data from 18 cats over 22 deployments between August 2016 and May 2017 within the Arid Recovery study site. There were 57 recorded stops (defined as per cluster fixes as movement less than 10 m in 5 min or longer) and of these, 18 involved hunting, 31 involved other and eight were sleeping. For the hunting events, only 39% were successful, the others were unsuccessful sit-and-wait ambush and pounces. The successful hunting events included rabbits, rodents, a gecko, and one instance where a cat ate nine caterpillars. All prey were eaten at the location where they were captured. Within the 104 h video collar dataset, there were 58 other hunting events recorded that were less than 5 min long, consisting entirely of small prey (e.g. reptiles, insects) or failed hunting attempts. There was a strong significant inverse relationship between confirmed hunting events and log-duration of stationary visit (coeff = -1.38 , SE = 0.665, $z = -2.075$, $P = 0.038$ *, Supplementary 1). The probability of a cat hunting declined significantly for bouts more than 60 min in duration, approximately where there was an inflexion point (at 54.6 min). In summary, when the cats were still for less than 60 min, 37% of these events included hunting, yet when bouts were greater than 60 min only 8% included hunting.

3.2. Site visits

From the 17 GPS collars, we recorded 165 full nights of high-frequency GPS fixes at 5 min intervals. During these nights, cats moved on average 7 km (6.6–7.6 km 95%CI and min 0.1 km max 16.2 km) and were active 23% of the night (19–26% 95%CI and 3–97% range).

In total we visited 1592 sites, 1172 at the Arid Recovery Reserve and 420 in the Flinders Ranges. Sites comprised 41% random non-visited sites (368 Arid Recovery, 124 Flinders Ranges), 32% single-fix sites (357 Arid Recovery, 147 Flinders Ranges) and 37% cluster sites (447 Arid Recovery, 149 Flinders Ranges). Of the cluster sites, 405 were less than 60 min in duration and 191 were greater than 60 min (Fig. 2). Only clusters less than one hour were used in our analyses, and most were less than 30 min in duration (Fig. 2).

3.3. Model outputs

Of the eight mixed-effect models comparing factors affecting visit duration (with individual cats as a random effect in all models), the top model included both vegetation cover and animal sign, and was more than $\Delta = 4$ from the next model (Table 1), indicating it was the only model with strong support. This model had a marginal R^2 of 0.2. Within this model, increasing vegetation cover was a strong predictor of visit duration, with cats spending approximately 20 min longer at sites with dense cover in the medium (coeff = 2.01, SE = 0.26) and tall vegetation classes (coeff = 1.85, SE = 0.27), over open sites (Table 2, Fig. 3 and 4). All vegetation height classes had a stronger influence on site visit than prey cues. Of the variables related to animal sign, cats spent significantly more time at sites

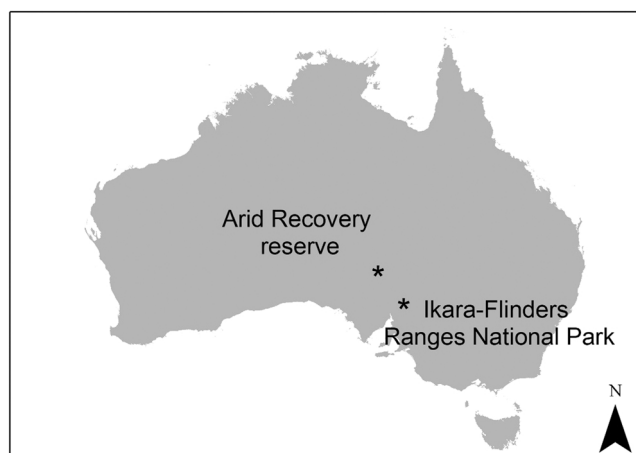


Fig. 1. Location of the two study sites in Australia.

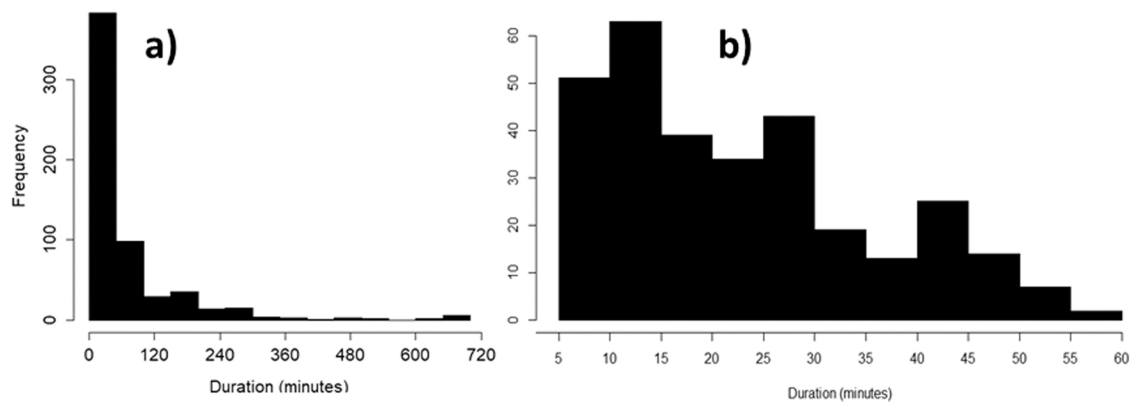


Fig. 2. Histogram of the duration of clusters (recorded stops from GPS collars) where feral cats were stationary for more than 5 min (a) and for stops of less than 60 min only (b).

Table 1

Model selection for duration of time spent at sites by feral cats for visits of less than 60 min in duration. The models compared contained different sets of fixed-effect variables, including site-specific vegetation cover ('Veg'), animal sign in the form of burrows, runways or scat ('Animal'), and/or landform category ('Landform'). Null model contained only the intercept. All models contained individual cat as a random-effect.

Model description	df	logLik	AICc	delta	weight
Veg + Animal	15	-2132.9	4296.2	0	0.894
Veg + Animal + Landform	21	-128.87	4300.4	4.25	0.106
Veg	6	-190.18	4392.4	96.27	0
Veg + Landform	18	-182.85	4402.2	106.05	0
Animal	12	-189.21	4402.6	106.48	0
Animal + Landform	12	-189.51	4403.2	107.08	0
Null	3	-256.29	4518.6	222.44	0
Landform	9	-254.33	4526.8	230.63	0

with rabbit and bettong warrens with multiple entrances (coeff=0.24, SE=0.05, up to 4 extra minutes dependent on number of entrances), small mammal burrows (coeff=0.65, SE=0.09, approx. 3 extra minutes), and sign of bilby activity (coeff=0.4, SE=0.1, approx. 1 extra minute, Table 2, Fig. 3 and 4). These mixed effects models indicated that there were strong trends across all cats in this study, but there was also variation between individual cats (random intercept -standard deviation of 0.231 for intercept and 1.234 for residuals). Landform was not present in the top model and different landforms were spread evenly between single, random and cluster sites (Supplementary 2).

