

Habitat preference for fire scars by feral cats in Cape York Peninsula, Australia

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Abstract

Context. Feral cats are implicated in the decline of terrestrial native mammals across northern Australia. Research in the Kimberley region of north-western Australia found feral cats strongly selected for fire scars when hunting, suggesting that intensifying fire regimes will have severe consequences for declining prey species.

Aims. We tested the generality of cat–fire interaction beyond the Kimberley, by measuring habitat selection of feral cats in relation to fire scars and habitat types in north-eastern Australia.

Methods. Our study was conducted at Piccaninny Plains Wildlife Sanctuary, Cape York Peninsula. We live-captured feral cats during the dry season of 2015, released them with GPS collars set to record fixes at 15-min intervals, and recaptured cats 4 months later. We created dynamic habitat maps of vegetation types, fire and wetlands, and compared cat habitat selection using discrete choice modelling. We also measured cat density from arrays of camera traps and examined cat diet by analysis of stomach contents.

Key results. We obtained GPS movement data from 15 feral cats. Feral cats selected strongly for recent fire scars (1 or 2 months old), but avoided fire scars 3 months old or older. Three long-distance movements were recorded, all directed towards recent fire scars. Cats also selected for open wetlands, and avoided rainforests. Density of cats at Piccaninny Plains was higher than recorded elsewhere in northern Australia. All major vertebrate groups were represented in cat diet.

Conclusions. We showed that feral cats in north-eastern Australia strongly select for recent fire scars and open wetlands. These results are consistent with those from the Kimberley. Together, these studies have shown that amplified predation facilitated by loss of cover is likely to be a fundamental factor driving mammal decline across northern Australia.

Implications. Reducing the frequency of intense fires may indirectly reduce the impact of feral cats at a landscape scale in northern Australia. We also suggest that managers target direct cat control towards open wetlands and recently burnt areas, which cats are known to favour.

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Introduction

Many species are threatened with extinction across the world, and the dominant threatening processes are generally well understood, such as land clearing, altered disturbance regimes and invasive species (Dirzo *et al.* 2014). Many species can survive one such threatening process operating in isolation; however, often these processes interact and their impacts magnify (Didham *et al.* 2007; Brook *et al.* 2008; Doherty *et al.* 2015b). Understanding such interactions enables the development of appropriate conservation actions. We examine the impacts of interacting altered fire patterns and predation by invasive species on small mammal populations in northern Australia.

A suite of small- to medium-sized native mammals has declined in distribution and abundance across the savannas of northern Australia since European settlement, particularly in recent decades (Woinarski *et al.* 2011; Ziemnicki *et al.* 2015). Predation by feral cat, *Felis catus*, has been established as a major driver of these declines (Fisher *et al.* 2014; Frank *et al.*

2014; Woinarski *et al.* 2015b). Recently, studies conducted in the central Kimberley, Western Australia, have shown that predation by feral cats on small mammals is facilitated by wildfire and grazing. This is because recently intensively burnt or heavily grazed savannas represent open habitats, where cats prefer to forage, as hunting success is relatively high (McGregor *et al.* 2014, 2015a). As a consequence, populations of small mammals in recently intensively burnt areas are exposed to high levels of predation by cats (Leahy *et al.* 2016). The results of these studies provide a mechanistic explanation for the decline of mammals in northern Australia and lead to a suite of management prescriptions to help mitigate these declines (Legge *et al.* 2008, 2011a).

An important caveat in generalising from studies of feral cat ecology in the central Kimberley is that savannas extend over a large area of northern Australia (~1.8 million km²) and encompass four major biogeographic regions (Kimberley, Top End, Gulf and Cape York Peninsula) with substantial differences in climate, vegetation, fauna and history of land-use modification

(Woinarski *et al.* 2007; Ziembicki *et al.* 2015). Rainfall is a key driver of environmental variation in the region, with a major distinction between relatively mesic (>1000 mm rainfall p.a.) and lower-rainfall savannas (Whitehead *et al.* 2014). In lower-rainfall savannas, where the central Kimberley is located, savanna woodlands are the dominant vegetation, and wildfires tend to occur at 2–3-year intervals in the absence of management (Legge *et al.* 2011b). With increasing rainfall, eucalypt forests, melaleuca forests, rainforests and wetlands become a more common component of the landscape, and fires increase in frequency and extent (Russell-Smith *et al.* 2003; Whitehead *et al.* 2014). Assemblages of small mammals also change from lower-rainfall to mesic savannas; many formerly widespread species now only persist in the more mesic parts of their range (McKenzie *et al.* 2007; Woinarski *et al.* 2015a), whereas forested habitats often support a suite of species absent from more open savannas (Bateman *et al.* 2010; Perry *et al.* 2015). These changes in habitat, fire regimes and faunal assemblages from lower rainfall to mesic savannas might be expected to influence the ranging and hunting behaviour of feral cats, and, in turn, the management prescriptions that might be deployed to mitigate their impacts.

To help determine the generality of results from studies of feral cats in the central Kimberley, we extended our research to the mesic savannas of Cape York Peninsula. In this area, the vegetation is a mosaic of savanna woodlands, grasslands, rainforest and vine thickets, wetlands are common, and fires are frequent and extensive (Perry *et al.* 2016). Recent studies have documented that small mammals are scarce or absent from many savanna sites in the region, although the absence of long-term monitoring makes it difficult to quantify historical decline (Kutt *et al.* 2012; Perry *et al.* 2015). Cats are considered a major threat to mammals in north-eastern Australia, although evidence is mostly circumstantial (Dickman *et al.* 2000; Kutt 2012). There have been no previous studies of the ecology of feral cats in north-eastern Australia (Bengsen *et al.* 2016).

