CSIRO PUBLISHING
Wildlife Research
https://doi.org/10.1071/WR19201

Distribution and diet of feral cats (*Felis catus*) in the Wet Tropics of north-eastern Australia, with a focus on the upland rainforest

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Abstract

Context. Feral cats have been identified as a key threat to Australia's biodiversity, particularly in arid areas and tropical woodlands. Their presence, abundance and potential impacts in rainforest have received less attention.

Aims. To investigate the distribution and diet of feral cats (*Felis catus*) in upland rainforest of the Wet Tropics.

Methods. We collated available occurrence records from the Wet Tropics, and data from upland camera-trapping surveys over an 8-year period, to assess geographic and elevational distribution of feral cats in the bioregion. We also assessed the diet of feral cats from scats collected at upland sites.

Key results. Feral cats are widespread through the Wet Tropics bioregion, from the lowlands to the peaks of the highest mountains (>1600 m), and in all vegetation types. Abundance appears to vary greatly across the region. Cats were readily detected during camera-trap surveys in some upland rainforest areas (particularly in the southern Atherton Tablelands and Bellenden Ker Range), but were never recorded in some areas (Thornton Peak, the upland rainforest of Windsor Tableland and Danbulla National Park) despite numerous repeated camera-trap surveys over the past 8 years at some of these sites. Scat analysis suggested that small mammals comprise ~70% of the diet of feral cats at un upland rainforest site. Multivariate analysis could not detect a difference in mammal community at sites where cats were detected or not.

Conclusions. Feral cats are widespread in the Wet Tropics and appear to be common in some upland areas. However, their presence and abundance are variable across the region, and the drivers of this variability are not resolved. Small mammals appear to be the primary prey in the rainforest, although the impacts of cats on the endemic and threatened fauna of the Wet Tropics is unknown.

Implications. Given their documented impact in some ecosystems, research is required to examine the potential impact of cats on Wet Tropics fauna, particularly the many upland endemic vertebrates. Studies are needed on (1) habitat and prey selection, (2) population dynamics, and (3) landscape source–sink dynamics of feral cats in the Wet Tropics.

Additional keywords: camera trap, invasive predator, prey, small mammal.

Received 18 October 2019, accepted 3 March 2020, published online 10 June 2020

Introduction

Feral cats (*Felis catus*) are recognised as a key threatening process for biodiversity in Australia (Doherty *et al.* 2017; Legge *et al.* 2017; Radford *et al.* 2018). Research has focussed on arid areas and tropical savannas and woodlands, where habitat simplification as a result of altered burning regimes and grazing may be enhancing the ability of cats to hunt prey (Fisher *et al.* 2014; McGregor *et al.* 2014, 2015, 2016). Cats have been implicated in the recent declines in small-bodied tropical mammals in open habitats (Fisher *et al.* 2014; Frank *et al.* 2014; Woinarski *et al.* 2015). However, we know very little about the distribution and abundance of cats in tropical and subtropical rainforests. Only a handful of studies have assessed this, and these have found that cats avoided rainforest (McGregor *et al.* 2016) or were present in smaller tracts, but appeared to be absent from large tracts of closed forest (Gordon 1991).

The lack of documented small-mammal declines in rainforest habitats has exonerated cats, with the suggestion that the effectiveness and impacts of their predation are limited in structurally complex environments (Fisher *et al.* 2014; Hohnen *et al.* 2016; McGregor *et al.* 2014, 2015, 2016). However, their impact will depend on how thoroughly they establish in rainforest (in terms of distribution and abundance), how they utilise this habitat, and what they prey on. There is limited information on the diet of feral cats in rainforests. Information on diet is critical to assessing potential impact on prey species and competition with co-occurring predators. Studies (including continental wide reviews) investigating the diet of feral cats across Australia have reported that small mammals are the most commonly consumed fauna group (Doherty *et al.* 2015; Woolley *et al.* 2019).

The Wet Tropics rainforest stretches as a fairly continuous band among Townsville, Cairns and Cooktown, in north-eastern Australia. It consists of lowland (<500 m above sea level (asl)), mid-elevation (500–900 m asl), and upland (>900 m–1630 m asl) rainforest. The Wet Tropics is World Heritage listed, in part because of the level of endemic diversity in the uplands. Approximately 35 vertebrates are restricted to the cool, wet mountaintops (Williams *et al.* 2010; Singhal *et al.* 2018), and many of these are of small size and, therefore, potentially prey for cats. The 'large' mammalian predators of the Wet Tropics are the endemic northern spotted-tailed quoll (*Dasyurus maculatus gracilis*), dingo (*Canis familiaris*) and feral cat. Introduced foxes (*Vulpes vulpes*) do not occur in the Wet Tropics, with a coastal northern limit near Townsville (Fairfax 2019; M. Chawla and C. Hoskin, unpubl. data). *Dasyurus m. gracilis* is listed as *Endangered* and one of the potential (yet unresolved) threats is competition with feral cats (Burnett and Marsh 2004; DELWP 2016).

The present study had two aims, namely (1) to describe the distribution of cats in the Wet Tropics using occurrence records collected from various sources, including from extensive camera trap surveys in upland areas, and (2) to assess the diet of feral cats from scats collected in the Wet Tropics uplands. We use our results to discuss research priorities and management implications.