Cluster sites of between 5 min and 60 min were more likely to be located at sites with thicker vegetation cover, bilby sign, warrens with more entrances and small mammal burrows than at random or single sites. Although duration was modelled as a continuous dependent variable we also present the results categorically for the purposes of easy visualisation and interpretation (Fig. 5). Cluster

Table 2

Model parameters for the top model (Table 1) of the duration of time spent at sites by feral cats for visits of less than 60 min. Properties for each variable at each site were measured in the field. For the variables under 'Animal sign', these refer to presence of burrows or sign (e.g. scats, diggings) for each species. For variables under 'Vegetation', these refer to the visually estimated cover of vegetation with three height classes.

Parameter	Estimate	Std. Error	t value	P	
(Intercept)	0.77	0.09	8.54	< 0.001	**
Animal sign					
Bilby burrow	0.44	0.24	1.79	0.073	
Rabbit/bettong warren	0.18	0.14	1.28	0.2	
Small mammal burrow	0.65	0.09	7.19	< 0.001	**
Warren entrances	0.24	0.05	5.18	< 0.001	**
Bettong sign	0.13	0.09	1.43	0.154	
Bilby sign	0.40	0.10	4.12	< 0.001	**
Rabbit sign	0.10	0.11	0.97	0.335	
Kangaroo sign	-0.09	0.19	-0.50	0.618	
Small mammal sign	0.11	0.15	0.77	0.444	
Vegetation					
Veg < 0.5 m	0.84	0.26	3.26	0.001	**
Veg 0.5–2 m	2.01	0.26	7.86	< 0.001	**
Veg > 2 m	1.85	0.27	6.82	< 0.001	**

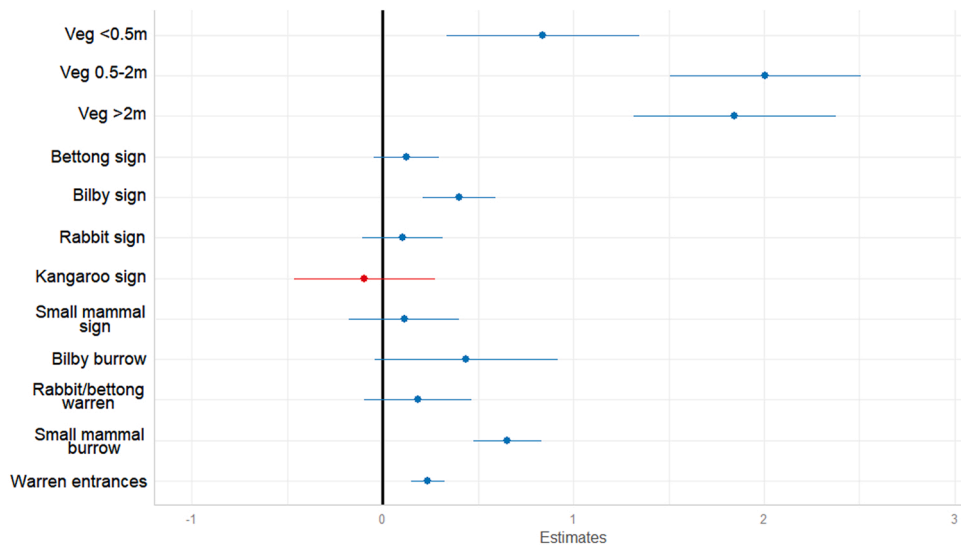


Fig. 3. Model estimates for variables included in the top model. Coloured dots indicate average, lines indicate 95% confidence intervals, and blue lines indicate a positive trend and red a negative trend.

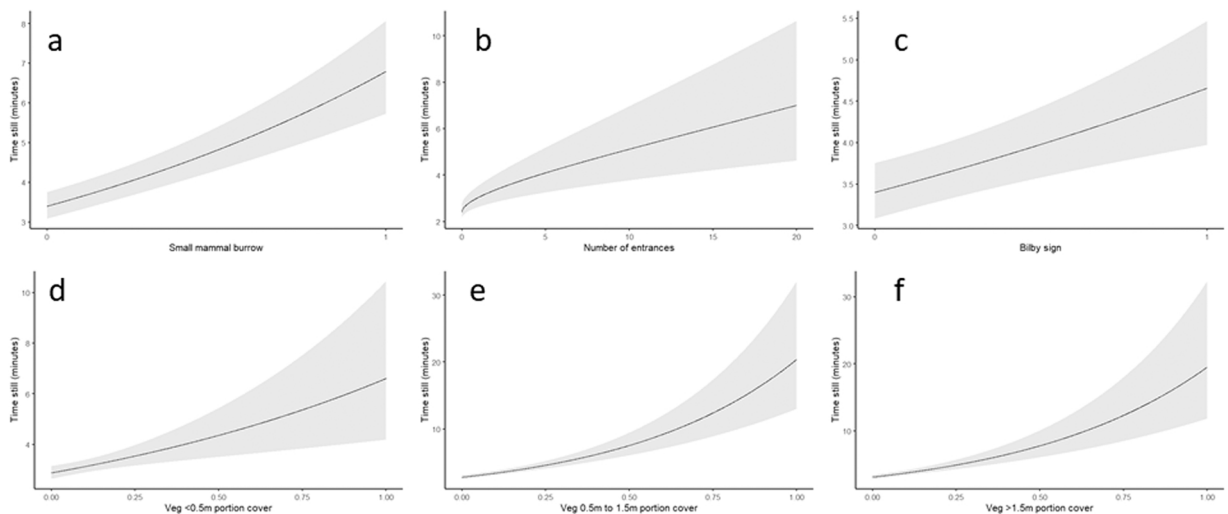


Fig. 4. modelled outputs of prey (a,b,c) and habitat (d,e,f) variables relative to time spent still at a location (5–60 min).

sites supported on average twice as much vegetation cover as random sites: clusters 8% cover of tall vegetation, 14% cover of medium vegetation and 10% cover of low vegetation (total 31% cover) compared with random sites 3%, 5% and 7% respectively (total 15%, Fig. 5). Additionally, 37% of cluster sites were at small mammal burrows compared with 10% of random sites and 16% of single fix sites. Cluster sites had an average of 3 warren entrances per site compared with 1 at single and random sites (Fig. 5).

3.4. Field observations

At Arid Recovery, carcasses were found at 5% of cluster sites and at 1.4% of single and 0.5% of random fix sites (Table 3, Fig. 6). These carcasses included adult and juvenile bilbies, adult and juvenile bettongs, rabbits, a bearded dragon, a cinnamon quail thrush, a crested pigeon and two unidentified small birds. There was a significant difference in the proportion of prey remains found at cluster, single and random fix sites (chi-squared=18.42, df=2, $P < 0.01$). In the Flinders Ranges, remains of rabbits and a bird were found at 3 cluster sites (2%) and not at any single or random fix sites.

