Feral cat abundance, density and activity in tropical island rainforests

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Abstract

Context. Introduced predators, especially cats, are a major cause of extinction globally. Accordingly, an extensive body of literature has focussed on the ecology and management of feral cats in continental and island systems alike. However, geographic and climatic gaps remain, with few studies focusing on rainforests or tropical islands of the south-western Pacific.

Aims. We aimed to estimate cat densities and elucidate activity patterns of cats and sympatric birds and mammals in tropical island rainforests. We hypothesised that cat activity would be most influenced by the activity of introduced rodents and ground-dwelling birds that are predominant prey on islands.

Methods. We used camera traps to detect feral cats, pigs, rodents and birds on four tropical islands in the south-western Pacific. We used spatial capture–recapture models to estimate the abundance and density of feral cats. Relative abundance indices, and temporal overlaps in activity were calculated for feral cats, pigs, rodents, and birds. We used a generalised linear model to test for the influence of pig, rodent, and bird abundance on feral cat abundance.

Key results. The species most commonly detected by our camera traps was feral cat, with estimated densities between 0.31 and 2.65 individuals km^{-2}. Pigs and introduced rodents were the second- and third-most commonly detected fauna respectively. Cat activity was bimodal, with peaks in the hours before dawn and after dusk. Cat abundance varied with site and the abundance of rodents.

Conclusions. Feral cats are abundant in the tropical rainforests of our study islands, where one bird and two mammal species are now presumed extinct. Introduced rodents possibly amplify the abundance and impacts of feral cats at our sites. Peak cat activity following dusk did not clearly overlap with other species detected by our camera traps. We postulate cats may be partly focussed on hunting frogs during this period.

Implications. Cats are likely to be a major threat to the highly endemic fauna of our study region. Management of feral cats will benefit from further consideration of introduced prey such as rodents, and their role in hyperpredation. Island archipelagos offer suitable opportunities to experimentally test predator–prey dynamics involving feral cats.

Introduction

Introduced predators have devastating impacts on wildlife and are responsible for the decline and extinction of faunas world-wide (Salo *et al.* 2007; Doherty *et al.* 2016). Islands are particularly vulnerable because they can support higher feral-predator densities than do mainlands, and prey communities can be naïve having evolved in the absence of such threat (Blumstein 2002; Legge *et al.* 2016). This is of major concern because islands support a disproportionate share of global terrestrial biodiversity (Kier *et al.* 2009) and often act as the last remaining refugia for species extirpated from broader continental ranges (Burbidge 1999; Whittaker and Fernández-Palacios 2007). Ninety-five per

cent of all recorded bird and mammal extinctions since 1500 have been insular species (including Australia; Loehle and Eschenbach 2012).

Feral cats (*Felis catus*) are one of a small number of mammal species responsible for the bulk of invasive impacts to island ecosystems (Courchamp *et al.* 2003; Nogales *et al.* 2013). Globally, they are responsible for at least 14% of insular bird, mammal and reptile extinctions and threaten a further 8% of critically endangered island vertebrates (Medina *et al.* 2011). Although cats appear common and have been held responsible for extinctions worldwide, major geographic and climatic biases remain in our understanding of their impacts (Medina *et al.* 2011). Few studies have focussed on the tropics, data from rainforests are lacking, and the western Pacific is an under-studied region (Bonnaud *et al.* 2011; Medina *et al.* 2011; Doherty *et al.* 2014; Legge *et al.* 2016).

Focus on the behaviour and ecology of feral cats in rain-forests may prove interesting because occupancy rates have been found to be lower in highly complex habitats (Doherty *et al.* 2014; Hohnen *et al.* 2016), and in higher-rainfall areas more generally (Legge *et al.* 2016). Moreover, in Australia where cats are partly responsible for the world's highest rates of mammal extinction and decline, rainforest species have been among those least affected (Hohnen *et al.* 2016; Woinarski *et al.* 2014, 2017).

The East Melanesian Islands of the south-western Pacific are a globally important biodiversity hotspot, with high proportions of fauna that are found nowhere else on Earth (Mayr and Diamond 2001; Mittermeier *et al.* 2004; McCoy 2006; Pikacha *et al.* 2008; Lavery *et al.* 2016). Three birds, and two mammals, are presumed extinct in Solomon Islands. The thick-billed ground dove (*Gallicolumba salamonis*), Choiseul pigeon (*Microgoura meeki*), Makira woodhen (*Gallinula silvestris*), Emperor rat (*Uromys imperator*), and Guadalcanal rat (*U. porculus*) were all ground-dwelling species apparently lost in the late 1800s or early 1900s (Parker 1972; Flannery 1995; Tennent 2009; Dutson 2011). In all instances, introduced pre-dators have been the suspected primary drivers of extinction (Parker 1972; Flannery 1995; Tennent 2009; Dutson 2011). However, data on prevalence and behaviour of introduced species are unavailable to support these assumptions.