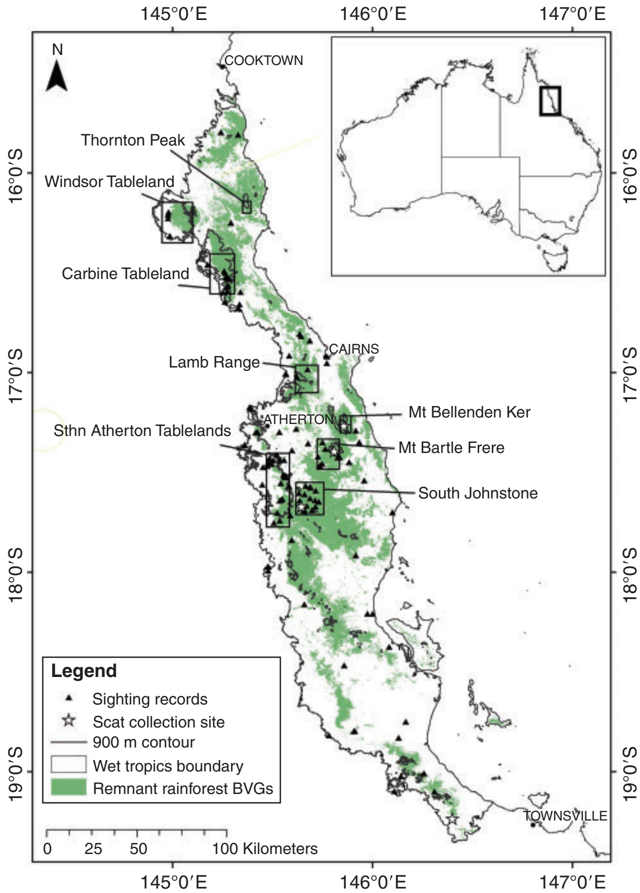

Fig. 1. Map of the Wet Tropics bioregion, showing remnant rainforest (as defined by broad vegetation groups (BVGs); Queensland Herbarium 2018), 900 m asl contour line, and feral cat occurrence records. Boxed areas highlight the upland areas where camera trapping was undertaken in the present study (listed in Table 1).

Materials and methods

Study area

The present study confines itself to Queensland's Wet Tropics bioregion (Fig. 1). The bioregion extends along the coast and ranges from the Bluewater Range, near Townsville, north to Big Tableland, near Cooktown, being a length of ~400 km. It encompasses a discrete and almost continuous area of rainforest, separated by dry habitat barriers from other rainforest areas to the south and north. Our focus was particularly on the upland areas (>900 m elevation), which are distributed in a disjunct fashion across mountaintops throughout the length of the Wet Tropics (Fig. 1). These cool, wet uplands are climate refuges that support high levels of biodiversity, including many endemic invertebrates and vertebrates (Moritz *et al.* 2005; Williams *et al.* 2010).

Distribution of cats

We compiled a database of feral cat occurrence records from the following sources: incidental records (including sightings, scats and tracks) made by ourselves and colleagues, publicly available records from the Atlas of Living Australia (ALA 2019) and WildNet (2019), the Queensland Historical Fauna Database, and upland camera-trap surveys conducted by the authors over the past 8 years (outlined below). We selected all records that had a precision within 9 km and checked these by plotting them and geospatially verifying them against any associated locality notes. Many of the occurrence records had associated elevation data (derived from a GPS in the field); however, for those that did not, we determined an elevation from a 30-m digital elevation model (DEM) layer in ArcMap (version 10.6.1). Occurrence records were also plotted on the broad vegetation-group (BVG) mapping layer (Queensland Herbarium 2018) and clipped to the Wet Tropics bioregion boundary, so as to derive which BVGs the records occurred in. When mapping elevation trends in cat occurrence records and undertaking data analyses described below, we excluded our own 41 records (i.e. those derived from upland forest camera trap surveys) because they were biased to higher elevations (they were obtained primarily during research on *D. m. gracilis*).

Camera-trapping surveys

Our camera-trapping data consisted of 378 camera stations in upland simple to complex notophyll vine forest and microphyll vine-fern forest (all broadly termed 'rainforest' herein) between Thornton Peak in the north and Tully Falls National Park (NP) in the south (Table 1). Stations spanned an elevation range of 500–1570 m asl and were each operated for between 4 and 109 nights.

Table 1. List of regions, sites, survey period/s (month and year), number of camera-trap stations surveyed (number of cameras) and trap nights (TrapN) from camera trap surveys
Number of individual cats detected (Indiv), total number of cat detections (*D*), image detection rate (IDR), and elevation/elevational range of cat records or camera stations (Elevation) are also shown