Many cluster sites were in slightly elevated areas that afforded good unobstructed views of bettong and rabbit warrens. Some clusters were located in piles of dead branches with litter, within thick bushes, within tree root buttresses, under logs or under single large trees that were prominent in the environment. Even in gibber swales where vegetation cover was low, cluster sites were often in

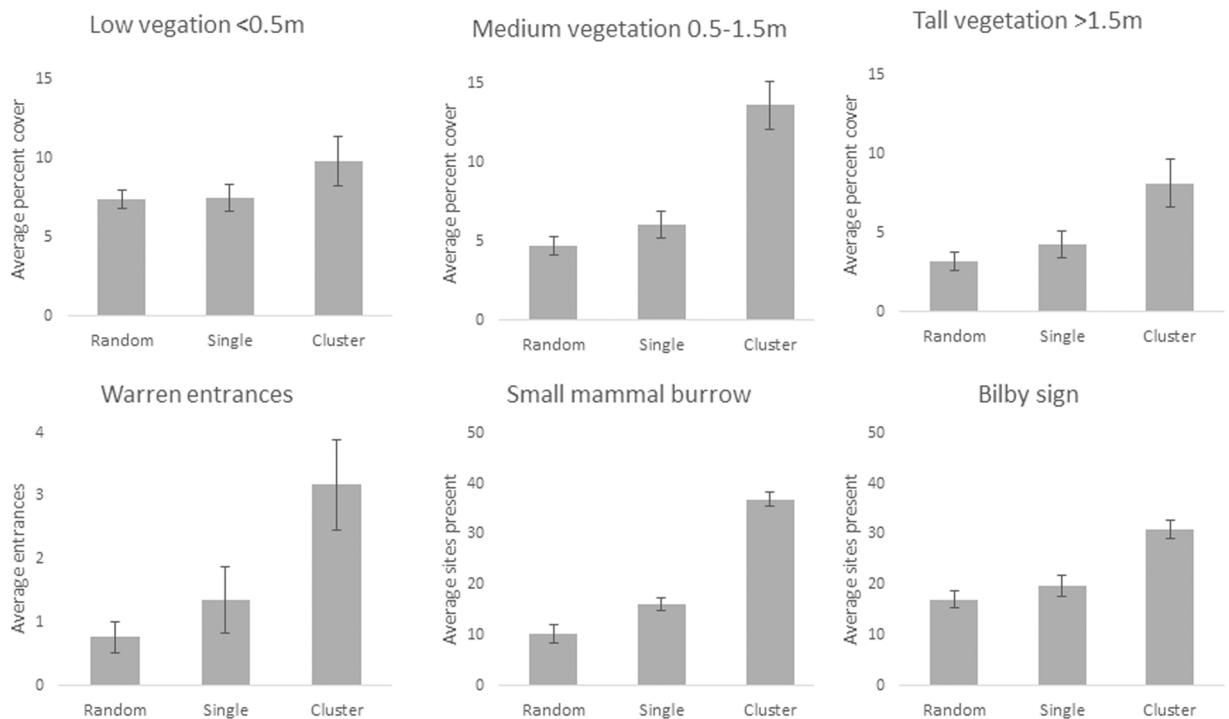


Fig. 5. Average values for variables in the top model explaining the duration of time (<1 h) spent by cats at different locations. Although duration was modelled as a continuous variable, it is presented here categorically for random fixes, single GPS fixes and cluster sites 5–60 m in duration for the purpose of visualisation only. Values were averaged for each cat, and the average of all cats is presented. Bars represent 95% confidence intervals.

Table 3

Carcass remains of different prey species recorded at sites surveyed at the two study areas (Arid Recovery and Flinders Ranges). Sites are based on GPS movements of feral cats, with 'Cluster' sites being those where a cat remained stationary for more than 5 min, 'Single' sites those where a cat was present for less than 5 min (e.g. was moving), and 'Random' sites at nearby randomised locations. Sites were visited within four days of the cat movement being recorded, and the number of sites with prey carcasses present is included.

	N	Rabbit	Bettong	Bilby	Bird	Reptile	Rodent	Sites with prey remains (%)
ARID RECOVERY								
Cluster	448	5	9	3	3	1	1	22 (5%)
Single	357	0	4	1	0	0	0	5 (1.4%)
Random	368	0	2	0	0	0	0	2 (0.5%)
FLINDERS RANGES								
Cluster	149	2	n/a	n/a	1	0	0	3 (2.0%)
Single	147	0	0	0	0	0	0	0
Random	124	0	0	0	0	0	0	0

patches of tall grass close to warrens. In areas where small mammal burrows were present in the swales, cluster sites were usually immediately in front of a burrow entrance, often with another subsequent cluster site at a second burrow entrance a few metres away.

When only cluster sites with prey carcasses found were included in analysis, the top model was the same as when all clusters between 5 and 60 min were included (Supplementary 3). Within this top model, output from percent vegetation cover in different height classes remained significant, however, for animal sign only presence of rabbit/bettong warren was significant (compared to small mammal burrow, bilby sign and burrow entrances for the model with all clusters included).

4. Discussion

Although broadscale habitat features such as habitat type, roads, slope and elevation are known to influence movement patterns of predators (Phillips et al., 2004; Whittington et al., 2005; Nisi et al., 2021), the factors that influence fine scale movement patterns are often overlooked (but see Recio et al., 2013, 2014). In particular, most studies of cat movement concentrate on home range size and broad habitat use preferences (Edwards et al., 2001; Moseby et al., 2009b; Bengsen et al., 2012, 2016). Our results suggest that fine scale features have a significant influence on feral cat movement patterns and in particular that feral cats spend significantly more time