Tropical islands of the south-western Pacific offer distinct opportunities for understanding the ecology and impacts of feral cats. First, the predominant vegetation is rainforest. Second, prey communities are simplified because vertebrate diversity per land area is low compared with continents, but endemism is high (Whittaker and Fernández-Palacios 2007; Kier *et al.* 2009). Third, prey assemblages have evolved in the absence of mam-malian predators, and because wild dogs are largely absent, cats are the only exotic carnivore present. The abundance and activity of cats is, thus, unencumbered by the influences of competition with native or introduced carnivores (e.g. Bogdan *et al.* 2016).

We surveyed primary rainforests on four large tropical islands in the south-western Pacific by using camera traps. Our aims were to estimate abundance, density and activity patterns of feral cats, and the abundance and activity patterns of other locally occurring birds and mammals. We postulated that the primary prey for feral cats at our study sites would be introduced rodents and ground-dwelling birds, expecting that

(1) the abundance of feral cats would be most influenced by abundances of introduced rodents and ground-dwelling birds, and (2) temporal overlaps in activity would be greatest between feral cats and these taxa.

Materials and methods

Study area

Data were collected at five sites spanning four islands, namely, Guadalcanal (5302 km^2), Malaita (4307 km^2), Choiseul (3837 km^2) and Kolombangara (687 km^2; Fig. 1, Table 1). All sites were located within primary lowland or lower montane rainforest and varied in elevation from 248 m to 1100 m above sea level (Table 1). On Guadalcanal, we surveyed two sites ~27 km apart, namely, Kovi, on the northern coast, ~4 km from the outskirts of Honiara, and Valevahalo, a former village site that was abandoned in the 1970s (J. Kera, pers. comm.). On Kolombangara, our site was on the western side of the island, inland from Poitete village and within a designated conservation area above the 400-m contour. On Choiseul, our site was close to Mount Maetembe in the middle of the island, and, on Malaita, we worked at the Kwainaa'isi Conservation Area in the high-lands of East Kwaio.

The Kovi and Poitete sites supported lowland rainforest, and higher-elevation sites (Kwainaa'isi, Mount Maetembe, Valevahalo) were in areas of lower montane rainforest. Lowland rainforests in Solomon Islands are dominated by 12 common tree species (genera *Calophyllum*, *Dillenia*, *Elaeocarpus*, *Endospermum*, *Parinari*, *Maranthes*, *Pometia*, *Gmelina*, *Schizomeria*, *Terminalia* and *Campnosperma*), with a canopy typically between 25 and 35 m high. Lower montane forests are shorter (15–20 m), with an increasing infiltration of *Syzygium*, *Metrosideros*, *Ardisia*, *Psychotria*, *Schefflera*, *Ficus*, *Rhododendron*, *Dacrydium*, and *Podocarpus pilgeri* (Müeller-Dombois and Fosberg 2013).

Camera-trap surveys

We collected data on feral cats and sympatric fauna by using camera traps (Reconyx, Models HC500, HC550 and PC900, Holmen, WI, USA). Cameras were programmed using a high-sensitivity trigger to capture five images per event at rapid-fire intervals, with no delay between triggers. We deployed cam-eras as linear transects (Guadalcanal, Kolombangara), or opportunistically as a cluster of three cameras (Choiseul) or six cameras (Malaita) spaced between 94 m and 679 m apart (Table 1). Each camera was fixed to the trunk of a tree ~50 cm above the ground, facing perpendicular to fauna trails. We placed a bait in front of each camera (2–3 m away), which consisted of a cannister containing peanut butter on fibre wadding. The use of baits has been shown to have limited influence on detection rates of feral cats in other environments (Read *et al.* 2015; Stokeld *et al.* 2015). However, rodents attracted to our baits could, in turn, have attracted feral cats and increased detection rates.