Our study aimed to address questions of habitat selection by feral cats in mesic savannas, by recording movements of feral cats using GPS collars, and comparing these movements among different vegetation communities, wetland types and time-since-fire categories. We also obtained information on density, home range, long-distance movements and diet of cats in this region. The study was conducted at Piccaninny Plains Wildlife Sanctuary, where the results of research are used to refine land management in an adaptive framework.

Materials and methods

Study area

Piccaninny Plains Wildlife Sanctuary is a 1700-km² property located near the centre of Cape York Peninsula, northern Queensland, Australia (Fig. 1; 13°13'S, 142°46'E). The property was acquired in 2008 by Australian Wildlife Conservancy (AWC) and Tony & Lisette Lewis Foundation – WildlifeLink, and is managed for conservation by AWC. The dominant vegetation type on Piccaninny Plains is savanna woodland, transitioning to grassland on cracking clay soils. The savannas are dissected by gallery rainforests and vine thickets along major watercourses; rainforest patches are also present in

fire-sheltered locations. The floodplains of the Archer and Wenlock Rivers support numerous permanent and ephemeral wetlands. The region has a tropical monsoon climate with three broad seasons of the wet (December–April), early dry (May–July) and late dry (August–November); average rainfall is 1400 mm per year. As a result of the relatively high rainfall, long dry season and few natural barriers to the spread of fire, central Cape York Peninsula is subject to a high frequency of late dry-season wildfire (Drucker *et al.* 2008). Fire management by AWC on Piccaninny Plains utilises prescribed burns in the early dry season (while weather and grass layer conditions are favourable) to reduce fuel loads and create fire breaks, with the primary aim of reducing the incidence of late dry-season wildfires. Since 2008, prescribed burning on Piccaninny Plains has reduced the average annual extent of late dry-season fire from 54% to 26% of the property and the total area burnt from 75% to 63% of the property (Webb *et al.* 2015). Feral pigs, cattle and horses, which are common on Cape York Peninsula, are subject to control programs on Piccaninny Plains to reduce densities and impacts.

Feral-cat capture

Feral cats were captured in June and September 2015 at two localities on Piccaninny Plains, namely (1) on the Archer River floodplain and (2) around the homestead paddocks (Fig. 1). To detect cats, we conducted nocturnal surveys from a vehicle driven at a maximum speed of 20 km h⁻¹. Two observers stood on the vehicle tray and looked for cat eyeshine using 350-lm LED head-torches. When a cat was observed, we attempted capture using two trained hunting dogs. If the dogs picked up fresh scent, they would chase the cat until it escaped or ran up a tree. Cats were darted with a 0.5-mL dart with a gel-collar fired from a CO₂-powered X-caliber[®] dart rifle (Pneu-dart, Williamsport, PA, USA). We used tiletamine–zolazepam at a rate of 0.5 cc kg⁻¹. Once immobilised, cats fell from the tree and were caught in a sheet. Each cat was fitted with a GPS collar (Quantum 4000 enhanced, Telemetry Solutions, California, USA). Cats weighing between 2 and 3.3 kg were fitted with a 70-g collar and cats exceeding 3.3 kg were fitted with a 100-g collar (ensuring that all collars were <3% of bodyweight). Cats weighing less than 2 kg were killed. GPS units were programmed to record fixes every 15 min for 2-day bouts, starting and finishing at 1200 hours. These bouts were separated by intervals of 2 days where no fixes were taken. Units were programmed to search for a satellite for 60 s, and then remain on for 10 s to refine the fix. Sedated cats were released at the point of capture 2–6 h after capture, once full muscle control was regained; non-sedated cats were released as soon as possible (2–5 min after collars were fitted).

Habitat mapping

A vegetation map of the study area was developed by defining vegetation types and their extent (minimum of 0.5 ha) from stereoscopic examination of black-and-white aerial-photo contact prints, taken between 1972 and 1974, at a scale of 1 : 80 000, with minor refinements based on recent (2015) satellite imagery in Google Earth. Boundaries of vegetation types were informed by land-form and geology; aerial interpretation was subject to