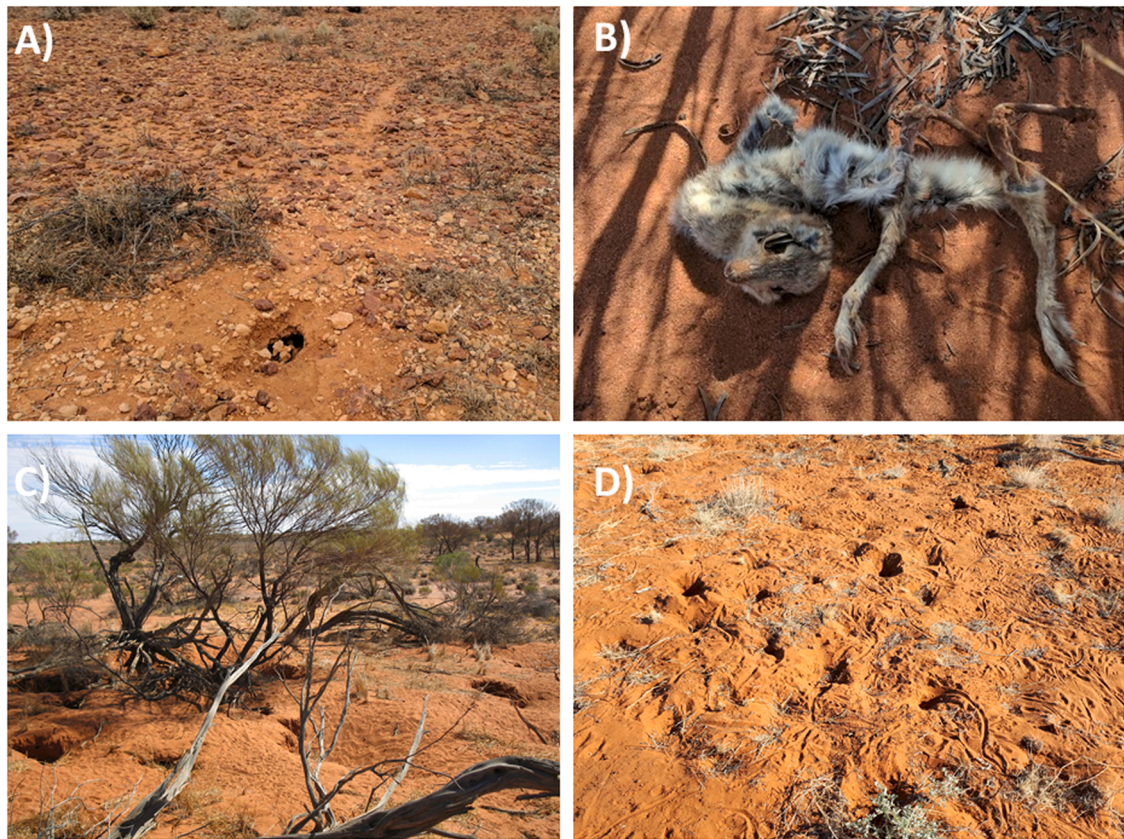


Fig. 6. Photographs of typical habitat features at ‘cluster’ sites, where cats spent between 5 and 60 min, including small mammal burrows and runways (A), kill sites (B), bettong/rabbit warrens with multiple entrances (C) and at sites with evidence of bilby sign (foraging digs and scats) (D).

in areas that contain prominent prey cues such as foraging digs and burrows, regardless of landform.

Previous studies have found predator species alter their space use to maximise interactions with prey. For example, [Kittle et al. \(2016\)](#) found lions preferentially used landscape attributes such as water sources and embankments where total prey abundance or ambush opportunities were highest. Our study found prey cues and microhabitat features were selected by feral cats at very fine scales and were prey specific. Cats have a broad and flexible diet ([Doherty et al., 2015](#)) and the use of different prey cues for different prey species is likely related to the species-specific variation in cue conspicuousness and the proportion of time prey spend there. The most conspicuous prey cues for small rodents are arguably their burrows which have spoil heaps of excavated dirt at their entrance. Conversely, bilbies do not have permanent burrows and move continually between them, often digging new burrows or reusing old ones ([Moseby and O’Donnell, 2003](#)). Burrows are usually small with only 1 or 2 entrances and can be hidden under logs or vegetation. However, they dig conspicuous foraging pits and deposit scats in these areas where preferred food items are present ([Southgate et al., 2019](#)) and reuse these areas over time. Cats in our study spent significantly more time at sites with bilby sign (scats and foraging digs) than bilby burrows suggesting they found it easier to locate conspicuous foraging sites that contain scats than cryptic burrows, or had learned that encounter rates were likely to be higher at foraging sites than at transient burrows that might not be occupied. In comparison, cats spent significantly more time at bettong and rabbit warrens, particularly those with more active entrances. These prey species build permanent warren systems that are used daily and the number of active entrances is significantly related to the number of residents in the warren ([Parer, 1982; Palomares, 2001](#)). At our study site, bettongs can build single burrows that house one individual but more often build complex warren systems that house an average of 4–5 individuals ([Moseby et al., 2018](#)). Historical accounts record some large warrens housing up to 50 or 60 individuals ([Flannery et al., 1990](#)). Larger warrens that support more prey would increase encounter rate. Warrens also provide shelter for a range of commensal reptile, mammal and invertebrate species that are also preyed on by cats ([Read et al., 2008; Dawson et al., 2019](#)), possibly contributing to their attractiveness. Our results are supported by [Read et al. \(2015\)](#) who found higher camera detections of cats at rabbit warrens compared with other sites. At a broader scale, other studies have reported higher cat activity in areas where rabbit density is high ([Recio and Seddon, 2013; Moseby et al., 2021](#)).

Interestingly, rabbit latrine sites were not foci sites for predator activity despite the fact that they are prominent in the environment and visited regularly by male rabbits. However, cats are thought to use auditory and visual cues more than olfactory cues when hunting ([Fisher et al., 2015](#)) which may explain the lower interest at latrine sites. Additionally, rabbit latrine sites are mainly used by male rabbits whereas warrens are foci for breeding thus providing opportunities for both adult and juvenile prey. Warrens are also used by

cats as shelter sites (Moseby et al., 2009b) thus increasing their time spent at these locations. Multiple prey cues were often present at a site e.g. runways at warrens or scats at bilby foraging digs, making it difficult to determine which cues were predominantly being used by cats.

Unfortunately, we were unable to determine if prey were present at focal sites used by cats at the time cats were present or if cats waited at prey cue sites for prey to visit. The former suggests that prey cues are just a proxy for prey presence and that cats are simply responding to visual sightings of prey, and the latter suggests cats seek out prey cues in order to increase possible encounter rate with prey. We postulate that the latter is more likely for several reasons: There was a very low incidence of carcass remains found at cluster sites suggesting that many hunting attempts were unsuccessful either due to prey not always being present at prey cue sites or attempts to catch prey being unsuccessful; the frequency of duration of time spent at cluster sites declined at a steady rate implying varying time spent at prey cue sites. If prey were always present then the time periods spent at cluster sites would likely be shorter and similar in duration. Finally, rabbits, bettongs, bilbies and rodents in our study region spend considerable time foraging away from their burrows and warrens (up to 1 kilometre, Finlayson and Moseby, 2004; Moseby et al., 2005; Moseby and Read, 1999) and if cats were responding only to the visual presence of prey then we would expect less focus of clusters within 10 m of warrens. A limitation of our study was that we were unable to differentiate between the use of thick cover for hunting vs prey consumption but the video data suggested prey were eaten immediately after capture without being moved suggesting that thick cover may be used for both hunting and prey consumption.