Region	Site	Survey period/s	Number of cameras	TrapN	Indiv	*D*	IDR	Elevation (m)
Daintree	Thornton Peak	Aug. 2018	11	172	0	0	–	606–1295
Windsor Tableland	Rainforest	June 2011	12	45	0	0	–	843–1347
		June 2013	17	101	0	0	–	843–1347
		June 2015	17	164	0	0	–	843–1347
		June 2016	20	226	0	0	–	843–1347
		June 2017[A]	20	622	0	0	–	843–1347
		Sep. 2017[A]	36	403	0	0	–	843–1347
		Nov. 2017[A]	40	458	0	0	–	843–1347
		Dec. 2017[A]	40	415	0	0	–	843–1347
		Apr. 2018[A]	79	812	0	0	–	843–1347
		June 2018[A]	19	254	0	0	–	843–1347
		Sep. 2018[A]	19	258	0	0	–	843–1347
	Wet–dry sclerophyll forest	Aug 2018[B]	24	351	2	3	0.008	1182–1186
Carbine Tableland	Mount Lewis	June 2017	24	384	2	2	0.005	1078–1157
		June 2018[A]	29	400	3	3	0.008	1022–1217
		Sep. 2018[A]	20	277	3	3	0.011	1097–1172
	Mount Spurgeon	July 2016	10	96	0	0	–	1108–1233
		May 2018[A]	23	195	0	0	–	1143–1324
Lamb Range	Danbulla National Park	June 2015	21	260	0	0	–	871–1154
		June 2016	18	802	0	0	–	871–1154
		Sep. 2016	10	80	0	0	–	871–1154
		June 2017	15	298	0	0	–	871–1154
		June 2018[A]	15	337	0	0	–	871–1154
	Kahpalim Rock (Dinden National Park)	Apr. 2018[A]	12	101	1	1	0.010	1012
Bellenden Ker Range	Mount Bartle Frere area	June 2018[A]	35	530	3	3	0.006	1412–1568
		Sep. 2018[A]	5	56	1	1	0.018	703
	Mount Bellenden Ker	Sep.–Nov. 2016	26	314	3	10	0.032	1430–1585
Southern Atherton Tablelands	Towalla Road	Sep. 2018[A]	5	75	3	4	0.053	663–680
	Mount Hypipamee National Park	Apr. 2019[A]	3	42	0	0	–	964–995
	Herberton Range National Park	Apr. 2019[A]	4	56	1	2	0.036	1141–1210
	Mount McHugh–Misty Mountain Nature Refuge	Apr. 2019[A]	5	75	1	2	0.027	1102–1151
	Southern Atherton Tableland Nature Refuges: Cassowary Crossing, Lemuroid Leap, Ringtail Crossing, Dirrans End, Taylor's Hill	Apr. 2019[A]	10	142	0	0	–	833–1138
	Mount Fisher (Malaan National Park)	Apr. 2019[A]	5	70	1	1	0.014	1277
	Majors Mountain (Tully Gorge National Park)	Sep. 2016	5	50	2	2	0.040	1053–1143
		Sep. 2018[A]	7	105	1	1	0.010	1077
	South Johnstone area (Wooroonooran National Park)	Sep. 2016	5	70	1	1	0.014	592
		Aug. 2018[A]	45	478	4	4	0.008	600–735
		Sep. 2018[A]	8	128	1	1	0.008	712
	Tully Falls National Park	Apr. 2019[A]	16	224	1	1	0.004	837

[A]Site and survey period with prey species listed in Table 5.
[B]Non-rainforest site.

All camera-trapping records come from within the period of June 2011 to May 2019 (Table 1). The majority of cameras were placed near (i.e. within ~50 m of) roads and walking trails through the rainforest, although not on the roads and trails themselves.

Four trail camera models were used during the camera surveys (Bestguarder SG-990V, Reconyx HC550 Hyperfire, ScoutGuard/BolyGuard 562-C and Bushnell NatureView HD, Faunatech, Mount Taylor, Vic., Australia). All cameras were programmed to take three or more still images per detection event, with no time gap between trigger events. At each camera station, a single camera was placed on a tree at a height of 10–50 cm above the ground and facing horizontally, and on a slight downwards angle, towards a bait. Cameras were baited with one or two raw chicken frames, or up to four raw chicken necks. Baits were housed in a plastic mesh bag or an open-ended (i.e. vented), enclosed PVC cylinder, and the bait was placed 1.4–3 m from the camera (Rowland *et al.* 2020). Bait was not replaced or replenished during each of the survey periods. Each survey period was generally a minimum of 2 weeks' duration. Camera stations were spaced between 200 m and 1 km apart and were set in a line transect or grid formation.

Images obtained from camera traps were tagged with species and individual metadata, using the camera-trap management program Camelot (Hendry and Mann 2018). A detection event was defined as any image of an individual captured more than 10 minutes after the previous detection of that species. Image-detection rate (IDR) was determined by dividing the number of detection events by the number of camera-trap nights during a survey period, and this measure was used as an index of cat and prey species activity. Wherever possible, we identified individual cats from the images using aspects of head, body and tail pattern.

Data analysis

We used goodness-of-fit tests and their standardised residual values to explore patterns in cat distribution across the Wet Tropics in relation to (1) broad vegetation type and (2) elevation. Because of low expected frequencies in some vegetation and elevation categories, we collapsed the cat records into broad vegetation types and elevational bands. For vegetation communities, the categories were (1) dry sclerophyll woodland and forest, (2) wet sclerophyll forest and rainforest, and (3) non-remnant vegetation (Table 2). The non-remnant category included all habitats significantly disturbed by humans, such as urban and cropping land, heavily thinned or logged vegetation, and regrowth (Neldner *et al.* 2019).

For elevation, using ArcMap (version 10.6.1), a 1-s Shuttle Radar Topography Mission (SRTM)-derived smoothed DEM layer (DNRM 2011) was used to reclassify elevational bands into 100-m increments from 0 m to 1600 m. We, then, binned 100-m-asl elevational zones into the following five broad elevation categories: (1) 0–300 m, (2) 301–600 m, (3) 601–900 m, (4) 901–1200 m, and (5) >1200 m (Table 3). Our objective was to test whether there was a significant association between cat occurrence records and elevation. However, we also wanted to account for human activity (and, hence, associated cat reporting bias) across elevations. We, therefore, incorporated an index of human activity in the form of road density. To do this, we calculated the total length of roads (in kilometres) by using the Queensland baseline roads and tracks layer (DNRME 2019), for each elevational category (Table 3). We, then, tested for an association between cat records and the road-corrected elevational categories.