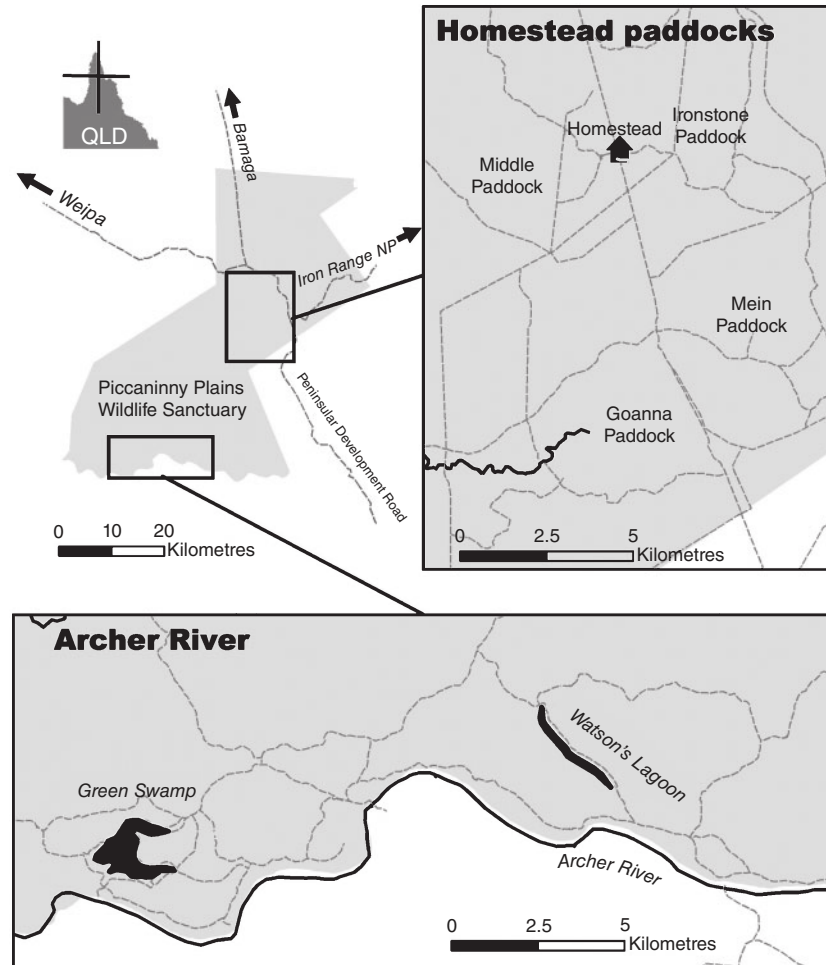


Fig. 1. Map of Piccaninny Plains Wildlife Sanctuary, with details of the two areas where cats were captured and spotlighted. Only major wetlands are depicted.

ground-trothing (detailed assessment of vegetation composition and structure) at 318 sites. Vegetation boundaries were marked directly on the aerial photos with white ink in a 0.25-mm drafting pen, and digitised into ArcMap v.10. The vegetation map was used to define nine habitat types and six broad vegetation types considered likely to be relevant to cats (Table 1).

Attributes of ground structure were sampled at six sites, each being 0.003 ha in extent, within each vegetation type. At each site, we placed a touch pole 50 times, 1 m apart each time. For each touch, we recorded the composition of the ground (bare ground, leaf litter, grass litter or grass tussock) and the number of grass or shrub intercepts on the pole between 10 cm and 1 m above ground in three categories (0, 1–10, >10). On the basis of this, we derived the following attributes for each site: ‘ground cover’ (percentage cover at a ground level that was not bare ground), ‘grass cover’ (percentage of pole deployments with at least one grass intercept between 10 cm and 1 m) and ‘tussock cover’ (percentage of plot with grass tussock on the ground, or with more than 10 grass intercepts between 10 cm and 1 m).

Habitat attributes were recorded for all 112 wetlands greater than 0.25 ha in the vicinity of collared cats. Wetlands were

classified as ‘open’ (ground cover dominated by reeds and lilies, open canopy cover), ‘melaluca dominated’ (*Melaluca viridiflora*-dominated canopy), or ‘lagoon with fringing riparian forest’ (no ground cover vegetation, dense trees on banks). Each wetland was visited once a month and classified as deep, shallow (>10% of the wetland had exposed ground) or dry. This information was used to make a dynamic wetland map (see Fig. S1, available as Supplementary Material to this paper).

Fire patterns were mapped by digitising fire scars from satellite (Landsat 7) images. The date of each fire was recorded. Fire scars were categorised by age in months. A variable ‘fire-grass edge’ was created to represent boundaries of fires with unburnt grassland, as a 50-m buffer. In 2015, all fires in the vicinity of collared cats were prescribed burns conducted in the early dry season (between May and June). Although these fires were not extensive (i.e. <40% of property burnt), field inspection showed that many fires removed almost all ground cover within the mapped fire scar.

Other variables mapped in the study included roads (10-m buffer around any vehicle track), distance to water (any wetland classified as deep or shallow, or permanent river), and day–night period (before–after sunrise–sunset).

Table 1. Details of the vegetation types mapped at Piccaninny Plains, against which cat movements were compared

Ground, grass and tussock cover is the average % cover from six sites sampled in each vegetation type. Amalgamated code refers to the secondary clumping of each variable

Broad vegetation type	Amalgamated vegetation type	Ground-cover percentage (s.e.)	Grass-cover percentage (s.e.)	Tussock-cover percentage (s.e.)	Canopy
Ironstone woodland	Savanna woodland	38 (2)	52 (4)	0 (3)	Mixed
Sandhill woodland	Savanna woodland	65 (2)	76 (3)	5 (3)	Mixed
Savanna woodland	Savanna woodland	46 (2)	78 (7)	10	Mixed
Blacksoil plains	Savanna woodland	37 (4)	100 (0)	80 (8)	Open
Dense woodland	Dense woodland	81 (1)	66 (8)	5 (4)	Dense
Rainforest	Rainforest	91 (2)	10 (1)	3 (0)	Complete cover
Open wetland – shallow	Moist open wetland	71 (7)	38 (14)	1 (4)	Open
Open wetland – dry	Dry or tree-covered wetland	24 (7)	20 (10)	5 (8)	Open
Melaluca-dominated wetland – shallow	Dry or tree-covered wetland	24 (7)	20 (10)	5 (8)	Dense
Melaluca-dominated wetland – dry	Dry or tree-covered wetland	24 (7)	20 (10)	5 (8)	Mixed
Lagoon with fringing riparian forest	Dry or tree-covered wetland	0	0	0	Mixed
Fire scar – 1, 2, 3 or 4 months old	Fire scar – 1, 2, 3 or 4 months old	20 (11)	4 (1)	0 (0)	As pre-burn habitat