Our results suggest that mammal species with conspicuous burrows, latrine sites and foraging diggings are more likely to be susceptible to cat predation than those that move frequently and do not have permanent warren systems. Cats apparently modified their behaviour to increase time spent at these sites which would maximise the chance of encountering and detecting prey, key steps in the predation cycle (Saul and Jeschke, 2015). Increased detection is particularly important for predator species that hunt in habitats with low productivity where prey species are often at low density and patchily distributed. Our study was conducted in large arid and semi-arid areas with low annual rainfall, and cat home range size is known to be significantly higher at these sites than in more mesic areas (Bengsen et al., 2016). Repeating this study at more mesic sites would provide insights into whether this focus on prey cues is related to productivity. Limited battery life meant we only recorded crepuscular and nocturnal activity during the cooler months when reptiles are inactive and cats are known to prey more on nocturnal mammals (Read and Bowen, 2001; Woinarski et al., 2017). More data collected during daylight hours and the summer months would reveal hunting behaviour on birds and reptiles and provide information on whether cues are also used for these taxa. We predict that reptiles with prominent warrens systems and birds with conspicuous accessible nests will also be targets for feral cat hunting behaviour. In support of this prediction, a number of skink species that have conspicuous latrine sites and warren systems have declined in Australia and are listed as threatened by feral cats including the great desert skink (*Egernia kintorei*) (McAlpin, 2001). In a similar behaviour to that recorded in our study, cats have been observed waiting outside warren entrances for these skinks to emerge (McAlpin, 2001).

Feral cats and other predators have been found to prefer certain habitat types (Moseby et al., 2009b) and change their movement patterns in relation to broad features like roads and elevation (Wang et al., 2017; Whittington et al., 2005; Dickson et al., 2005; Phillips et al., 2004). However, we did not find landform to significantly influence time spent at sites less than 60 min in duration suggesting landform may have a stronger influence on broader movement patterns.

The vegetation cover at cluster and single fix sites was significantly higher than at random sites, particularly in the medium and tall height categories, indicating cats prefer to spend time in more structurally complex and denser microhabitat patches within the sparse vegetation of our study sites, at least when hunting. The preference for denser vegetation patches could be indirectly related to prey preferring to forage or shelter in thicker cover and/or due to a preference for cats to use dense vegetation to hide during sit and wait hunting strategies or feeding bouts. GPS fix locations suggested an ambush hunting strategy at prey warrens, burrows and foraging dig sites where short stationary periods, usually less than 15 min, were spent hiding or feeding in thick vegetation at prey cue sites before moving to areas where other prey cues were present. These results were supported by field observations where cluster sites were often located in thicker vegetation patches close to prey cue sites where cats would have clear line of sight of prey whilst being hidden from view. The importance of concealment is supported by studies on other feline species that use thick vegetation cover during hunting (Loarie et al., 2013). Lion kill sites were twice as likely to be found in areas of thick vs open cover (Davies et al., 2016). Interestingly, this preference for denser vegetation cover is in direct contrast to studies that found feral cats prefer habitats with an open understorey and low structural complexity (fire scars or areas with high herbivore grazing; Hohnen et al., 2016; McGregor et al., 2016; Stobo-Wilson et al., 2020). This discrepancy could be explained by open habitats providing more opportunity to move freely and locate prey visually but denser microsites being used at a fine scale to hide during stalk and pounce hunting, and/or for consuming prey.

We are confident that a large proportion of the cluster sites we analysed constituted hunting bouts: significantly more prey remains were found at cluster sites than single and random sites; kangaroo sign, a species that is not hunted by cats, was not a focus of cat activity; and video camera data found stationary periods less than 60 min in length were most likely to constitute hunting bouts. Additionally, our reanalysis of just the GPS clusters where carcasses were recorded yielded similar results to the full dataset. Within this smaller dataset some variables such as small rodent burrows were not significant but this could be because cats are likely to eat these animals whole and so less cluster sites would contain prey remains of rodents and smaller prey. Our use of GPS fix clusters to locate hunting sites is supported by studies of larger predators such as Eurasian lynx (*Lynx lynx*) where GPS fix clusters have been used to locate fresh kills (Krofel et al., 2013). The number of carcasses found at our kill sites were low in comparison with other carnivore studies (McPhee et al., 2012) but cats take smaller prey and often quickly ingest prey whole. Carcass remains of all prey species whose cues significantly influenced stop duration were found at cluster sites (bilby, bettong, rabbit) and all have been reported in the diet of cats (Bannister et al., 2021; Ross et al., 2019; Read and Bowen, 2001).

Video collar data were used to determine the duration of GPS fix stops most likely to constitute hunting behaviour. However, we

cannot discount that some longer duration stops of more than 60 min may have included hunting bouts, and video collar data suggests that some single fix sites are likely to have included hunting bouts. Furthermore, a portion of our clusters less than 60 min may have involved other stationary behaviour. More video collar data are needed to differentiate resting from hunting and other behaviours, and accelerometers could be used in conjunction with GPS and video collars to enable hunting behaviour to be identified more accurately (Brown et al., 2013). Cats at our study site are known to take refuge down rabbit and bettong warrens during the day, especially in hot weather (Jones and Coman, 1982; Moseby et al., 2009b, KM pers obs 2018). We only included crepuscular and nocturnal movement thus reducing the chance of including diurnal rest stops. However, regardless of motivation, warrens represent a significant feature in the environment where cats spend considerable time either for hunting or resting.

Our results have implications for management of predators. If predators predictably spend more time at certain locations within their home range then these areas may be ideal sites for implementing control or monitoring activities. Warrens are likely to be optimum places to place control devices, potentially increasing efficacy and reducing non-target uptake, an issue reported for many control programs (Hohnen et al., 2019). Similarly, small patches of thick, taller vegetation within open landscapes are likely to be used preferentially by cats and should be targeted for monitoring or control sites. Open pasture with patchy shrub cover has been shown to be important habitats used by feral cats in New Zealand with implications for trap and bait placements (Recio et al., 2017). Perhaps most importantly for control applications, the preference for cats to spend longer at sites with conspicuous prey cues suggests they may invest in learning where these features are, making them an important part of their home range (Sensu Powell and Mitchell 2012). Other studies have found individual predators increase their efficiency at locating prey using olfactory prey cues over time (Nams, 1997; Price and Banks, 2017). If so, removing knowledgeable resident cats may reduce predation pressure on prey populations, even if immigration rates are high and density remains relatively constant. Immigrating cats may take time to learn prey cues and hunting points in their new environment thus providing a temporary reprieve to resident prey. Other management actions such as olfactory manipulation of prey cues (Price and Banks, 2020) may be successful in reducing predator impacts on vulnerable prey.