Table 2. Proportional occurrence of 99 cat records (our 41 camera-trap records excluded) and the broad habitats in which they originated
Wet sclerophyll forest and rainforest are shown separately below, but these were combined for Chi-squared testing

Habitat type	Number of cat records	Proportional area of habitat type
Dry sclerophyll	25	0.332
Wet sclerophyll	3	0.04
Rainforest	47	0.39
Non-remnant	24	0.23

Table 3. Proportional occurrence of 99 cat records (our 41 camera-trap records excluded) and the broad elevational zone in which they were detected

Elevational band (m)	Number of cat records	Proportion of road lineal extent in band
0–300	17	0.635
301–600	18	0.086
601–900	33	0.210
901–1200	25	0.077
>1200	6	0.002

Cat diet

Cat scats were collected during 350 km of road-based walking transects throughout the Wet Tropics uplands between 1991 and 1997, as part of a project focussed on spotted-tailed quolls (Burnett 2001). All carnivore scats were collected and cat scats were identified from those of the other candidate mammalian carnivores (i.e. dingoes or wild dogs and *D. m. gracilis*), first, by size and general appearance of the scat, and, second, by retrieval of grooming hairs where possible. In terms of broad diagnostics, dingo scats are readily distinguished from scats of cats and *D. m. gracilis* by being much larger (>2.5 cm in diameter). Scats from *D. m. gracilis* can be identified from cat scats by their twisted, rope-like appearance and their persistent pungent smell, even after 24 h of exposure to the atmosphere.

Grooming hairs and mammalian prey species found in scat contents were identified by Barbara Triggs through hair and skeletal analyses, by using the method described by Brunner and Coman (1974). Mammal remains in scats were identified to species level, and non-mammalian material was identified to class level. The hair of two sympatric species, *Rattus fuscipes* and *R. leucopus*, could not be distinguished and, hence, they are included together as *Rattus* spp.

Cat association with mammal community

We used the camera-trap images to quantify the potential prey community of mammals at our survey areas (Table 1). Potential bird prey species captured on camera traps were not considered in the analysis because there were relatively few bird detections in comparison to mammal detections. The methodology for assessing the camera images of potential mammalian prey was the same as that for the cat images (above), except that we did not attempt to identify individuals of prey species. In all analyses, we combined the visually similar *Rattus fuscipes* and *R. leucopus* into a single category, *Rattus* spp., and the three visually similar potential *Antechinus* species (*A. adustus*, *A. flavipes rubeculus*, *A. godmani*) into *Antechinus* spp.

To assess the relationship between cat presence/absence and mammal prey communities, we visualised the mammal communities at sites with cat detections on the camera traps *versus* at sites without cat detections using non-metric multidimensional scaling (NMDS). We used a Bray–Curtis dissimilarity matrix and the metaMDS function of the *vegan* package (Oksanen *et al.* 2011) in R ver. 3.4.3 (R Development Team Core 2017). We visually compared the rank-order composition of the mammal community at each site (as shown by camera trapping), using the number of independent detections of each species as a surrogate of their abundance. These count data were transformed using the power of one-fourth to standardise data to a range of between 0 and 10, and, thus, reduce the effects of the more abundant species on our analyses.

We used Permanova to test for statistically significant differences in the composition of the mammal faunas at sites with and without cat detections. We tested the assumption that data from sites with and without cats had homogeneous dispersions using the 'permutest' function in *vegan*. With that assumption met ($P = 0.48$), we then performed a Permanova on the mammal community data. This was achieved using the 'adonis' function in R package *vegan* set to perform 999 permutations and the Bray–Curtis distance measure.

We also performed a correlation between cat IDR and prey IDR across sites. Average cat IDR was calculated for each site with prey data, and a Spearman correlation was performed.

Results

Distributional patterns

One-hundred and forty cat-occurrence records were compiled from all sources. Cats occur from the coastal lowlands to the summits of the highest mountains in the Wet Tropics bioregion (including on top of the highest peaks in Queensland, Mount Bartle Frere and Mount Bellenden Ker, ~1600 m asl; Figs 1, 2). The combined cat dataset (i.e. including our own data) shows clusters of cat records in the southern Atherton Tablelands region, South Johnstone section of Wooroonooran National Park, and the Bellenden Ker Range (Mount Bartle Frere and Bellenden Ker). The earliest record of a feral cat in the bioregion is in the early 1880s, in the vicinity of Abergowrie, north-west of Ingham (WildNet 2019). This is followed by a record from the 1930s, collected at Babinda. Available records then accumulated in the 1970s and 1980s, and then increased substantially over the following three decades (Fig. 3*a*). We compared the accumulation of cat records against that of 12 co-occurring mammalian prey species (WildNet 2020): *Antechinus adustus*, *A. flavipes rubeculus*, *A. godmani*, *Cercartetus caudatus*, *Isoodon macrourus*, *Melomys cervinipes*, *Perameles pallescens*, *Pseudochirulus herbertensis*, *Rattus fuscipes*, *R. leucopus*,

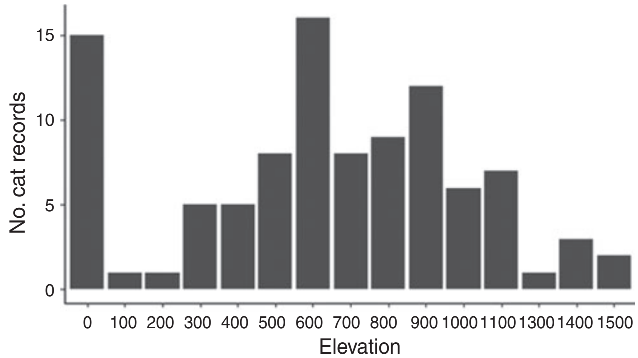

Fig. 2. Cat records in the Wet Tropics, binned to 100-m elevational bands, where 0 refers to elevations from 0–99 m asl, 100 refers to elevations 100–199 m asl, and so on.