Feral-cat habitat selection

GPS data were cleaned in the following steps. All fixes were removed where the altitude reading was wildly inaccurate (the study area was 70–150 m above sea level; all fixes <0 m or >300 m above the sea level were removed), or where there were implausible ‘spikes’ in movement (distance from last fix >100 m and turn angle >170°, subsequently returning to within 50 m of the previous fix). We quantified GPS error by setting six GPS units in the study area to record 300 fixes at various intervals, with three in savanna woodland and three within rainforest. The true location was taken as the average point from all fixes, and error defined as distance from this point. On the basis of this test, 95% of fixes were within 30 m of the true location, which was defined as the GPS error in the present study. Although there was substantial difference in GPS accuracy between savanna and rainforest fixes on ‘cold’ start fixes (those with greater than an hour between fixes), there was no significant difference on ‘hot’ starts when fixes were 15 min apart. We defined cat activity as any fix where the distance between successive fixes was greater than the GPS error.

Habitat selection was determined using step selection functions analysed with mixed-effects discrete-choice modelling (Forester *et al.* 2009; McGregor *et al.* 2014; Thurfjell *et al.* 2014). In this approach, each pair of sequential GPS fixes from an animal are considered a step, and random points are generated around every step representing locations cats could have moved to. The habitats available to an animal (the random points) are compared with the habitats selected (the actual GPS location) to determine preference. Habitat availability was modelled by intersection with five points created around each fix based on probability distributions of turn-angles and distances between fixes for male and female cats. Each individual cat was included as a random effect. Only moving fixes were considered, because these were when cats were selecting habitats. We used the R library ‘coxme’ for the analysis (Therneau 2014).

We generated 10 different habitat models with the following three broad themes: detailed vegetation types, amalgamated vegetation classes and structural habitat models. The detailed vegetation types compared different floristic communities, and included all mapped habitat, wetland and fire categories

(Table 1), as well as roads and fire edges. The amalgamated vegetation types clumped floristic communities with similar structure to reduce the number of variables within these models. The structural models considered only vegetation structure, and included terms with ground cover, grass cover, tussock cover, canopy cover, distance to water, roads, and day–night interaction terms. A global model was added as well. All different models were compared in an information theory framework (Burnham and Anderson 1998).

For ease of interpretation, we present the coefficients of discrete-choice modelling not as odds ratios but as the percentage change in likelihood of selection compared with a reference habitat, that with the greatest spatial coverage in the study area (unburnt savanna woodland). For example, if ‘Habitat A’ had an odds ratio of 0.2:1, this would be converted to a negative odds ratio of –5 (as in 1:5) and then to the percentage change from the intercept (–400%). In this example, an odds ratio of 0.2:1 is presented as a cat being 400% less likely to select Habitat A over savanna woodland.

Cat density, home range, long-distance movements and diet

Cat density was estimated from detections of cats on arrays of camera traps. We set a total of four arrays of cameras, including one in 2014 and three in 2015. Each array comprised 15 and 25 cameras spaced 500–1000 m apart, following methods outlined in McGregor *et al.* (2015c). The array set in 2014 was located in Goanna Paddock, and both Goanna Paddock and Watson’s Lagoon (see Fig. 1 for location names) were sampled in 2015. For each array, cameras were placed 20–60 cm above ground, directed across a road or into a corral, and set for between 3 and 4 weeks. Individual cats were identified, and reviewed by H. Mc. and H. C. until we reached an agreement on identities. A capture history was created for each cat and camera, where each cat was either detected or not during a 3-day block. The spatial patterns of detection were used to estimate the centres of each cat’s home range. Density was determined by spatially explicit mark–recapture analysis (Borchers and Efford 2008; Rich *et al.* 2014). For each array, we compared multiple models with differing covariates for estimating home-range use

(detection functions half-normal, hazard-rate and exponential), home-range size (σ) and detection probabilities (g_0). Time-series covariate, behavioural response and sex differences were also considered (see McGregor *et al.* 2015c for more detail). Because cat densities in Goanna Paddock appeared to vary among habitats, we also ran an analysis including habitat as a variable against cat density. The most parsimonious model was selected within an information-theory framework.

We also documented both home range and long-distance journeys made by cats. The long-distance journeys were classed as any movement greater than 5 km; all such movements were unambiguous. Home-range size and boundaries were determined using the non-parametric kernel *a*-LoCoH method (Getz *et al.* 2007), with *a* set to the maximum distance between any two points. We did not include long-distance movements in deriving these estimates. We report on 95% utilisation values. All analysis was conducted in the 'adehabitatHR' package (Calenge 2006) using R (R Development Core Team 2014).

Cat diet in the study region was presented from the stomach-content analysis of cats captured during this study and euthanased at study end-point.

