

Effects of habitat alteration and disturbance by humans and exotic species on fosa *Cryptoprocta ferox* occupancy in Madagascar's deciduous forests

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Abstract Anthropogenic habitat alteration and invasive species are threatening carnivores globally. Understanding the impact of these factors is critical for creating localized, effective conservation programmes. Madagascar's Eupleridae have been described as the least studied and most threatened group of carnivores. We investigated the effects of habitat degradation and the presence of people and exotic species on the modelled occupancy of the endemic fosa *Cryptoprocta ferox*, conducting camera-trap surveys in two western deciduous forests, Ankarafantsika National Park and Andranomena Special Reserve. Our results indicated no clear patterns between habitat degradation and fosa occupancy but a strong negative association between cats *Felis* sp. and fosas. Cat occupancy was negatively associated with birds and positively associated with contiguous forest and narrow trails. In contrast, dog *Canis lupus familiaris* occupancy was best predicted by wide trails, degraded forest and exotic civets. Our results suggest fosas are capable of traversing degraded landscapes and, in the short term, are resilient to contiguous forest disturbance. However, high occupancy of cats and dogs in the landscape leads to resource competition through prey exploitation and interference, increasing the risk of transmission of potentially fatal diseases. Management strategies for exotic carnivores should be considered, to reduce the widespread predation of endemic species and the transmission of disease.

Keywords Ankarafantsika, deforestation, Eupleridae, fosa, feral cat, habitat degradation, invasive species, Menabe

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Introduction

The fosa *Cryptoprocta ferox* is Madagascar's largest endemic carnivore. The species plays a critical role in ecosystems across Madagascar as an apex predator of lemurs, small mammals, reptiles and birds (Dollar et al., 2007; Hawkins & Racey, 2008). Weighing 6–7 kg (Hawkins, 1998; Dollar, 2006), male fosas have been estimated to occupy large home ranges of up to 50 km² (Lührs & Kappeler, 2013) at low densities of 0.18–0.26 per km² in deciduous forests (Hawkins & Racey, 2005) and 0.20 per km² in rainforests (Murphy et al., 2018b). Currently categorized as Vulnerable on the IUCN Red List (Hawkins, 2016), fosas are threatened by bushmeat hunting (Golden, 2009; Farris et al., 2015b; Merson, 2018), retaliatory killing in response to poultry predation (Hawkins, 2016; Merson, 2018), exotic species (Gerber et al., 2012b; Farris et al., 2015c) and habitat loss (Gerber et al., 2012a; Farris et al., 2015b).

Deforestation has significantly reduced Madagascar's overall forest cover, and much of the remaining forest is severely degraded (Allnutt et al., 2013; Vieilledent et al., 2018). However, there has been little research on the effects of anthropogenic disturbance on Madagascar's endemic species (Irwin et al., 2010). In addressing these empirical deficits, the fosa is a useful focal species because its innate biological characteristics (large body size and home range, low population density) make it potentially more susceptible to human-caused extinction (Ripple et al., 2014).

Research documenting the fosa's persistence in human-disturbed landscapes is mostly limited to Madagascar's eastern rainforests. Camera-trap studies have reported broad patterns of lower native, and higher exotic carnivore occupancy in more degraded forests (Gerber et al., 2012a; Farris et al., 2014, 2015b; Murphy et al., 2017). However, despite these advances in the knowledge of anthropogenic disturbance in eastern Madagascar, no similar research has yet been published from Madagascar's deciduous forests, a globally important, threatened ecoregion (Waeber et al., 2015).

Deforestation in western Madagascar has reduced much of its deciduous forest cover (Scales, 2012), with high annual rates of loss continuing (Zinner et al., 2014). Many narrow-ranged endemic taxa occupy these forests (Waeber et al., 2015), and are potentially capable of responding differently to anthropogenic change in rainforests compared to deciduous forests