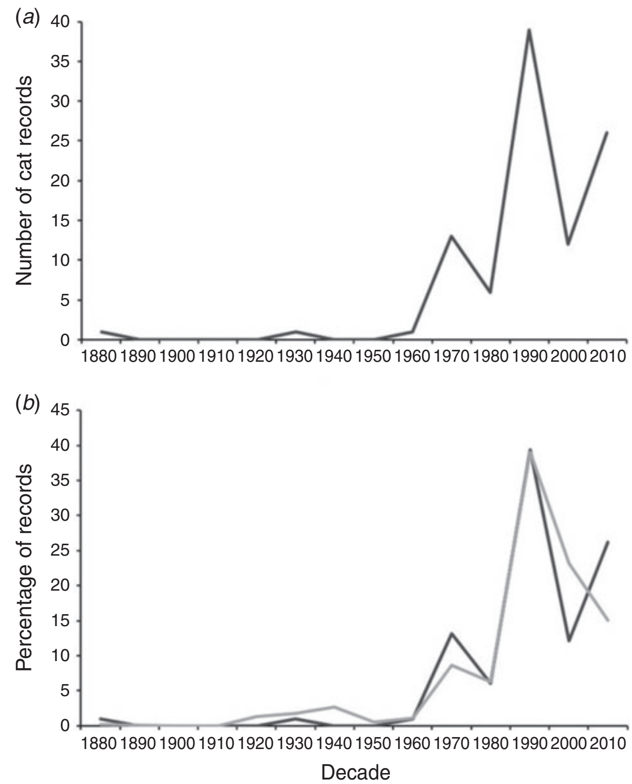

Fig. 3. (*a*) Decadal trends of cat records in the Wet Tropics from 1880 to 2020. (*b*) Decadal trends of the accumulation (%) of cat records (dark grey line) versus mammal prey records (light grey line) in the Wet Tropics from 1880 to 2020.

Uromys caudimaculatus and *U. hadrourus*. The accumulation of records appears similar (Fig. 3*b*), suggesting that the increase in cat records since the 1990s reflects increased general survey effort and reporting, rather than an increase in cat abundance.

Cat records in the Wet Tropics occur across a range of vegetation types, including rainforest communities, tall wet sclerophyll forests, a range of sclerophyll woodlands, forests and shrublands, mangroves and non-remnant habitats including urban and rural environments (Table 2). There is no discernible

Table 4. Diet of cats in the upland areas of the Wet Tropics bioregion from 123 scats collected from transects between 1991 and 1997
BF, Bartle Frere; BK, Bellenden Ker; SJ, South Johnstone; PR, Paluma Range. F, frequency occurrence of prey species in scats; P, percentage of all prey items (therefore, total P sums to >1). Note that 120 scats came from BF, and just one scat from each of BK, SJ and PR

Prey species	BF		BK	SJ	PR	Total	
	F	P	F	F	F	F	P
Rattus species	42	32.5	1	0	0	43	33.3
Antechinus godmani/adustus	30	23.3	0	0	0	30	23.3
Cercartetus caudatus	2	1.5	0	0	0	2	1.5
Melomys cervinipes	11	8.5	0	1	1	13	10.1
Pogonomys sp.	1	0.75	0	0	0	1	0.75
Uromys hadrourus	5	3.8	0	0	0	5	3.8
Total small mammal	91	70.5	1	1	1	94	72.9
Dasyurus hallucatus	1	0.75	0	0	0	1	0.75
Perameles pallescens	6	4.7	0	0	0	6	4.7
Uromys caudimaculatus	8	6.2	0	0	0	8	6.2
Pseudochirulus herbertensis	1	0.75	0	0	0	1	1
Total medium mammal	16	12.4	0	0	0	16	12.4
Isoodon macrourus	6	4.7	0	0	0	6	4.7
Total large mammal	6	4.7	0	0	0	6	4.7
Bird	16	12.4	0	0	0	16	12.4
Total number scats	120		1	1	1	123	
Total number of prey items	129		1	1	1	132	

association of cats with any of our three defined broad vegetation categories ($\chi^2 = 2.97$, d.f. = 2, $P = 0.23$). Cat records are not distributed in proportion to the amount of road in each broad altitudinal band ($\chi^2 = 3019$, d.f. = 4, $P < 0.001$; Table 3). Standardised residual values suggest that a higher number of cats are recorded above 900 m than expected from the lineal extent of roads in that elevational band ($rv_{901\text{–}1200\ m} = 6.2$, $rv_{1200\ m+} = 15.2$), and fewer cat records than expected in the 0–300 m asl band ($rv_{0\text{–}300\ m} = -5.68$) than would be expected based on human activity there.

Upland camera-trap records

Cats were detected at 12 of the 16 mid-elevation and upland camera-trapping survey areas, on 41 of 378 camera stations over a total of 9926 camera-trap nights (Table 1). We had a total of 45 feral cat detections of an estimated 35 individuals (Table 1). The camera trapping suggested that feral cats are widespread but patchily distributed in the uplands of the Wet Tropics. Cat IDR ranged from 0 to 0.053 (Table 1). Rainforest sites on the southern Atherton Tablelands, Bellenden Ker Range, and South Johnstone area had the highest detection rates (Table 1). Cats were not detected at some sites on the southern Atherton Tablelands, on Thornton Peak, Mount Spurgeon (central Carbine Tableland), the upland rainforest at Windsor Tableland, and the Danbulla National Park section of the Lamb Range (i.e. Kauri Creek and Mount Edith Roads). Some of these were single surveys and, hence, we cannot conclude they were real absences; however, the lack of detections at two of these sites (upland rainforest at Windsor Tableland and Danbulla National Park) may reflect real absence because the camera-trapping effort was substantial over many years. Interestingly, cats were detected on camera traps in sclerophyll forest adjacent to the rainforest at Windsor Tableland (albeit at low abundance, Table 1), and have been observed in sclerophyll open forest at Lamb Range.