Results

Spotlighting and cat capture

Spotlighting to capture feral cats was conducted in June and September 2015. Over this period, surveys were conducted on 740 km of tracks over 98 h. Thirty-eight cats were seen while spotlighting, of which 20 were captured (10 males, 10 females). Adult male cats weighed an average of 4720 g (s.e. = 290 g) and females 3180 g (s.e. = 160 g). In total, 3 of the 20 cats were subsequently killed because they were not heavy enough to carry a GPS collar. The remaining 17 cats were fitted with a GPS collar and released.

Habitat selection

We obtained GPS data from 15 of the collared cats, resulting in movement data at 15-min intervals from 492 full 24-h bouts. After data were cleaned, we considered 17 335 'steps' for analysis. From the nine different mixed-effect discrete-choice

models of cat habitat selection, the most parsimonious model of cat habitat selection included the six amalgamated vegetation classes, time since fire and 'fire-grass edge' as explanatory variables (see Table 2, Fig. 2). Within this model, cats displayed a very strong preference for recent fire scars (up to 1 month old). Selection for fire scars decreased over time, becoming negative after 3 months (Figs 2, 3; Table 3). Cats also selected for fire-grassland edges, but only to a minor extent (6% preference over savanna woodland). Cats selected for wetlands with little canopy cover and shallow water, but avoided wetlands that had dried up and wetlands with a dense tree cover. Cats also avoided dense woodland and rainforest (Table 3).

Density, home range and long-distance movements

Cat densities varied markedly between the two arrays of remote camera-traps. The most parsimonious model of cat density for Watsons Lagoon in 2015 considered a half-normal detection function with a time-series effect, and estimated a density at 0.18 km^{-2} (s.e. = 0.05). In Goanna Paddock in 2014, the most parsimonious model considered density to vary within the array; cats were much more abundant in the blacksoil plains (3.56 km^{-2} , s.e. = 1.04) than elsewhere on the array (0.09 km^{-2} , s.e. = 0.03). In 2015, the most parsimonious model assumed sex differences in the home-range size, and estimated density at 1.09 km^{-2} (s.e. = 0.43).

Home ranges estimated as the 95% utilisation distribution with the *a*-LoCoH method were on average 444 ha (s.e. = 82) for adult male cats; female home ranges averaged 237 ha (s.e. = 74). Long-distance movements were recorded in 3 of 17 GPS-collared cats (Fig. 4). One cat's GPS did not work while it journeyed, so movements were determined with VHF tracking.

Diet

A broad range of taxa were found in the 18 cat stomachs assessed during the study, including three mammal species (one ground-dwelling, one arboreal and one volant species), four species of reptile, one ground-dwelling bird and, from one cat collected from around a wetland, a large number of frogs (Table 4).

Table 2. Comparison of the 10 different models explaining feral-cat habitat choice using information theory

Ground cover is percentage cover below 10 cm of rock/gravel, leaf litter, grass litter and tussock. Grass cover is percentage of dense or light grass over >10 cm. Tussock cover is % of plot with either tussock <10 cm or dense grass >10 cm. AIC, Akaike information criterion. R^2_{LR} represents likelihood-ratio-based pseudo-R-squared

Model description	d.f.	logLik	AIC	delta	Akaike weight	R^2_{LR}
Amalgamated veg types + fire edge	22	-143603	282990	0	0.992	0.546
Amalgamated veg types	21	-143608	283000	10	0.005	0.546
Amalgamated veg types + roads	22	-143608	283002	12	0.003	0.546
Broad vegetation types + fire edge	26	-148169	288178	5188	0	0.501
Broad vegetation types + roads	26	-148178	288195	5205	0	0.501
Broad vegetation types	25	-148181	288198	5209	0	0.501
Global model	33	-148285	288282	5292	0	0.5
Structural model 1 (ground cover, tussock cover, road, fire, canopy and day-night interaction)	21	-149304	290711	7721	0	0.487
Structural model 2 (ground cover, tussock cover, road, fire)	19	-149442	291040	8050	0	0.488
Structural model 3 (grass cover, road, fire, canopy and day-night interaction)	19	-149658	291356	8366	0	0.474

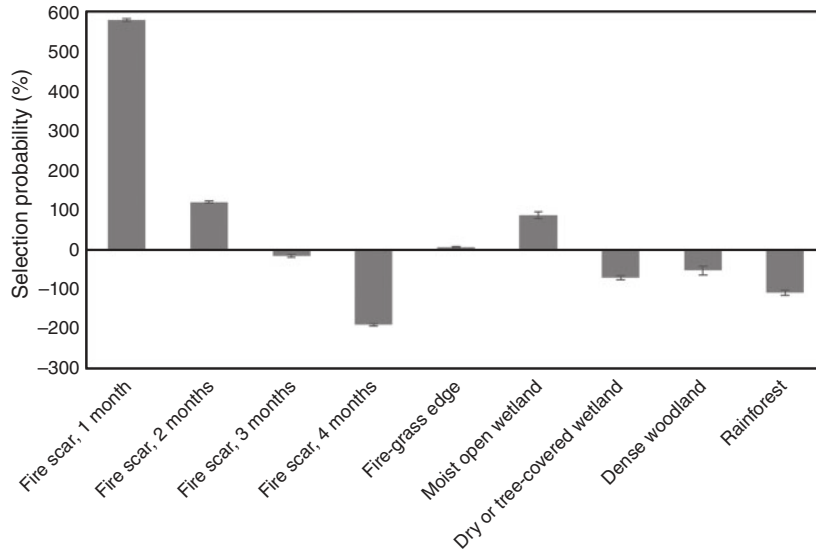


Fig. 2. Relative selection of different habitat types by feral cats compared with the most prevalent habitat type (savanna woodland). For example, cats were 600% more likely to choose to move to recent fire scars (less than a month old) than to unburnt savanna woodland.