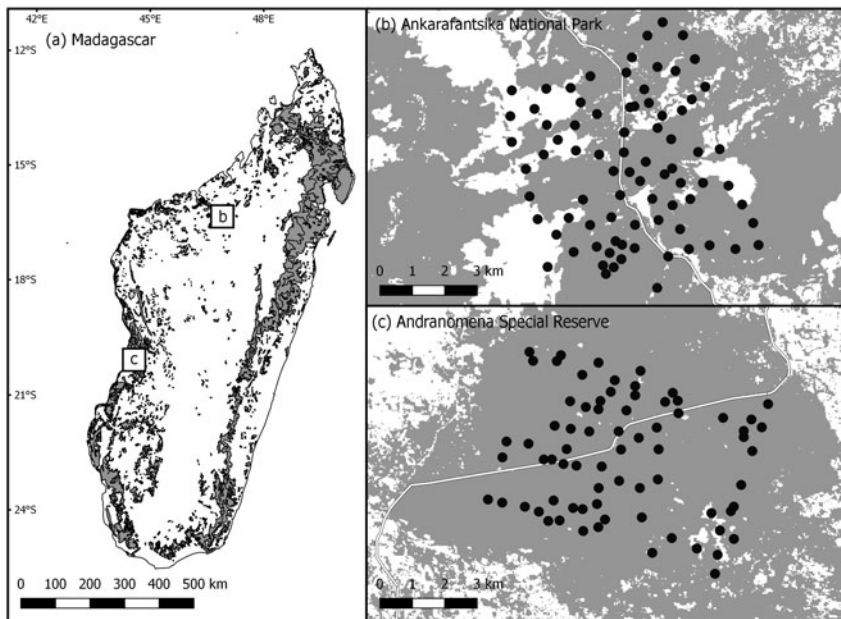


FIG. 1 (a) Forest cover (shaded) and location of study sites in north-west and western Madagascar where the camera-trap surveys were conducted during 2014–2015, with location of camera traps in (b) north-west Ankarafantsika National Park and (c) western Andranomena Special Reserve.

(Gardner, 2009; Irwin et al., 2010). With these species now facing greater anthropogenic disturbance, understanding this relationship is more important than ever.

This study investigated the effects of anthropogenic disturbance on fosa living in deciduous forest. Surveys were conducted in two forests, Ankarafantsika National Park and Andranomena Special Reserve, contrasting in degradation, forest cover and human occupation. Our objectives were to examine (1) the effects of human and exotic species presence on fosa occupancy, (2) the effects of various landscape variables (measures of forest degradation) on fosa occupancy, and (3) differences in fosa occupancy between the two forests.

Study area

Ankarafantsika National Park is Madagascar's largest continuous dry deciduous forest (1,350 km²; Fig. 1). The 37.73 km² study site within the Park includes four villages and is characterized by old-growth forest (defined as continuous forest that has experienced some human disturbance), savannah, raffia plantations and rice fields. It is used recurrently by local people and frequented by exotic species, including the zebu *Bos primigenius indicus*, free-ranging dogs *Canis lupus familiaris* and cats *Felis* sp., bushpig *Potamochoerus larvatus*, small Indian civet *Viverricula indica*, and another endemic carnivore, the western fanouc *Eupleres major* (Merson et al., 2018).

Andranomena Special Reserve (64 km²) is located in the central-western region of Menabe. The 35.45 km² study site within the Reserve encompasses contiguous, mostly old-growth forest, with two villages on its boundary. The area is bisected by a grid system of trails established by the former

Forestry Commission (Fig. 1). Despite the cessation of commercial logging, widespread illegal logging was evident throughout the study site. The Reserve is home to another euplerid, the endemic bokiboky *Mungotictis decemlineata*.

Methods

Eighty pairs of camera traps (Cuddeback Ambush IR 1187, De Pere, USA) were placed along trails in Ankarafantsika National Park for 80 days during April–June 2014, and in Andranomena Special Reserve for 35 days during May–June 2015. Trails were chosen to maximize the detection of fosas and exotic species for occupancy analysis (O'Connell et al., 2010). Camera stations were c. 500 m apart, improving the detection of *E. major* and *M. decemlineata*, which have smaller home ranges than *C. ferrox*. Stations were set up following the methodology of Gerber et al. (2012a). Pairs of independently operated cameras were placed flanking trails, 20–30 cm above the ground, to improve detection and account for potential camera-trap failure. Camera stations operated for 1–3 months to ensure sufficient data were collected, and to minimize violation of the assumption of population closure for occupancy modelling (MacKenzie, 2006).