We placed cameras a minimum of 100 m away from informal walking trails. The degree to which feral cats travel along these features in our study region is unknown. However, their prox-imity could potentially result in increased detection rates of cats, and there was potential bias owing to differing levels of habitat
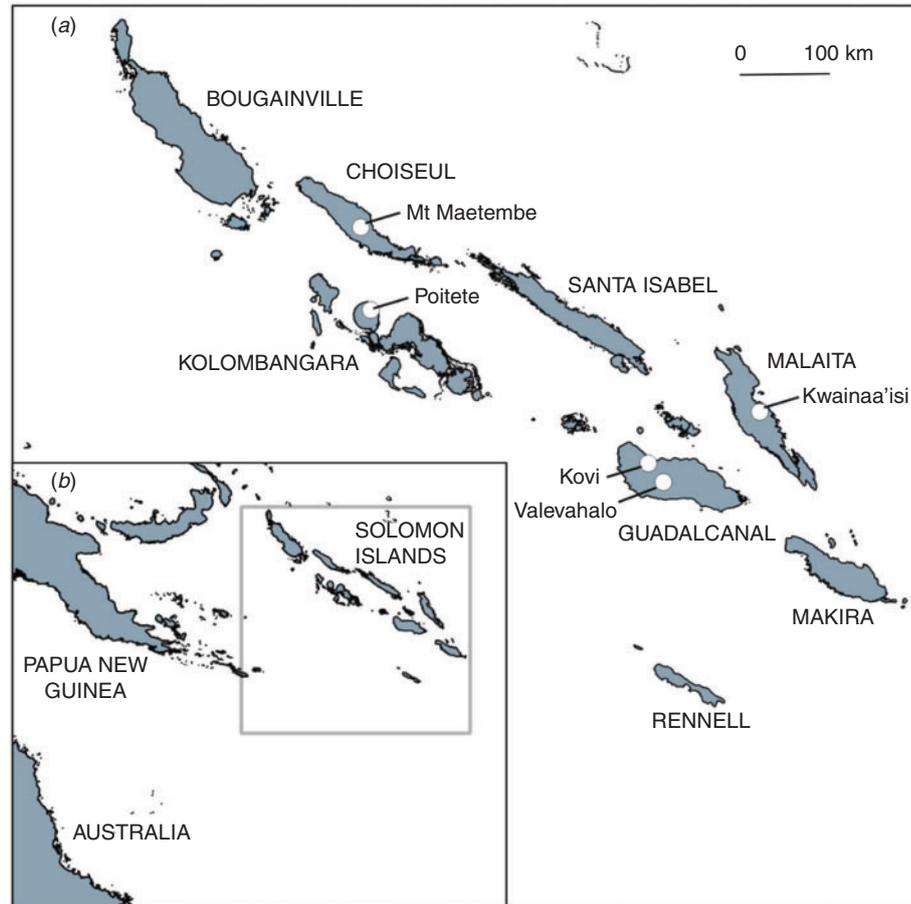
Fig. 1. Location of study sites on Guadalcanal and Kolombangara Islands: (*a*) within Solomon Islands; and (*b*) within the wider southern Pacific.

disturbance and modification in these areas (e.g. people dispersing or planting fruit trees *en route*).

We used the program Camelot (Hendry and Mann 2018) to process camera-trap images by identifying and tagging fauna to species level where possible. Cats were individually identified using pelage colour patterns, sex, body and tail shape, and carriage. A proportion of photographs captured only distal body parts (e.g. ears, tails), individuals with no defining marks or tabby cats whose pattern could not be recognised, and these were coded as unidentified. Other taxa recorded by our camera traps were not individually identified because of a lack of discerning features. Photographs were defined as events when the delay between two consecutive images of a species exceeded 10 min.

Abundance and densities

We generated density and abundance estimates of feral cats for our transect sites by using spatial capture–recapture models that are ideal where a proportion of the population can be identified via unique markings (Forsyth *et al.* 2019). These incorporate data on both identified and unidentified individuals under the critical assumptions that unidentified animals are a random sample from the population, and that they are distributed throughout the defined state space (Forsyth *et al.* 2019). A

suitable buffer width for defining the state space (the maximum distance from each individual's home-range centre where detection was zero) was identified using the 'secr' library in R (Efford 2019). Values of Akaike information criterion (AIC) were used to assess which functional form (half-normal, exponential, hazard-rate) best fitted our data by comparing for each model. The detection function with the lowest AIC was then used as the basis for estimating the buffer. Our sites were within large contiguous patches of forest remote from landscape features that may be impassable by feral cats; thus, we did not expect the geometry of home ranges to be distorted by these features (e.g. large rivers, vertical terrain).