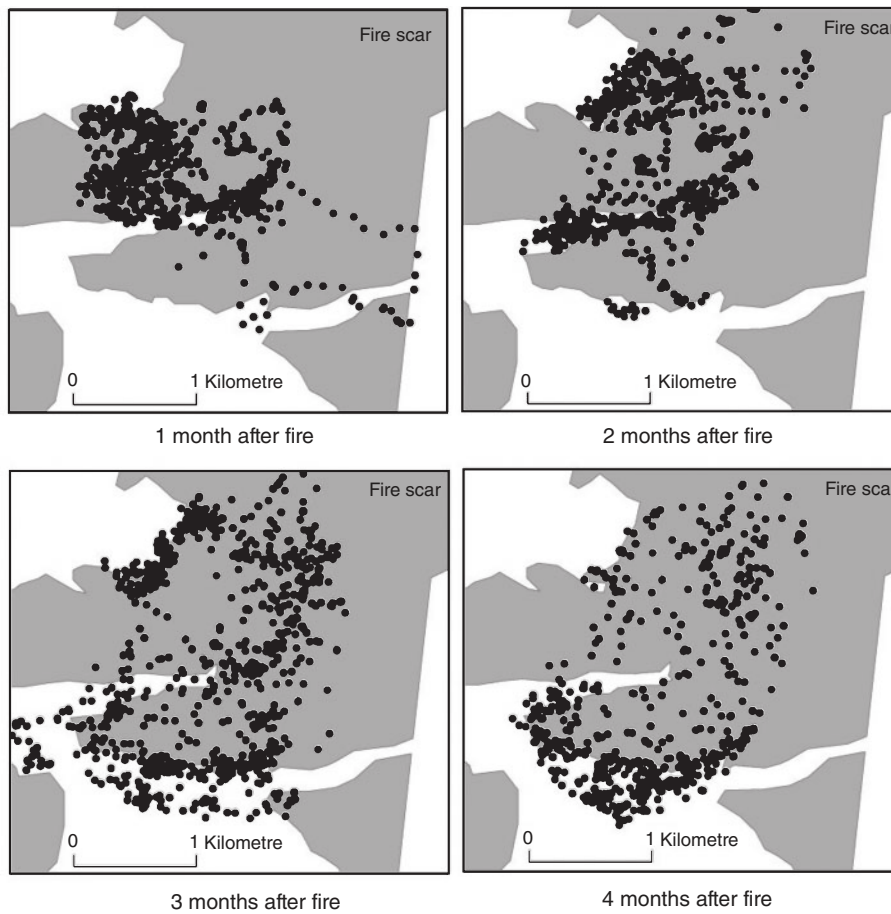


Fig. 3. GPS locations of a male feral cat through time in relation to a fire scar (grey), from up to 1 month post fire (top left) until 3–4 months post fire (bottom right). Note how the concentration of points in the fire scar compared with surrounding savanna woodland decreases through time.

Table 3. Details of coefficients with the most parsimonious model of cat habitat selection

Relative selection % is the percentage increase or decrease in the likelihood of habitat selection of feral cats choosing that habitat, compared with the most prevalent habitat type (savanna woodland)

Variable	Coeff.	s.e.	Odds ratio	Relative selection % (s.e.)
Fire Scar, up to 1 month	1.94	0.03	6.79	579 (3)
Fire Scar, 1–2 months	0.79	0.03	2.2	120 (3)
Fire Scar, 2–3 months	–0.16	0.03	0.86	–16 (3)
Fire Scar, three or more months	–1.1	0.03	0.34	–190 (3)
Fire-grass edge	0.07	0.02	1.07	7 (2)
Moist open wetland	0.8	0.09	1.87	87 (10)
Dry or tree-covered wetland	–0.51	0.05	0.58	–71 (5)
Dense woodland	–0.43	0.11	0.65	–53 (12)
Rainforest	–0.68	0.07	0.48	–108 (7)

Discussion

We have conducted the first detailed study of the ecology of feral cats in north-eastern Australia and the first in the mesic savannas of northern Australia. At Piccaninny Plains, cats displayed a very strong preference for recent fire scars and a preference for moist open wetlands; they avoided rainforest and dense eucalypt forest, wetlands with no moisture, and fire scars more than 3 months old. Despite substantial differences between Cape York Peninsula and the central Kimberley in cat density, rainfall, vegetation and native mammal fauna, a key aspect of the behaviour of feral cats was remarkably similar in each region. In both regions, cats strongly selected for recent fire scars (less than 3 months old) and travelled long distances to hunt in those areas; and in both regions they avoided older fire scars (McGregor *et al.* 2014, 2015b). This could be because cats hunt more effectively in recent fire scars (McGregor *et al.* 2015a; Leahy *et al.* 2016), but, within a few months, they (and other predators) deplete prey abundance until hunting in older fire scars becomes inefficient. We presume that favourable hunting opportunities explain habitat selection by feral cats on Piccaninny Plains; those habitats most strongly selected for by cats (recent fire scars and open shallow wetlands) were both likely to have abundant prey or at least prey easily accessible to cats, because of the lack of cover. The consistency between results in the Kimberley and Cape York Peninsula suggests that the fundamental drivers of how feral cats and fire interact are similar across the savannas of northern Australia.