Cat diet

In all, 123 cat scats were collected from upland rainforest, and prey species remains identified. Nearly all of these scats (120) came from a 3-km section of the Mount Bartle Frere summit trail. The other three came from the summit area of Mount Bellenden Ker, the South Johnstone area of Wooroonooran National Park, and Paluma Range National Park (Fig. 1). The scats contained traces of 12 mammal species and an unknown number of bird species (Table 4). Small terrestrial and scansorial mammals, weighing less than 250 g as adults, make up almost three-quarters (72.9%) of prey occurrences in cat scats. The remainder of the diet is made up of medium-sized mammals up to adult weight of 2 kg (12.4% frequency occurrence) and birds (12.4% frequency occurrence; Table 4).

Cat association with mammal community

Sixteen potential prey taxa were detected from baited camera-trap surveys at mid-elevation and upland sites from June 2017 to May 2019 (Table 5). Mount Lewis had the highest IDR for potential prey species (3.196), followed by Thornton Peak, Danbulla National Park, and Mount Bartle Frere (Table 5). Sites on the southern Atherton Tablelands generally had the lowest detection rate for potential prey species. *Rattus* spp., which were the most common food items in the feral cat scat analysis, were detected at every site. *Antechinus* spp., which were the next most common food items, were detected at most sites except the southern Atherton Tablelands sites, where they were rarely detected (Table 5). There is no indication of an obvious difference in small mammal communities between sites with and those without cat detections (NMDS, Permanova $P = 0.726$; Fig. 4).

We found no correlation between average cat IDR and prey IDR across sites ($C_s = -0.334$, $P = 0.202$; Fig. 5). This is driven by the fact that sites with a low cat IDR have highly variable prey IDR.

Table 5. Potential prey species detected from baited camera-trap surveys in upland rainforest habitat, from June 2017 to May 2019

Prey species richness, total prey detections, total trap-nights, image detection rate (IDR), and detections and numbers of feral cat individuals are also shown. Bold type indicates the sites with a high IDR for prey species. Southern Atherton Tablelands sites: TR, Towalla Road; MH, Mount Hypipamee National Park (NP); HR, Herberton Range NP; McH/MMNR, Mount McHugh/Misty Mountain Nature Refuge; MM, Majors Mountain; SJ, South Johnstone area; MF, Mount Fisher; TF, Tully Falls NP; ST, Southern Atherton Tableland Nature Refuges

Species	Daintree	Windsor Tableland	Carbine Tableland		Lamb Range		Mount Bartle Frere	Southern Atherton Tablelands								
	Thornton Peak		Mount Lewis	Mount Spurgeon	Danbulla NP	Dinden NP		TR	MH	HR	McH/ MMNR	MM	SJ	MF	TF	ST
Antechinus godmani					X		X	X							X	
Antechinus species	X	X	X	X	X	X	X						X			
Cercartetus caudatus							X									
Dactylopsila trivirgata							X									
Hydromys chrysogaster	X	X	X		X		X	X	X	X	X	X	X	X	X	X
Hypsiprymnodon moschatus	X	X	X	X	X	X	X	X					X		X	
Isoodon sp.												X				
Melomys cervinipes		X			X		X		X	X	X		X	X		X
Perameles pallescens	X	X	X	X	X	X	X	X	X		X	X	X		X	X
Rattus species	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X
Pseudochirulus herbertensis							X									
Sminthopsis leucopus													X			
Thylogale stigmatica		X	X		X	X	X		X		X	X	X	X	X	X
Trichosurus vulpecula					X											
Uromys caudimaculatus		X	X	X	X	X	X						X	X	X	
Uromys hadrourus	X		X	X			X	X								
Total prey detections	514	3410	2164	281	652	109	1074	69	9	18	26	53	834	41	76	80
Total trap nights	172	3250	677	195	337	101	586	75	42	56	75	105	606	70	224	142
IDR	**2.988**	1.049	**3.196**	**1.441**	**1.935**	1.079	**1.833**	0.92	0.214	0.322	0.346	0.505	1.376	0.586	0.339	0.691
Prey species richness	6	8	8	6	10	6	12	6	4	3	4	5	9	5	7	5
Felis catus detections (individuals)	0	0	6 (5)	0	0	4 (4)	4 (3)	4 (3)	0	2 (1)	2 (1)	1 (1)	5 (5)	1 (1)	1 (1)	0

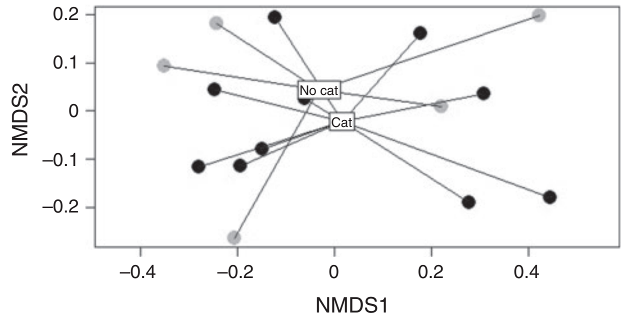

Fig. 4. Non-metric multidimensional scaling (NMDS) plot of prey species communities at each surveyed site with cats (grey circles) and without cats (black circles). Stress = 0.09; $k = 2$.