We fitted spatial capture–recapture models using Markov-chain Monte Carlo (MCMC) sampling in NIMBLE version 0.8.0 (de Valpine *et al.* 2017), following the methods described by Forsyth *et al.* (2019). We defined the state space around camera locations by using our buffer estimate (2 km) and drew 110 000 samples from the MCMC algorithm from each of three chains, using diffuse initial values with a thinning rate of 10. The first 10 000 samples were discarded, leaving 100 000 samples from each chain to form the posterior distribution of the parameters. Model convergence was assessed by calculating $\hat{R}$ and by visual inspection of the chains.

Table 1. Site details for camera-trap surveys for feral cats

Island	Site	Survey method	Survey date	Elevation (m)	Number of cameras	Number of trap nights	Transect length (km)	Average distance between cameras (m)	Latitude (camera centroid)	Longitude (camera centroid)
Guadalcanal	Kovi	Transect	5 Sep. 2015–26 July 2016	248–427	14	2676	3.92	299	−9.46124	159.89374
Guadalcanal	Valevahalo	Transect	16 Sep. 2015–9 Nov. 2016	867–1100	11	2369	1.17	125	−9.64805	160.04524
Kolombangara	Poitete	Transect	19 July 2017–16 Nov. 2017	323–991	10	1178	3.64	401	−7.92478	157.11258
Choiseul	Mount Maetembe	Opportunistic	20 Feb. 2017–14 Nov. 2017	746–823	3	726	n.a.	194	−7.09367	157.01260
Malaita	Kwainaa 'isi	Opportunistic	24 Aug. 2017–14 Jan. 2018	718–900	6	510	n.a.	265	−8.95344	161.00630

For cats, pigs, birds and rodents, we calculated relative abundance indices (number of event counts per 100 camera-trap nights) at each study site. Problems associated with relative abundance indices are well acknowledged in that they do not adequately account for imperfect and variable detection probabilities across species, time and space (Sollmann *et al.* 2013). However, suitable alternatives are unavailable for unmarked species that are unlikely to be detected across multiple camera-trap stations in a given study (e.g. species of rodent in this case). Here, we have used relative abundance indices for comparisons of the same species across multiple sites where survey methods were consistent.

Temporal overlaps and associations

We analysed the pair-wise temporal overlap between cats and pigs (*Sus scrofa*), buff-headed coucals (*Centropus milo*), Melanesian megapodes (*Megapodius eremita*), Stephen's emerald dove (*Chalcophaps stephani*, bronze ground dove (*Gallicolumba beccarii*) and rodents Pacific rat (*Rattus exulans*) and black rat (*R. rattus*) by using the R statistical environment package 'overlap' (Meredith and Ridout 2014). Two species of introduced rodent (*R. exulans* and *R. rattus*), and two species of ground-foraging doves from the family Columbidae (*C. stephani* and *G. beccarii*) were each pooled together for the analysis. We pooled data from all study sites and calculated overlaps between cats and pigs, buff-headed coucals, Melanesian megapodes, columbid doves and rodents. Survey effort was standardised by partitioning event counts into single month periods of camera-trap deployment. The measure generated using this method ranges from 0 where there is no overlap, to 1 where species completely overlap. Confidence intervals were obtained as percentile intervals from 1000 bootstrap samples.

To examine species spatial associations between cats and other vertebrates, we used a negative binomial generalised linear model (GLM) implemented using MASS library in R (Venables and Ripley 2002). We regressed event counts of cats against event counts of pigs, buff-headed coucals, Melanesian megapodes, columbid doves and rodents. Site was included as a variable.

Results

Eighteen species were detected from 44 camera-trap stations over 7459 camera-trap nights. The most frequently recorded (event counts) were cats (303), pigs (*Sus scrofa*; 260), introduced rodents (Pacific rat (*Rattus exulans*) and black rat (*R. rattus*) (192)), Melanesian megapode (*Megapodius eremita*; 168), buff-headed coucal (*Centropus milo*; 91) and Stephen's emerald dove (*Chalcophaps stephani*; 32). We also recorded water monitor (*Varanus indicus*; 22), dogs (*Canis lupus familiaris*; 21), bronze ground dove (*Gallicolumba beccarii*; 16), nankeen night heron (*Nycticorax caledonicus*; 14), northern common cuscus (*Phalanger orientalis*; 11), Roviana rail (*Gallirallus rovianae*; 4), Nicobar pigeon (*Caloenas nicobarica*; 3), and single events of variable goshawk (*Accipiter hiogaster*), white-billed crow (*Corvus woodfordi*), Sanford's sea eagle (*Haliaeetus sanfordi*) and golden whistler (*Pachycephala pectoralis*).