Piccaninny Plains appears to have a greater density of feral cats than do other locations surveyed across northern Australia (in the central Kimberley and the Northern Territory; McGregor *et al.* 2015c). Consistent with this result, home ranges of cats on Piccaninny Plains were about half the size of home ranges from the central Kimberley (McGregor *et al.* 2015c); the activity of cats on Piccaninny Plains is also reported to be higher than in most other locations in northern and central Australia (Brook *et al.* 2012; Stokeld *et al.* 2015). Whereas the density of cats presumably reflects the underlying prey base, the relatively high density of cats on Piccaninny Plains is a potential concern for conservation management, because even a low density of feral cats may have a severe impact on native mammal populations (Frank *et al.* 2014).

At Piccaninny Plains, we found that rainforests and dense woodlands were avoided by feral cats, and, as a result, may offer refuge to native mammals. Such habitats typically support a much greater abundance and richness of small to medium-sized mammals than do open savanna woodlands in north-eastern Queensland (Bateman *et al.* 2010; Perry *et al.* 2015). At Piccaninny Plains, several small to medium-sized mammals have been recorded only or primarily in rainforests and dense woodlands, including the Cape York rat, *Rattus leucopus*, grassland melomys, *Melomys burtoni*, and black-footed tree rat, *Mesembriomys gouldii* (AWC, unpub. data). In the dense woodlands, it is likely that such animals have protection from the dense tussock grasses, where it is harder for cats to hunt (McGregor *et al.* 2015a). There are numerous possible explanations as to why cats avoid rainforest. Such habitats typically contain more arboreal than terrestrial species, which would be more difficult for cats to hunt successfully. It might be harder for cats to hunt for reptiles with the almost complete cover of leaf litter.

Open wetlands with shallow water were favoured by feral cats on Piccaninny Plains, and they avoided dry wetlands and those covered in trees. Such open shallow wetlands are likely to have more easily available frogs and reptiles to hunt, both of which can form a substantial portion of cat diet if available (Doherty *et al.* 2015a; McGregor *et al.* 2015a). One cat caught on the banks of such a wetland contained ~70 frogs in its stomach. Shallow wetlands were also moderately degraded by feral pigs (Mulder *et al.* 2014), and it is possible that there is an interaction between these two invasive species. Pigs remove the large reeds and tussocks, and simplify the vegetation structure (Doupé *et al.* 2010), which may enable cats to hunt more effectively. We could not test for this interaction during the present study, because all open wetlands in the vicinity of collared cats were subject to similar levels of pig disturbance. However, this warrants further testing and investigation, because such synergies between threatening processes can have a severely detrimental impact for conservation (Brook *et al.* 2008; Doherty *et al.* 2015b).

Management implications

On the basis of the outcomes of similar research in the Kimberley, we have argued that a reduction in the frequency of intense fires (fires that remove most ground cover) has the potential to reduce the impacts of feral cats on native wildlife at a landscape scale (McGregor *et al.* 2014). In general, this can be achieved by a reduction in the frequency of late dry-season fires, because such fires tend to be more extensive, burn more intensely and leave less ground cover than do fires earlier in the dry season (Russell-Smith and Edwards 2006; Lawes *et al.* 2015). The results of the present study are consistent with that research and further support those management recommendations.

Nevertheless, a proportion of early dry-season fires can burn intensely (Russell-Smith and Edwards 2006). In our study, the prescribed fires lit early in the dry season (May and June) were mostly small and linear; however, these early dry-season fires burned intensely and removed virtually all ground cover from within burnt areas. These fire scars were favoured for hunting by feral cats. A similar result was obtained in the