Recent technological advances in GPS collars and satellite imagery have led to a focus on broad scale predator movement patterns and the influence of macrohabitat features. However, these analyses tell us little about how animals use their environment at a fine scale, the level at which predators must operate to catch prey successfully. At this level, prominent prey cues and microhabitat features such as vegetation cover significantly influence hunting behaviour with likely implications for susceptibility of prey species. We urge researchers working on cryptic predators to consider what drives movement patterns at fine scales as this information is likely to be critical for long term management of introduced predator species.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are indebted to M. Jensen, P. Hodgens, T. Moyle and J. Read for assistance with field work. Your astute field observations and data recordings were invaluable, thank you. Thanks to Arid Recovery, in particular K. Tuft, for ongoing support and encouragement and to SA DEW for permission to access areas in the Ikara-Flinders Ranges National Park. Thank you to J. Jansen for assistance with cat radiocollaring. Research was conducted under ethics approval from the University of NSW Ethics Committee approval no. 17/107A. Funding was provided by the Australian Research Council through an ARC Discovery Early Career Researcher Award- DE160100123.

Conflict of interest statement

The authors declare no conflicts of interest.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2022.e02093](https://doi.org/10.1016/j.gecco.2022.e02093).

References

- Alterio, N., Moller, H., Ratz, H., 1998. Movements and habitat use of feral house cats *Felis catus*, stoats *Mustela erminea* and ferrets *Mustela furo*, in grassland surrounding yellow-eyed penguin *Megadyptes antipodes* breeding areas in spring. *Biol. Conserv.* 83, 187–194.
- Anderson, C.R., Lindzey, F.G., 2003. Estimating cougar predation rates from GPS location clusters. *J. Wildl. Manag.* 67, 307–316.
- Austin, D., Bowen, W.D., McMillan, 2004. Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator. *Oikos* 105, 15–30.
- Bannister, H., Letnic, M., Blumstein, D., Moseby, K.E., 2021. Individual traits influence survival of a reintroduced marsupial only at low predator densities. *Anim. Conserv.* <https://doi.org/10.1111/acv.12690>.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48.
- Bengsen, A.J., Butler, J.A., Masters, P., 2012. Applying home-range and landscape-use data to design effective feral-cat control programs. *Wildl. Res.* 39, 258–265.
- Bengsen, A.J., Algar, D., Ballard, G., Buckmaster, T., Comer, S., Fleming, P.J.S., Friend, J.A., Johnston, M., McGregor, H., Moseby, K.E., Zewe, F., 2016. Feral cat home-range size varies predictably with landscape productivity and population density. *J. Zool.* 298, 112–120.