Eight species (cat, pig, Pacific rat, black rat, Melanesian megapode, buff-headed coucal, Stephen's emerald dove and

Table 2.   Abundance and density estimates for the most common vertebrates recorded on camera traps

RAI, relative abundance index (number of event counts per 100 camera-trap nights); $\hat{N}$, posterior distribution of abundances; $\hat{D}$, number km^{-2}. CrL, 2.5% and 97.5% credible limit; n.a., species distribution does not extend to site

Parameter	Guadalcanal–Kovi			Guadalcanal–Valevahalo			Kolombangara–Poitete			Malaita–Kwainaa'isi	Choiseul–Mount Maetembe Loboro
	RAI	$\hat{N}$	$\hat{D}$ (CrL)	RAI	$\hat{N}$	$\hat{D}$ (CrL)	RAI	$\hat{N}$	$\hat{D}$ (CrL)	RAI	RAI
Cats	5.16	13.10	0.31 (0.24–0.45)	4.81	59.10	2.65 (1.30–4.00)	2.72	23.7	0.65 (0.19–1.37)	1.77	1.38
Pigs	0.67			8.10			0.68	–	–	0	5.79
Columbid doves	1.16	–	–	0.63	–	–	0.09	–	–	0.20	0
Coucals	1.61	–	–	0.93	–	–	2.29	–	–	n.a.	n.a.
Megapodes	2.62	–	–	1.22	–	–	6.03	–	–	0	0.41
Rattus spp.	0.71	–	–	3.97	–	–	6.54	–	–	1.37	0

bronze ground dove) accounted for 93.1% of all event counts. Dogs were recorded in a total of 21 instances across Malaita (7), Kolombangara (1), Guadalcanal (Kovi, 10), and Choiseul (3). In all instances, these were identified as hunting dogs owned by people in nearby villages.

We assigned 89.7% of feral cat images to known individuals. At Kovi, we identified nine individual cats, 12 at Valevahalo and five at Poitete. The predominant colours of cats were classic tabby (9), spotted tabby (6), black ± tuxedo (5), brindle (3), plain white (2), mackerel tabby (1) and tabby and white (1).

Abundance and densities

Cat density estimates from spatial capture–recapture ranged from 0.31 km^{-2} at Kovi, close to Honiara, to 2.65 km^{-2} at the more remote site Valevahalo. On Kolombangara, we estimated a density of 0.65 cats km^{-2} (Table 2).

Relative abundance indices (number of event counts per 100 camera-trap nights) varied among species and sites (Table 2). Values for cats ranged from 5.16 at Kovi, to 1.38 at Mount Maetembe. At our two Guadalcanal sites, feral cat density estimates were far greater at Valevahalo than Kovi. However, the relative abundance index was highest at Kovi, indicating that fewer individuals were recorded more frequently over the longer Kovi transect (Tables 1, 2). Pig indices were greatest at the more remote sites of Valevahalo and Mount Maetembe (8.10 and 5.79 respectively), and they were not detected at Kwainaa'isi. The greatest abundances of *Rattus* spp., Melanesian megapodes and buff-headed coucals were all detected at Poitete. The greatest abundance of columbid doves was at Kovi, and none were detected at the Kwainaa'isi site.

Temporal overlaps and associations

Cats were predominantly nocturnal and activity was bimodal, with peaks following dusk (between 1800 hours and 1900 hours) and before dawn (between 0500 hours and 0600 hours; Fig. 2a–e). In relation to other vertebrates, the highest overlap in activity was with pigs, followed by introduced rodents, Melanesian megapodes, columbid doves and buff-headed coucals (Table 3, Fig. 2a–e).

Our generalised linear model showed that the number of cat-event counts captured by cameras varied significantly with survey site (fewer cats were detected on cameras set at Kwainaa'isi and Poitete than at other sites; Table 4). Cat-event counts were positively associated with the number of event counts of introduced rodents (Table 4).

Discussion

The present study has contributed to the sparse literature on ecology and impacts of feral cats in rainforests (Doherty *et al.* 2014; Legge *et al.* 2016), and helped fill a geographic information gap in the south-western Pacific (Medina *et al.* 2011). Feral cat was the species most commonly recorded in our study. Density estimates from spatial capture–recapture models ranged between 0.31 cats km^{-2} and 2.65 cats km^{-2} and our relative abundance indices ranged from 1.38–5.16 event counts per 100 camera-trap nights. The single density estimate made from our lower montane sites (Valevahalo, 2.65 cats km^{-2}) was higher than those from our lowland site on the same island (Kovi, 0.31 cats km^{-2}) and the lowland site on Kolombangara (Poitete 0.65 cats km^{-2}). We suspect that this may reflect higher abundances of prey and increased carrying capacity at our montane site. Rodent trapping data have shown that Pacific rat is often extremely abundant at high-elevation sites in Solomon Islands (T. H. Lavery, unpubl. data), but such data specific to our sites are unavailable. Relative abundance of rodents (event counts per 100 camera-trap nights) at our Valevahalo site (3.97) was indeed higher than at Kongulai (0.71). However, the highest relative abundance of rodents was recorded at Poitete (6.54). More reliable estimates of prey density, and a greater number of sites and elevational ranges are needed to draw more specific conclusions about the factors influencing variations in cat density on our study islands.