Analysis

We used occupancy modelling to investigate the effects of camera-station level, landscape-level and species-level (i.e. species presence) variables on the probability of fosa presence (MacKenzie & Nichols, 2004). Photographic data were converted into detection histories (1, detection; 0, non-detection) for the fosa, and for key exotic species (Table 1)

TABLE 1 Forest area and summary statistics of the camera-trap surveys conducted during 2014–2015 in Ankarafantsika National Park and Andranomena Special Reserve, Madagascar (Fig. 1), with the camera-trap station, landscape-level and species-level covariates (i.e. trap success) at each site.

	Ankarafantsika National Park	Andranomena Special Reserve
Study site and survey summary		
Forest area (km ²)	1,350	64
Survey date	12 Apr. 2014–12 July 2014	20 May 2015–28 June 2015
Camera-trap grid area (km ²)	37.73	35.45
Mean no. of days camera traps deployed ± SD	79.14 ± 9.24	35.91 ± 6.18
Total no. of camera-trap stations	79	69
Mean station spacing (m)	579.4	464.9
Total camera-trap effort (nights)	6,252	2,478
Camera-trap level covariates¹		
Mean trail width (m) ^{2,3,4}	3.2	3.1
Forest type ³	Various	Various
Trail type	Various	Various
Landscape-level covariates¹		
Mean distance to village (m) ²	1,616.9	5,113.9
Mean distance to forest edge (m) ^{3,4}	357.5	2,489.8
Mean distance to road (m) ^{2,4}	1,471.9	1,604.9
GFC20 ^{2,3,4}	75.3	97.2
VCF ^{1,2}	49.5	48.1
Mean total edge (m) ²	2,921.9	1,023.3
Mean total core area (m ²) ^{2,4}	30.3	42.6
Mean no. of patches ³	7.7	3.0
Mean landscape patch index ³	1.9	95.4
Mean distance to water (m) ^{2,4}	2,127.1	958.8
Drainage (m) ⁴	3,348.8	1,088.5
Mean elevation (m)	146.3	26.4
Trap success (number of species detections/total sampling days × 100)		
Fosa <i>Cryptoprocta ferox</i>	3.6	3.6
Dog <i>Canis lupus familiaris</i> ¹	13.7	3.9
Cat <i>Felis</i> sp. ¹	3.4	11.2
Civet <i>Viverricula indica</i> ^{2,3}	1.2	0.0
Pig <i>Potamochoerus larvatus</i> ³	1.8	2.8
Zebu <i>Bos primigenius indicus</i> ^{2,3}	18.9	1.3
Lemur (multiple sp.) ^{1,2}	0.3	0.7
Bird (multiple sp.) ^{1,3}	3.2	6.6
Human	104.8	32.2

¹Forest type, forest classification (old-growth, degraded, savannah); Trail type, game trail, Madagascar National Park trail, disused logging trail, trail actively used by local people; GFC20, mean % global forest cover (forest cover at 20% threshold level at 30 m resolution); VCF, mean vegetation continuous field (% forest cover at 250 m resolution; Drainage, mean distance (m) to nearest drainage point (lowest point of elevation).

^{2,3,4}Indicates the best performing uncorrelated covariates included in the final fosa², dog³ and cat⁴ occupancy models.

used as covariates. All detections within a 30-minute period were considered a single detection (Linkie & Ridout, 2011). A complete camera-trap day involved at least one of two cameras operating during the 24 hours. Capture histories for each species were created through the collapsing of individual days into 5-day periods, improving temporal independence and model convergence (Otis et al., 1978). Species-level covariates were the encounter rates of exotic animals and humans at each camera-trap station and were calculated by evaluating trap success (number of detections/total days × 100) per species. Two survey covariates were included to account for detection probability: the site

surveyed (Site), and the number of days a station was active during each 5-day sampling period (Effort).

Camera station-level covariates were included to assess the impact of station geography. Trail width, trail type and forest type were included as they have been reported to be important metrics in fosa occupancy (Farris et al., 2015b). Trail width was estimated by averaging the width of the trail at the camera-trap station and at 10 m either side. Forest type was categorized subjectively and visually as either old-growth (intact forest with some disturbance), degraded (low forest cover, with few native plant species) or savannah (anthropogenic grassland). Trail type was

confirmed by a local guide and categorized as Madagascar National Park trail, local (actively used by local people), disused-local (formerly used by local people), game (animal trail), logging (actively used by loggers), or disused-logging (formerly used by loggers).