- Bolton, J., Moseby, K.E., 2004. The activity of Sand Goannas *Varanus gouldii* and their interaction with reintroduced Greater Stick-nest Rats *Leporillus conditor*. *Pac. Conserv. Biol.* 10, 193–201.
- Bradshaw, J., Casey, R.A., Brown, S.L., 2012. *The Behaviour of the Domestic Cat*, second ed. CABI, Wallingford, Oxfordshire, UK; Boston, MA.
- Brown, D.D., Kays, R., Wikelski, M., Wilson, R., Klimley, A.P., 2013. Observing the unwatchable through acceleration logging of animal behavior. *Anim. Biotelem.* 1, 20.
- Courchamp, F., Chapuis, J.L., Pascal, M., 2003. Mammal invaders on islands: impact, control and control impact. *Biol. Rev.* 78, 347–383.
- Criffield, M., van de Kerk, M., Leone, E., Cunningham, M.W., Lotz, M., Oli, M.K., Onorato, D.P., 2018. Assessing impacts of intrinsic and extrinsic factors on Florida panther movements. *J. Mammal.* 99, 702–712.
- Davies, A.B., Tambling, C.J., Kerley, G.I., Asner, G.P., 2016. Effects of vegetation structure on the location of lion kill sites in african thicket. *PLoS One*. <https://doi.org/10.1371/journal.pone.0149098>.
- Dawson, S.J., Broussard, L., Adams, P.J., Moseby, K.E., Waddington, K.I., Kobryn, H.T., Bateman, P.W., Fleming, P.A., 2019. An outback oasis: the ecological importance of bilby burrows. *J. Zool.* <https://doi.org/10.1111/jzo.12663>.
- Dickson, B.G., Jenness, J.S., Beier, P., 2005. Influence of vegetation, topography, and roads on cougar movement in southern California. *J. Wildl. Manag.* 69, 264–276.
- Doherty, T.S., Davis, R.A., van Etten, E.J.B., Algar, D., Collier, N., Dickman, C.R., Robinson, S., 2015. A continental-scale analysis of feral cat diet in Australia. *J. Biogeogr.* 42, 964–975.
- Doherty, T.S., Glen, A.S., Nimmo, D.G., Ritchie, E.G., Dickman, C.R., 2016. Invasive predators and global biodiversity loss. *Proc. Natl. Acad. Sci.* 113, 11261–11265.
- Edwards, G.P., De Preu, N.D., Shakeshaft, B.J., Crealy, I.V., Paltridge, R.M., 2001. Home range and movements of male feral cats (*Felis catus*) in a semiarid woodland environment in central Australia. *Austral. Ecol.* 26, 93–101.
- Elliot, N.B., Cushman, S.A., Loveridge, A.J., Mtare, G., Macdonald, D.W., 2014. Movements vary according to dispersal stage, group size, and rainfall: the case of the African lion. *Ecology* 95 (10), 2860–2869.
- Faulquier, L., Fontaine, R., Vidal, E., Salamolard, M., Le Corre, M., 2009. Feral cats *Felis catus* threaten the endangered endemic Barau's Petrel *Pterodroma baraui* at reunion island (Western Indian Ocean). *Waterbird. Int. J. Waterbird Biol.* 32 (2), 330–336.
- Finlayson, G.R., Moseby, K.E., 2004. Managing confined populations: the influence of density on the home range and habitat use of re-introduced burrowing bettongs (*Bettongia lesueur*). *Wildl. Res.* 31, 457–463.
- Fisher, P., Algar, D., Murphy, E., Johnston, M., Eason, C., 2015. How does cat behaviour influence the development and implementation of monitoring techniques and lethal control methods for feral cats? *Appl. Anim. Behav. Sci.* 173, 88–96.
- Flannery, T., Kendall, P., Wynn-Moylan, K., 1990. Burrowing bettong (*Bettongia lesueur*). In: Flannery, T., Kendall, P. (Eds.), *Australia's Vanishing Mammals: Endangered and Extinct Native Species*. RD Press, Surrey Hills, pp. 98–101.
- Fryxell, J.M., Hazell, M., Börger, L., Dalziel, B.D., Haydon, D.T., Morales, J.M., McIntosh, T., Rosatte, R.C., 2008. Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proc. Natl. Acad. Sci.* 105, 19114–19119.
- Funston, P., Mills, M., Biggs, H., 2001. Factors affecting the hunting success of male and female lions in the Kruger National Park. *J. Zool.* 253 (4), 419–431.
- Getz, W.M., Saltz, D., 2008. A framework for generating and analyzing movement paths on ecological landscapes. *Proc. Natl. Acad. Sci. USA* 105, 19066–19071.
- Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evolut. Biol.* 24 (4), 699–711.
- Hayward, M.W., Hayward, G.J., Druce, D.J., Kerley, G.I., 2008. Do fences constrain predator movements on an evolutionary scale? Home range, food intake and movement patterns of large predators reintroduced to Addo Elephant National Park, South Africa. *Biodivers. Conserv.* 18 (4), 887–904.
- Heupel, M.R., Simpfendorfer, C.A., 2015. Long-term movement patterns of a coral reef predator. *Coral Reefs* 34, 679–691.
- Hohnen, R., Tuft, K., McGregor, H.W., Legge, S., Radford, I.J., Johnson, C.N., 2016. Occupancy of the invasive feral cat varies with habitat complexity. *PLoS One* 11 (9), e0152520.
- Hohnen, R., Murphy, B.P., Legge, S.M., Dickman, C.R., Woinarski, J.C., 2019. Uptake of 'Eradicat' feral cat baits by non-target species on Kangaroo Island. *Wildl. Res.* 47 (7–8), 547–556.
- Hughes, N.K., Price, C.J., Banks, P.B., 2010. Predators are attracted to the olfactory signals of prey. *PLoS One* 5 (9), e13114. <https://doi.org/10.1371/journal.pone.0013114>.
- Jones, E., Coman, B.J., 1982. Ecology of the feral cat, *Felis catus* (L.), in South-Eastern Australia III. Home ranges and population ecology in semiarid north-west victoria. *Wildl. Res.* 9, 409–420.
- Keitt, B.S., Wilcox, C., Tershy, B.R., Croll, D.A., Donlan, C.J., 2002. 'The effect of feral cats on the population viability of black-vented shearwaters (*Puffinus opisthomelas*) on Natividad Island, Mexico'. *Anim. Conserv.* 5, 217–223.
- Kittle, A.M., Bukombe, J.K., Sinclair, A.R.E., Mduma, S.A., Fryxell, J.M., 2016. Landscape-level movement patterns by lions in western Serengeti: comparing the influence of inter-specific competitors, habitat attributes and prey availability. *Mov. Ecol.* 4, 17. <https://doi.org/10.1186/s40462-016-0082-9>.
- Krofel, M., Skrbinišek, T., Kos, I., 2013. Use of GPS location clusters analysis to study predation, feeding, and maternal behavior of the Eurasian lynx. *Ecol. Res.* 28, 103–116.
- Lawson, R.R., Fogarty, D.T., Loss, S.R., 2019. Use of visual and olfactory sensory cues by an apex predator in deciduous forests. *Can. J. Zool.* 97 (5), 488–494.
- Loarie, S.R., Tambling, C.J., Asner, G.P., 2013. Lion hunting behaviour and vegetation structure in an African savanna. *Anim. Behav.* 85, 899–906.
- Mazeroll, M.J., 2017 *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)*. R package version 2.1–1. <https://cran.r-project.org/package=AICcmodavg>.
- McAlpin, S., 2001. *A Recovery Plan for the Great Desert Skink (Ehernia kintorei) 2001-2011*. Arid Lands Environment Centre, Alice Spring, Australia.
- McGregor, H., Moseby, K.E., Johnson, C.N., Legge, S.M., 2019. The short-term response of feral cats to rabbit population decline: are alternative native prey more at risk? *Biol. Invasions* 22, 799–811.
- McGregor, H.W., Cliff, H.B., Kanowski, J., 2016. Habitat preference for fire scars by feral cats in Cape York Peninsula, Australia. *Wildl. Res.* 43 (8), 623–633.
- McKenzie, H.W., Merrill, E.H., Spiteri, R.J., Lewis, M.A., 2012. How linear features alter predator movement and the functional response. *Interface Focus* 2205–2216. <https://doi.org/10.1098/rsfs.2011.0086>.
- McPhee, H., Webb, N., Merrill, E.H., 2012. Hierarchical predation: wolf (*Canis lupus*) selection along hunt paths and at kill sites. *Can. J. Zool.* 90, 555–563.
- Medina, F.M., Bonnaud, E., Vidal, E., Tershy, B.R., Zavaleta, E.S., Josh Donlan, C., Keitt, B.S., Corre, M., Horwath, S.V., Nogales, M., 2011. A global review of the impacts of invasive cats on island endangered vertebrates. *Glob. Change Biol.* 17, 3503–3510.
- Morato, R.G., Thompson, J.J., Paviolo, A., de La Torre, J., Lima, F., McBride Jr, R.T., Rogério, C.P., 2018. Jaguar movement database: a GPS-based movement dataset of an apex predator in the Neotropics. *Ecology*. <https://doi-org.proxy.library.adelaide.edu.au/10.1002/ecy.2379>.
- Moseby, K.E., O'Donnell, E., 2003. Reintroduction of the greater bilby, *Macrotis lagotis* (Reid) (Marsupialia:Thylacomyidae), to northern South Australia: survival, ecology and notes on reintroduction protocol. *Wildl. Res.* 30, 15–27.
- Moseby, K.E., Jensen, M.A., Tatler, J., 2021. Dietary flexibility and high predator efficacy facilitate coexistence in a novel predator interaction. *Journal of Mammalogy*. <https://doi.org/10.1093/jmammal/gyab120>.
- Moseby, K.E., Read, J.L., 1999. Population dynamics and movement patterns of Bolam's Mouse, *Pseudomys bolami*, at Roxby Downs South Australia. *Aust. Mammal.* 20, 353–368.
- Moseby, K.E., De Jong, S., Munro, N., Pieck, A., 2005. Improving control methods of European rabbits (*Oryctolagus cuniculus*) in arid South Australia. *Wildl. Res.* 32, 305–311.
- Moseby, K.E., Nano, T., Southgate, R., 2009a. *Tales in the Sand: A Guide to Identifying Arid Zone Fauna Using Spoor and Other Sign*. Ecological Horizons.
- Moseby, K.E., Stott, J., Crisp, H., 2009b. Improving the effectiveness of poison baiting for the feral cat and European fox in northern South Australia: the influence of movement, habitat use and activity. *Wildl. Res.* 36, 1–14.
- Moseby, K.E., Read, J.L., Paton, D.C., Copley, P., Hill, B.M., Crisp, H.M., 2011. Predation determines the outcome of 11 reintroduction attempts in arid Australia. *Biol. Conserv.* 144, 2863–2872.