The limited number of feral cat studies in rainforests or on tropical islands makes it difficult to appreciate how our results compare to similar contexts. On other tropical islands, cats can be entirely absent from rainforests. For example, camera trap surveys in the Philippines failed to detect any cats inside primary rainforests (Bogdan *et al.* 2016). The Tenkile Conservation Alliance have deployed 50 camera traps since 2011 (across a 185 000-ha rainforest conservation area in the Torricelli Mountains of northern New Guinea) and no cats have been detected despite their being common in the 50 villages around the park (J. Thomas, pers. comm.). Conversely, in Australia's Wet Tropics, camera-trap detection rates of cats in upland rainforest were highly variable across 16 sites (Rowland *et al.* 2020). Cats were abundant at three sites
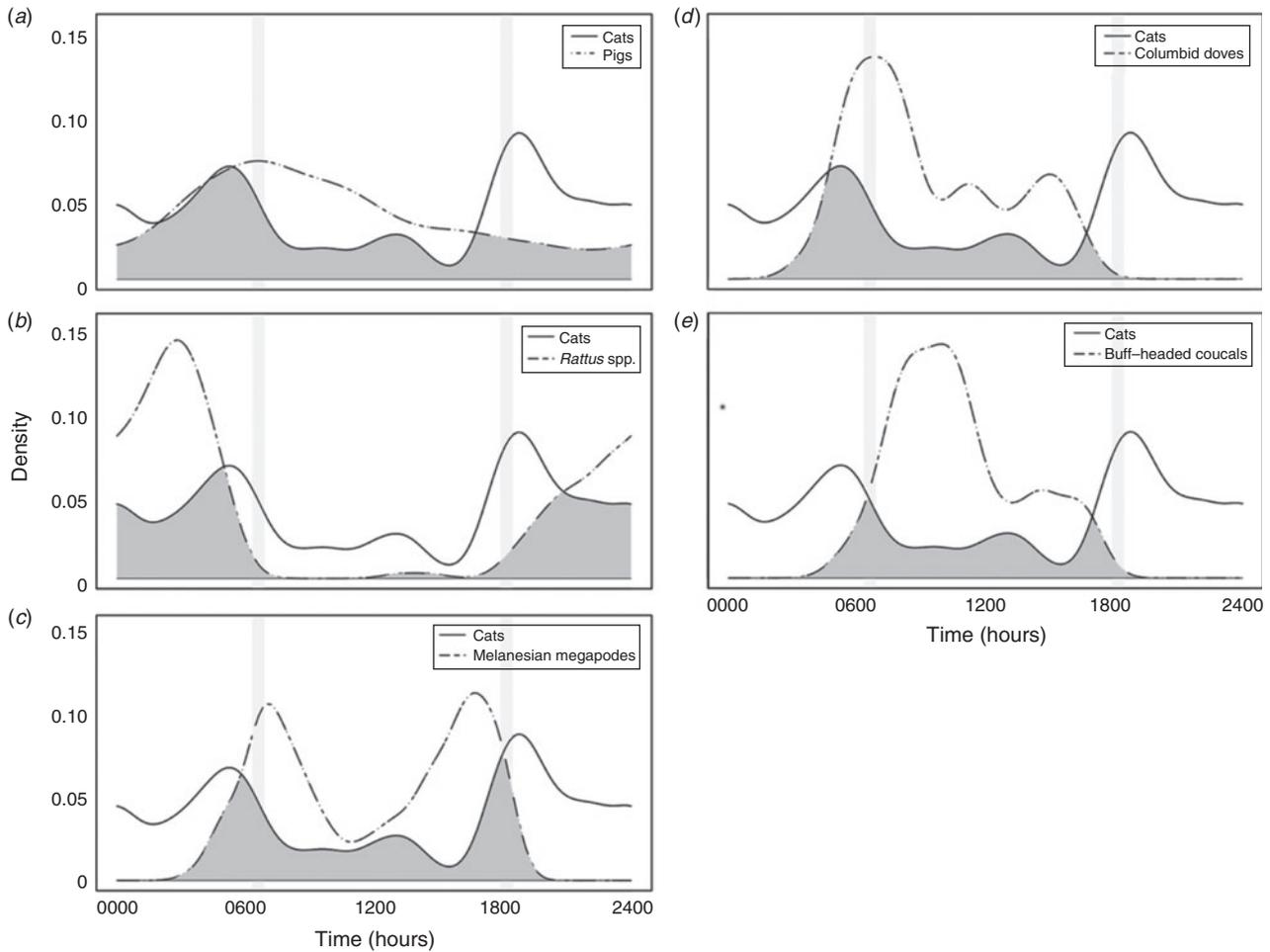
Fig. 2. Temporal overlap between cats (solid lines) and other species (dotted lines): (*a*) feral pigs; (*b*) *Rattus* spp. (*R. exulans* and *R. rattus*); (*c*) Melanesian megapodes (*Megapodius eremita*); (*d*) columbid doves (*Chalcophaps stephani* and *Alopecoenas beccarii*); and (*e*) buff-headed coucals (*Centropus milo*). Grey vertical bars indicate approximate times of sunrise and sunset at the study sites.