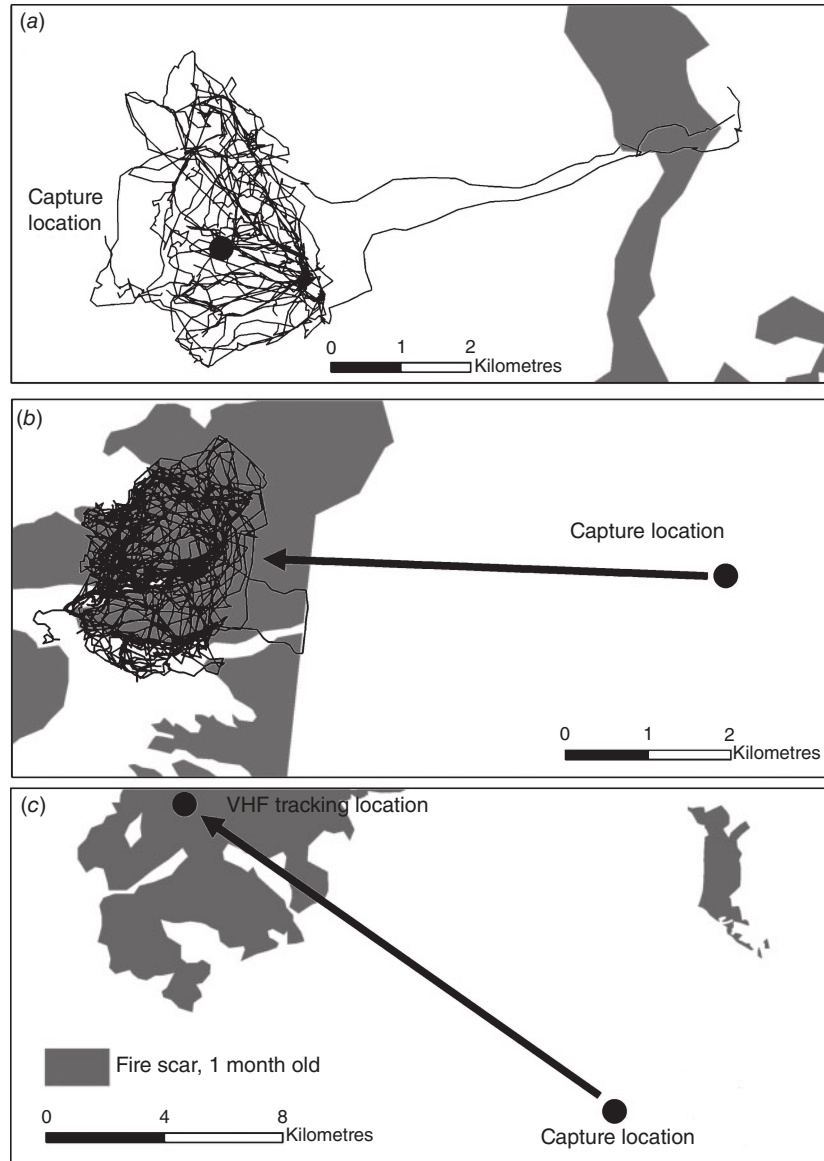


Fig. 4. Map of all recorded long-distance movements made by cats, and fire scars 1 month old at time of travel. Cat (a) made two short trips to a fire scar 6 km away. Cat (b) travelled 8 km from capture location to set up a new home range in the centre of fire scar just before GPS collar began recording. Cat (c) travelled 17 km after capture to hunt at a fire scar on the neighbouring pastoral station; however, this cat's GPS collar failed.

Kimberley, where cats focussed hunting at intense fire scars, regardless of season (McGregor *et al.* 2014; Leahy *et al.* 2016). These results caution against the view that early dry-season fires are necessarily positive for wildlife (see Perry *et al.* 2016 for a more detailed discussion of this issue). Nevertheless, prescribed burning is the only tractable means of reducing the extent of larger, high-intensity fires that typically occur later in the year in northern Australia. For example, prescribed burning on Piccaninny Plains helped prevent the incursion of late-season fires that burnt extensive areas on the southern, eastern and north-western boundaries of the property in 2015 (Webb *et al.* 2015).

Studies of feral-cat ecology on Cape York Peninsula and the central Kimberley have suggested that efforts to directly control feral cats (e.g. by shooting) could be more effective if targeted at their preferred habitats, that is, at recent fire scars and, where present, shallow open wetlands. Detections of feral cats in favoured habitats may be up to two to six times greater than in neighbouring habitats. At Piccaninny Plains, targeted hunting around Watson's Lagoon during the late dry season of 2013, when the banks of the wetland were open and shallow, resulted in 50 cats being shot in 2 months (AWC, unpubl. data). However, localised hunting is unlikely to reduce densities of cats over the long-term or at a landscape scale (Lazenby *et al.* 2015), given

Table 4. Animals found in the stomach contents of 18 feral cats killed at Piccaninny Plains

Common name	Scientific name	Individuals eaten	Cats	%
Insect	Various spp.	11	4	24
Spotty leopard-skink	<i>Ctenotus spaldingi</i>	11	4	24
Six-toothed rainbow-skink	<i>Carlia sexdentata</i>	5	3	18
Gecko	Various spp.	2	2	12
Two-lined dragon	<i>Diporiphora bilineata</i>	5	4	24
Frogs	Various spp.	70	1	6
Quail	Unknown spp.	2	2	12
Sugar glider	<i>Petaurus breviceps</i>	1	1	6
Microbat	<i>Vespudalus</i> spp.	1	1	6
Canefield rat	<i>Rattus sordidus</i>	4	4	24

that cats are ubiquitous in the savannas of northern Australia and readily travel long distances (McGregor *et al.* 2015b).

This research has provided further demonstration that fire events and regimes must be considered as a whole-of-ecosystem process, and there is potential synergy between fires and many other processes and threats (Brooks *et al.* 2004; Bowman *et al.* 2016). Ecosystems such as these savannas in north-eastern Australia are affected by a multitude of threats, including feral predators, feral herbivores, altered fire regimes, intensified pastoral impacts and weed invasion (e.g. Whytlaw *et al.* 2013; Stanton *et al.* 2014; Perry *et al.* 2015). Our research has highlighted how these threats can interact and magnify (Folke *et al.* 2004; Brook *et al.* 2008; Doherty *et al.* 2015b), and has implied that cat impacts could be mitigated by managing interacting ecosystem processes. This result is important because there are currently no direct methods of broad-scale cat control known to be effective at a landscape scale in northern Australia, whereas there are effective methods for broad-scale control of grazing by large herbivores and altered fire regimes (Legge *et al.* 2011b; Price *et al.* 2012).

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