- Moseby, K.E., Blumstein, D., Letnic, M., West, R., 2018. Choice or opportunity? Are post-release social groupings influenced by familiarity or reintroduction protocols? *Oryx*. <https://doi.org/10.1017/S0030605318000054>.
- Nams, V.O., 1997. Density-dependent predation by skunks using olfactory search images. *Oecologia* 110, 440–448.
- Nisi, A.C., Suraci, J.P., Ranc, N., Frank, L.G., Oriol-Cotterill, A., Ekwanga, S., Williams, T.M., Wilmers, C.C., 2021. Temporal scale of habitat selection for large carnivores: balancing energetics, risk and finding prey. *J. Anim. Ecol.* doi:10.1111/1365-2656.13613.
- Palomares, F., 2001. Comparison of 3 methods to estimate rabbit abundance in a mediterranean environment. *Wildl. Soc. Bull.* 29 (2), 578–585.
- Parer, I., 1982. Census methods: European rabbit (Australia). In: Davis, D.E. (Ed.), *CRC Handbook of Census Methods for Terrestrial Vertebrates*. CRC Press, Boca Raton, FL, USA., pp. 136–138.
- Phillips, M.L., Clark, W.R., Nusser, S.M., Sovada, M.A., Greenwood, R.J., 2004. Analysis of predator movement in prairie landscapes with contrasting grassland composition. *J. Mammal.* 85 (2), 187–195.
- Powell, R.A., Mitchell, M.S., 2012. What is a home range? *Journal of Mammalogy* 93, 948–958. <https://doi.org/10.1644/11-MAMM-S-177.1>.
- Price, C.J., Banks, P.B., 2017. Food quality and conspicuousness shape improvements in olfactory discrimination by mice. *Proc. R. Soc. B* 284, 2016–2629.
- Price, C.J., Banks, P.B., Brown, S., Latham, M.C., Latham, A., David, M., Pech, R.P., Norbury, G.L., 2020. Invasive mammalian predators habituate to and generalize avian prey cues: a mechanism for conserving native prey. *Ecol. Appl.* 30 (8) e02200-e02200.
- R Development Core Team, 2020. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Read, J.L., Bowen, Z., 2001. Population dynamics, diet and aspects of the biology of feral cats and foxes in arid South Australia. *Wildl. Res.* 28, 195–203.
- Read, J.L., Carter, J., Moseby, K.E., Greenville, A., 2008. Ecological roles of rabbit, bettong and bilby warrens in arid Australia. *J. Arid Environ.* 72, 2124–2130.
- Read, J.L., Parkhurst, B., Delean, S., 2015. Can Australian bush birds be used as canaries? Detection of pervasive environmental impacts at an arid Australian mine site. *EMU* 115, 117–125.
- Read, J.L., Bengsen, A.J., Meek, P.D., Moseby, K.E., 2015. How to snap your cat. Optimum lures and their placement for attracting mammalian predators in arid Australia. *Wildl. Res.* 42, 1–12.
- Recio, M., Maloney, R., Mathieu, R., Virgos, E., Moore, T., Seddon, P., 2017. Optimizing control programmes by integrating data from fine-scale space use by introduced predators. *Biol. Invasions*. DOI: 10.1007/s10530-016-1274-3.
- Recio, M.R., Seddon, P.J., 2013. Understanding determinants of home range behaviour of feral cats as introduced apex predators in insular ecosystems: a spatial approach. *Behav. Ecol. Sociobiol.* 67, 1971–1981.
- Recio, M.R., Mathieu, R., Hall, G.B., Moore, A.B., Seddon, P.J., 2013. Landscape resource mapping for wildlife research using very high resolution satellite imagery. *Methods Ecol. Evol.* 4, 10.
- Recio, M.R., Mathieu, R., Virgos, E., et al., 2014. Quantifying fine-scale resource selection by introduced feral cats to complement management decision-making in ecologically sensitive areas. *Biol. Invasions* 16, 1915–1927. <https://doi.org/10.1007/s10530-013-0635-4>.
- Ross, A., Letnic, M., Blumstein, D., Moseby, K., 2019. 'Reversing the effects of evolutionary prey naiveté through controlled predator exposure'. *J. Appl. Ecol.* <https://doi.org/10.1111/1365-2664.13406>.
- Saul, W.C., Jeschke, J.M., 2015. Eco-evolutionary experience in novel species interactions. *Ecol. Lett.* 18, 236–245.
- Southgate, R., Dziminski, M.A., Paltridge, R., Schubert, A., Gaikhorst, G., 2019. Verifying bilby presence and the systematic sampling of wild populations using signbased protocols – with notes on aerial and ground survey techniques and asserting absence. *Aust. Mammal.* 41, 27. <https://doi.org/10.1071/AM17028>.
- Stevens, D., Krebs, J.R., 1986. *Foraging Theory*. Princeton University Press, Princeton, N.J.
- Stobo-Wilson, A., Stokeld, D., Einoder, L.D., Davies, H.F., Fisher, A., Hill, B.M., Mahney, T., Murphy, B.P., Stevens, A., Woinarski, J.C., Bawinanga Rangers, Warhaken Rangers, 2020. Habitat structural complexity explains patterns of feral cat and dingo occurrence in monsoonal Australia. *Divers. Distrib.* 26, 832–842.
- Symonds, M.R.E., Moussalli, A., 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's Information Criterion. *Behav. Ecol. Sociobiol.* 65, 13–21.
- Tambling, C.J., Cameron, E.Z., du Toit, J.T., Getz, W.M., 2010. A comparison of methods for locating african lion kills using global positioning system movement data. *J. Wildl. Manag.* 74, 549–556.
- Wang, Y., Smith, J.A., Wilmers, C.C., 2017. Residential development alters behavior, movement, and energetics in an apex predator, the puma. *Plos One*. <https://doi.org/10.1371/journal.pone.0184687>.
- Whittington, J., Clair St, C.C., Mercer, G., 2005. Spatial responses of wolves to roads and trails in mountain valleys. *Ecol. Appl.* 15, 543–553.
- Woinarski, J.C.Z., South, S.L., Drummond, P., Johnston, G.R., Nankivell, A., 2017. The diet of the feral cat (*Felis catus*), red fox (*Vulpes vulpes*) and dog (*Canis familiaris*) over a three-year period at Witchelina Reserve, in arid South Australia. *Aust. Mammal.* 40, 204–213.
- Woolley, L.A., Geyle, H.M., Murphy, B.P., Legge, S.M., Palmer, R., Dickman, C.R., Augusteyn, J., Comer, S., Doherty, T.S., Eager, C., Edwards, G., Harley, D.K.P., Leiper, I., McDonald, P.J., McGregor, H.W., Moseby, K.E., Myers, C., Read, J.L., Riley, J., Stokeld, D., Turpin, J.M., Woinarski, J.C.Z., 2019. Introduced cats *Felis catus* eating a continental fauna: inventory and traits of Australian mammal species killed. *Mammal. Rev.* 49, 354–368.