Table 3. Estimates of activity pattern overlap between cats and the five most commonly recorded vertebrate species or species groups

Numbers in parentheses are approximate 95% bootstrap confidence intervals. Values were calculated using the methods of Meredith and Ridout (2014)

Species	Overlap (95% CI)
Pigs	0.68 (0.60–0.74)
Rattus spp.	0.56 (0.48–0.62)
Melanesian megapodes	0.47 (0.40–0.54)
Columbid doves	0.41 (0.33–0.49)
Buff-headed coucals	0.29 (0.21–0.36)

Table 4. Summary statistics of the negative binomial general linear modelling (GLM) testing for the effects of site and abundances of five species or species groups on feral cat abundance

$***P < 0.001; **P < 0.01; *P < 0.05$

Parameter	Estimate ± s.e.	Z	P
Intercept	0.48 ± 0.13	3.70	***
Kwainaa'isi	-0.87 ± 0.4	-2.21	*
Mount Maetembe	-0.71 ± 0.4	-1.79	0.07
Poitete	-0.8 ± 0.28	-2.87	**
Valevahalo	-0.15 ± 0.19	-0.80	0.42
Rattus spp.	0.08 ± 0.03	2.40	*
Columbid doves	-0.11 ± 0.1	-1.17	0.24
Melanesian megapode	0.06 ± 0.05	1.16	0.25
Pigs	0.04 ± 0.03	1.45	0.15
Buff-headed coucals	-0.19 ± 0.11	-1.75	0.08

(3.2–5.3 event counts per 100 camera-trap nights); however, at many of the other sites, no cats were detected. This included two sites that had been extensively surveyed with camera traps over many years.

Legge *et al.* (2016) compiled a comprehensive review of 78 feral cat density estimates across Australia. No rainforest sites were available, although the study did incorporate 13 sites on small islands (mostly arid or temperate islands). Forty-four of the reviewed studies estimated densities by using camera traps.

Values derived from these non-rainforest environments ranged from 0 to 3.4 km^{-2}, with a mean value of 0.49 km^{-2} (95% CI: 0.28–0.70 cats km^{-2}). On the 13 island sites, the majority of density estimates were based on animal capture or removal. Of the four island sites that calculated density estimates by using camera traps, values ranged from 0.17 to 3.4 cats km^{-2}. Further data from rainforest habitats and tropical island sites are needed before our results can be further compared with those from other locations.

Species interactions

Cat activity was bimodal, with peaks in the hour before dawn and the hour following dusk. The greatest temporal overlap was with pigs, followed by introduced rodents. Rodent abundance was also influential to cat abundance in our generalised linear model. Globally, rats are one of the top three prey items for feral cats on islands (Bonnaud *et al.* 2011). In New Caledonia, they were the predominant prey found in scats from all habitats across seasons (Palmas *et al.* 2017). In the Philippines, Bogdan *et al.* (2016) identified introduced rodents as key prey for feral cats because activity overlaps between the two were high (0.48–0.62% in intermixed areas of secondary forest, villages and farms).