We used QGIS v. 2.12.1 (QGIS Development Team, 2015) and FRAGSTATS v. 4.2 (McGarigal et al., 2002) to create 12 landscape-level covariates, to examine the effects of human settlement, landscape degradation, and ecological variables on fosa occupancy (Table 1). A 500-m buffer was created around each camera-trap station and the mean value of the raster cells was calculated for each covariate.

Two metrics were used to measure forest cover: global forest cover (GFC; Hansen et al., 2013) and mean vegetation continuous field (VCF; DiMiceli et al., 2011). The per cent of GFC (which is at 30 m resolution) that can be classified as forest may be specified. We chose 10, 20, 30 and 50% and compared these within univariate models to find the best predictor of fosa occupancy. VCF provides a forest cover per cent at 250 m map resolution. Maps of GFC for Andranomena Special Reserve were unavailable for the survey year, and therefore the most recently available (2014) maps were used. Four measures of fragmentation (Table 1; Gerber et al., 2012a; Farris et al., 2015b) were calculated with FRAGSTATS.

Two measures of water proximity were calculated using a waterway raster containing Madagascar's major water sources (Mapcruzin, 2016) and a digital elevation model (Jarvis et al., 2008), facilitating the mapping of low-elevation areas that may represent drainage points and potential seasonal streams. The covariate mean elevation was created from the Shuttle Radar Topography Mission's 90 m raster (Carroll et al., 2009).

We used the R v. 3.3.3 (R Core Team, 2017) package *unmarked* v. 0.11-0 (Fiske & Chandler, 2011) to run single-species, single-season occupancy modelling of the fosa, cat, and dog. Prior to modelling, a Pearson's correlation test was used to eliminate multicollinearity. We removed correlated continuous predictors ($r > 0.6$; i.e. the predictor that performed worst in the univariate model) and normalized the remaining covariates. A stepwise approach was taken to reduce the total number of competing covariates to be included in each final occupancy model for fosa, cat and dog. Firstly, the detection probability was modelled, with the most significant combination of detection covariates (Site and Effort) selected. Secondly, potential occupancy covariates were modelled independently with selected detection covariates, with the best-performing uncorrelated covariates retained (Table 1). We used the Akaike information criterion (AIC) and model selection to rank competing models, and reported those with $AIC < 2.0$. Covariates that attained a summed model weight > 0.50 were considered to be important predictors of occupancy (Barbieri & Berger, 2004).

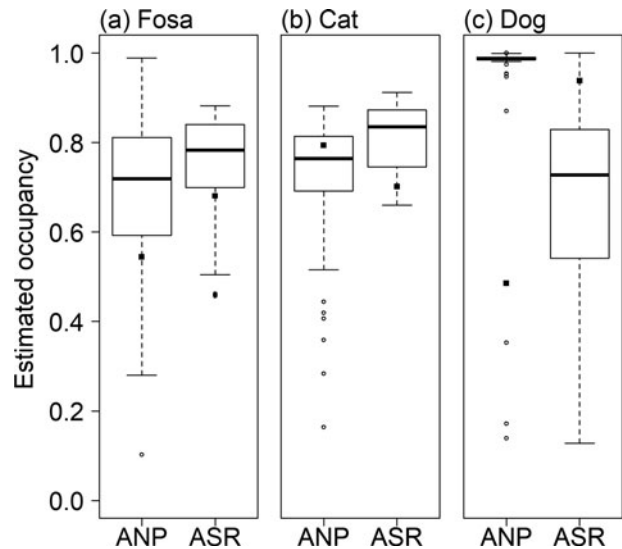


FIG. 2 Estimated site occupancy for the fosa *Cryptoprocta ferox*, cat *Felis* sp. and dog *Canis lupus familiaris* in Ankarafantsika National Park (ANP) and Andranomena Special Reserve (ASR) in Madagascar (Fig. 1). The boxes represent median site occupancy with upper and lower quartiles (25% greater and 25% lesser than the median); whiskers represent maximum/minimum values, black dots naïve occupancy, and white dots outliers.

We ran a goodness-of-fit test to examine the model's likelihood of being correct ($P > 0.05$) and determine how well it fitted the data (measuring overdispersion as \hat{c}). Species occupancy was predicted across both sites, accounting for the important covariate predictors.