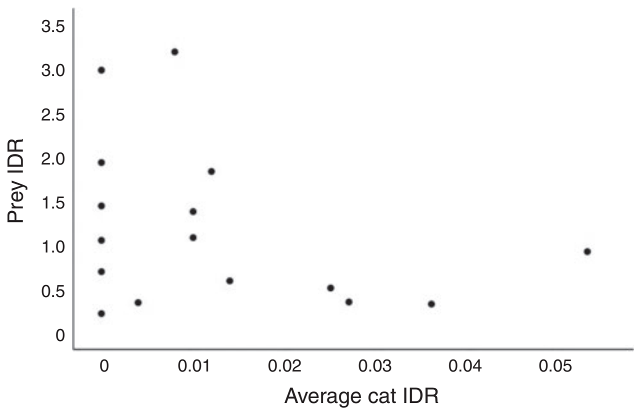

Fig. 5. Scatterplot of average cat image-detection rate (IDR) and total prey IDR for upland sites in the Wet Tropics. No significant correlation was found (see text).

Discussion

Distributional patterns

The occurrence records suggest that feral cats are widely spread throughout the Wet Tropics, and present across all elevations and in all broad vegetation types. Our data suggest that cats are more abundant (or at least more often reported) in the uplands than would be expected on the basis of human activity. Because the present study utilised opportunistically collected records, it cannot take account for sampling biases and, thus, we are unable to conclude definitively that cats are more abundant in the uplands. The trend may also come from people more often looking for wildlife in the higher elevations of the Wet Tropics, or more often reporting cats seen at higher elevations (often in protected areas such as National Parks). Regardless of possible biases, we can conclude that feral cats are present in many of the important upland areas of the Wet Tropics, and at seemingly high abundances in some of these locations.

We did not detect any association between the abundance of cat records and any of the broad habitat types. However, this result should also be treated cautiously because of the opportunistic nature of the present study and probable differences in detectability of cats in different habitats. Cats may be difficult to observe in rainforest, and cats observed in non-remnant ecosystems (e.g. agricultural landscapes) are less likely to be reported than are cats in rainforests or other remnant vegetation types. There is an obvious spike in cat records over the past three decades (Fig. 3*a*), although this is not likely to be a true indication of a sudden increase in cat abundance; rather, it is likely to reflect increased human use of the region, increased recognition of cats as an environmental issue (and, hence, better reporting), and an increased ability to collect and submit records. These broad drivers are supported by the fact that a subset of other mammal species show a similar pattern of accumulation of records over the same time period (Fig. 3*b*).

Despite potential biases, our results are significant in that they demonstrated the utilisation of tropical rainforests by resident feral cat populations for the first time on the Australian mainland. This is in contrast to other published studies. Gordon's (1991) review of cat distribution and habitat concluded that cats appear to be absent from large tracts of closed forest in Queensland, although they are present in smaller tracts. On Cape York Peninsula in north-eastern Australia, feral cats selected strongly for recent fire scars and open wetlands, and avoided rainforests (McGregor *et al.* 2016). In a targeted hair-tubing study along a powerline easement through eucalypt open forest in New South Wales, Goldingay and Whelan (1997) found no evidence of feral cats beyond 200 m into the forest from the powerline easement. However, Catling *et al.* (2002) modelled the distribution of feral cats in the forests of north-eastern New South Wales and indicated a preference for moist habitats with high structural complexity, particularly those with a medium to high density of ground and understorey shrub cover. These different findings may reflect the fact that selection of rainforest as cat habitat is region-specific and driven by local factors such as prey availability and, potentially, the presence of competitors and predators (e.g. Morrant *et al.* 2017). However, cats may widely use rainforests in Australia, but have been largely overlooked because of their cryptic nature in these dense habitats.

Interestingly, our camera-trapping data showed substantial variation in cat detection rate (and hence, probably, cat abundance) across upland areas. Cats were never detected in some upland areas despite considerable camera-trapping effort (including over many years), whereas they were readily detected in other upland areas, such as, for example, most sites in the southern Atherton Tablelands and the connected Bellenden Ker Range (Fig. 1). Furthermore, cats were detected in one part of some mountain ranges but not another (e.g. Dinden National Park versus Danbulla National Park respectively, in Lamb Range; Mount Lewis versus Mount Spurgeon respectively, on the Carbine Tableland). No detections were made in the more remote northern uplands of Thornton Peak, upland rainforest at Windsor Tableland, and central Carbine Tableland (Mount Spurgeon). Although survey effort was limited at some of these sites, intensive camera trapping has been conducted in the rainforest at Windsor Tableland and Danbulla National Park over many years, so the lack of detections reflects a genuine absence or rarity of cats in the rainforest. Interestingly, in both of these two areas, cats are known to be present in adjacent sclerophyll forests (Table 1, Fig. 1; WWF 2018).

This raises the important question of why cats appear to be seemingly common in some upland rainforest areas of the Wet Tropics and rare or completely absent in others. Working out the determinants of regional variation in cat abundance in the Wet Tropics is key to management. Candidates for such drivers include (1) proximity to source areas (e.g. residential and rural areas), (2) degree of access from source areas (e.g. along roads and tracks), (3) the presence and/or abundance of competitors and/or predators such as spotted-tailed quoll, dingoes or wild dogs, and lace monitor (*Varanus varius*), (4) abundance of small mammal prey, (5) provision of shelter from extreme rainfall by boulders or other natural structures, or human structures, or (6) interactions of these factors.