In Solomon Islands, the prehistorically introduced Pacific rat (*Rattus exulans*) is extremely abundant in primary forests from sea level to high-elevation summits (T. Lavery, unpubl. data). Smith and Quin (1996) suggested that abundant introduced rats and rabbits can sustain more abundant predator populations, increasing their propensity to hunt native species to extinction ('hyperpredation'). Accordingly, the impact of cats on islands is greater where exotic rodents or rabbits are present (Medina *et al.* 2011).

We postulate that hyperpredation may have contributed to the impacts of feral cats at our study sites. Our data indicated that ground-foraging columbid doves, Melanesian megapodes and buff-headed coucals were not principal prey targets. Temporal overlaps between birds and cats occurred in the morning, and bird activity following dusk (when cats were most active) was low. Furthermore, our generalised linear model indicated that counts of columbid doves, Melanesian megapodes and buff-headed coucals did not influence event counts of cats. Nonetheless, three ground-dwelling birds (and two ground-dwelling mammals) are now considered extinct in Solomon Islands because of feral cats (Parker 1972; Flannery 1995; Tennent 2009; Dutson 2011).

Our camera-trap images documented four instances of feral cat hunting behaviour. One image from Kolombangara portrayed a cat eating a large forest skink (most likely *Eugongylus albofasciolatus*). In the remaining three cases (two from Guadalcanal, one from Kolombangara), they were pursuing frogs on the forest floor. Islands can support extraordinarily high densities of organisms, including herpetofauna (Rodda and Dean-Bradley 2002). At our study sites, three large, ground-dwelling frogs occur at high densities (*Cornufer guentheri* at 3250 km^{-2}, *Cornufer solomonis* at 5480 km^{-2}, and *Cornufer weberi* at 7410 km^{-2}; Pikacha *et al.* 2008). These species are active in the early hours after dusk, and the peak in cat activity after dusk may reflect their exploiting this abundant resource. At Kwainaa'isi, where a cat control program has been implemented

across an area of ∼500 km^2 since 2015, the primary change recognised by communities has been an increase in the abundance of frogs (E. Kekeubata, pers. comm.). More broadly, the impacts of feral cats on amphibians seems to be an area of research that has received limited attention. For example, a global review of the impacts of cats on island endangered vertebrates did not include amphibians (Medina *et al.* 2011). Consideration of the role of introduced mammalian predators on global biodiversity loss also did not include amphibians because non-mammalian predators are a greater threat (Doherty *et al.* 2016). A recent review of the incidence of frogs in the diet of cats in Australia (Woinarski *et al.* 2020) helps redress this deficiency.

Images of dogs captured by our cameras were pairs or groups of three animals recorded during diurnal hours. Each dog photographed was conclusively recognised as a domestic hunting dog rather than a feral animal, and it is likely that they were recorded during hunting forays led by their owners. The activity of domestic hunting dogs (maximum 10 event counts per location at four of five sites) may have influenced the behaviour of cats, pigs and other species at our study sites. However, free-ranging wild dogs were not detected, and, thus, any influence was likely only sporadic. Dogs have been identified as a key contributor to several vertebrate extinctions in Solomon Islands (Tennent 2009; BirdLife International 2016*a*, 2016*b*). The apparent absence of wild dogs and rarity of hunting dogs in this study indicates cats are likely to be a far greater threat.

Biogeography of an introduced predator

Islands are often considered as natural laboratories useful for dissecting the influences of biotic and abiotic variables on ecology and biogeography (Mayr 1967). In Solomon Islands and the broader Pacific, natural variations in prey assemblages could provide useful opportunities to further understand the interactions between feral cats and vertebrate prey. For example, frog densities on our four study islands (Choiseul, Guadalcanal, Kolombangara Malaita) are higher than on smaller islands for which we were unable to obtain data (e.g. Tetepare, Gatokae, Ngella, Ranongga; Pikacha *et al.* 2016). In a broader Pacific island context, ectotherms progressively replace endotherms with an increasing isolation, and bird and mammal diversity decreases (Mayr and Diamond 2001; McNab 2002; Lavery *et al.* 2016). Conversely, birds become a more important prey item with an increasing isolation (Bonnaud *et al.* 2011). This biogeographic variation in vertebrate prey is likely to have fascinating implications for feral cat activity and densities. We recommend expansion of our study to cover a greater geographic area, incorporating a range of island sizes and isolation. Furthermore, as discrete units of land, islands also present suitable opportunities to manipulate prey assemblages. As such, there is potential to further understand the role of hyperpredation in vertebrate extinction through experimental removal of rodents. Research focus in these areas may greatly assist with prioritising management and eradication of feral cats for protection of island fauna globally.

Conflicts of interest

The authors declare no conflicts of interest.

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