Our data did not allow us to definitively test any of these potential drivers. Our observations suggested that the primary competitors and/or predators are present across sites both with and without cats (J. Rowland, C. Hoskin, and S. Burnett, unpubl. data), and our analysis of potential prey communities showed moderate to high diversity and abundance of small mammal prey across most sites. To some degree, our results appear to support Hypotheses 1 and 2 (proximity to disturbed areas and potential access pathways from these). The upland rainforest areas where cats appear to be absent are generally remote from human-modified landscapes, and if they are penetrated by a vehicular track, that track emerges from a dry landscape that does not typically carry a high biomass of small mammals or feral cats (S. Burnett, unpubl. data). In contrast, many of the sites where cats were readily detected are in close proximity to human-modified landscapes of high productivity, and often directly connected to these areas by roads and trails. Byrnes (2002) reported that cat tracks in sand traps in mid-elevation areas of the Wet Tropics suggested that cats may be using roads as feeding corridors to hunt in rainforest adjacent to cleared pasture areas. Similarly, a review by May and Norton (1996) concluded that it was important to determine the relative impact of exotic predators on native fauna from road formation, and how these potential impacts differ in forested areas with and without roads.

Diet and impacts on prey communities

Our finding that cats are present in many upland areas, including at an apparently high abundance in the core upland areas of the southern Atherton Tablelands and the Bellenden Ker Range, is of concern because most of the endemic vertebrates of the Wet Tropics are restricted to the uplands (Moritz *et al.* 2005; Williams *et al.* 2010). Most of these endemics are of small body size and may, therefore, be prey for feral cats.

Our scat analysis showed that feral cats in the rainforests of the Wet Tropics are preying primarily on small mammals, including a high proportion of rodents and *Antechinus*. It is important to highlight that our scat samples came almost entirely from one site, Mount Bartle Frere. However, this mountaintop site in the central Wet Tropics is probably broadly representative of the Wet Tropics uplands. A high diversity of small and medium-sized mammal species was found in the scats, including Wet Tropics upland endemics such as *Antechinus adustus*/*godmani* and *Uromys hadrourus*. We found no obvious difference in the composition of the small mammal communities between areas with and those without cat detections, although we note that the detection rate of all potential prey combined was generally low on the southern Atherton Tablelands (including low detections of *Antechinus*), the region where cat IDR was generally the highest. We also found no significant negative correlation between cat IDR and prey IDR across sites. However, it is interesting to note that sites with a high cat IDR (i.e. >0.01) generally have a low prey IDR (<1.0; Fig. 5). More detailed analysis is required to test the impact of cats on rainforest small mammal communities, and key endemic species.

There are no previous studies on the diet of feral cats in the Wet Tropics, and few studies on cat diets in other Australian mesic environments (e.g. McComb *et al.* 2019). The abundance of terrestrial mammal prey in our scat analysis concords with results from drier habitats in Australia (e.g. Kutt 2011; Mifsud and Woolley 2012; Yip *et al.* 2015; McDonald *et al.* 2018; Read *et al.* 2019; Wysong *et al.* 2019). Remains in the scats included those of small and medium-sized arboreal and semi-arboreal mammals, *Cercartetus caudatus*, *U. hadrourus* and *U. caudimaculatus*. McComb *et al.* (2019) reported evidence of cats preying on *Gymnobelideus leadbeateri* in high-elevation mesic habitats in Victoria, and Stokeld *et al.* (2018) found a medium-sized semi-arboreal rodent species (*Mesembriomys gouldii*) in cat diets at Kakadu National Park. Large mammal species were rare in the scat remains in our study, as found elsewhere in Australia (Kutt 2011; Wysong *et al.* 2019; but see records of large terrestrial mammal prey species up to 4 kg; Fancourt 2015; Read *et al.* 2019).

Implications and further research

Our research is a first-pass assessment of feral cats in the Wet Tropics. The opportunistic nature of our data means that we have not been able to control for some potential reporting biases. However, we can make important broad conclusions and, from these, we can provide a useful framework for future research. The occurrence records show that cats are widely distributed throughout the Wet Tropics rainforest, across all elevations and habitat types, and at an apparently high abundance in some upland areas. Intriguingly, cats are absent or extremely rare in some remote upland areas. We did not find evidence of population-level impacts on native mammals in the Wet Tropics; however, our analysis was coarse and more detailed studies are needed.

Research is required to resolve (1) the density of cats in rainforest habitats (Legge *et al.* 2017), (2) why they appear to be common in some areas versus absent or very rare in other areas, (3) what impact cats have on rainforest prey populations, (4) habitat and microhabitat selection and behaviour of feral cats in rainforests, (5) the importance of roads and tracks for cat access into rainforest, and (6) source–sink dynamics between cat populations in human-modified landscapes and the rainforest.

Cats have shown themselves to have a devastating impact on native fauna in other parts of Australia (Woinarski *et al.* 2015; Doherty *et al.* 2017) and we must not be complacent about their potential impacts in the Wet Tropics World Heritage Area. Resolving the determinants of distribution and abundance of cats in the Wet Tropics, and their potential impacts, is required so as to assess whether they are a management issue and, if so, what actions could be taken to reduce impacts. The unique upland communities of the Wet Tropics are predicted to be under acute threat from climate change (Williams *et al.* 2003). Populations of mountaintop mammals are likely to become increasingly localised and numerically small, and cats could prove to be a compounding pressure on some species.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

We kindly thank the numerous volunteers and students who assisted with camera trap surveys over the years. We acknowledge and appreciate the Jabalbina Aboriginal Corporation, Queensland Parks and Wildlife Service and Partnerships, Tree Kangaroo and Mammal Group, South Endeavour Trust, Bush Heritage Australia, and the Australian Wildlife Conservancy for their assistance and support of these surveys. We thank Stephen Trent for providing technical expertise in calculating road extents using ArcGIS. Surveys were funded by the Norman Wettenhall Foundation and the Wet Tropics Management Authority. Surveys were undertaken with permit WISP18606117, USC ethics permit (ANA15100) and JCU ethics permit (A2290). Comments from two anonymous reviewers and an associate editor improved an earlier version of the manuscript.

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Handling Editor: John Woinarski