Results

Landscape features and site detections

With a sampling effort of 8,730 nights across both sites, we recorded the presence of three native and three exotic carnivores (Table 1). The survey in Andranomena Special Reserve was shortened as a result of camera-trap theft (35 days vs 80 days in Ankarafantsika National Park). Overall, the landscape of the Park was more degraded (GFC 75.32%) than that of the Reserve (GFC 97.16%). The mean distance from camera stations to the nearest village and to the forest edge was considerably less in the Park than in the Reserve (Table 1).

In total, 311 independent detections of fosas were recorded (226 in the Park, 85 in the Reserve). In the Park, *E. major* was detected once, and in the Reserve *M. decemlineata* was detected twice. Small Indian civets were absent from the Reserve; in the Park they were detected almost exclusively in savannah and degraded land. These low detection rates prohibited occupancy modelling for these three species. Trap success was higher for dogs, zebu and humans in the Park, and for cats and birds in the Reserve (Table 1).

TABLE 2 Species covariate occupancy models for fosa, cat and dog, with Akaike information criterion corrected for a small sample size (AICc), relative change in Akaike information criterion from top model (Δ AICc), Akaike weight (AICc weight), number of parameters (K), and -2 log likelihood.

Species	Occupancy model ¹	AICc	Δ AICc	AICc weight	K	-2 log likelihood
Fosa	Cat + Dog + GFC20 + TCA	1,195.32	0.00	0.08	8	-589.11
	Cat + Dog + GFC20	1,195.54	0.22	0.07	7	-590.34
	Cat + GFC20	1,195.81	0.49	0.06	6	-591.59
	Cat + Dog + TCA	1,195.85	0.53	0.06	7	-590.50
	Cat + Dog + GFC20 + TCA + TW	1,196.20	0.89	0.05	9	-588.41
	Cat + Dog + Road + TCA	1,196.30	0.99	0.05	8	-589.60
	Cat + Dog + GFC20 + TW	1,196.41	1.09	0.04	8	-589.65
	Cat + Dog + GFC20 + Lemur	1,196.44	1.12	0.04	8	-589.67
	Cat + Dog + GFC20 + Lemur + TCA	1,196.49	1.17	0.04	9	-588.55
Cat	Bird + TW + VCF	1,558.00	0.00	0.23	7	-771.59
	Bird + TW	1,558.33	0.33	0.20	6	-772.86
Dog	Civet + Forest + NP + TW	1,288.57	0.00	0.10	9	-634.55
	Forest + Lemur + NP + TW	1,288.68	0.11	0.09	9	-634.61
	Civet + TW + VCF	1,289.17	0.60	0.07	7	-637.14
	FD + Forest + Lemur + NP + TW	1,289.46	0.89	0.06	10	-633.83
	Civet + FD + Forest + NP + TW	1,289.51	0.94	0.06	10	-633.85
	Forest + NP + TW + Zebu	1,289.56	0.99	0.06	9	-635.05

¹Cat, Dog, Lemur, Bird, Civet and Zebu, species encounter rates (total detections/total sampling days \times 100); GFC20, % global forest cover at 20% threshold level (30 m resolution); TCA, total core area in each patch (m²); TW, trail width (m); VCF, vegetation continuous field (% forest cover at 250 m resolution); Forest, forest classification (old-growth, degraded, savannah); NP, total patches of a class type; FD, distance to forest edge (m).

Covariate and model validation

Our two survey covariates (Site and Effort) were contained in the best performing detection model (Supplementary Table 1). Consequently, they were included in all subsequent modelling of occupancy with occupancy covariates. Our correlation matrix revealed significant correlations between competing covariates (Supplementary Table 2). Six covariates (Number of patches, Landscape patch index, VCF, Elevation, Mean distances to village and forest) were discarded prior to constructing the multivariate fosa occupancy model. The goodness-of-fit test indicated significant overdispersion, and consequently five sites were removed (42 detections in total).

Occupancy

There were no statistically significant differences in occupancy between the two study sites ($P < 0.05$). The mean fosa occupancy across both regions was 0.724, being marginally higher in the Reserve (0.757) than in the Park (0.692; $\chi^2 = 0.003$, $df = 1$, $P = 0.959$; Fig. 2). Mean cat occupancy was 0.736, and was marginally higher in the Reserve ($\chi^2 = 2.844$, $df = 1$, $P = 0.092$). Mean dog occupancy was 0.999, and was considerably higher in the Park ($\chi^2 = 2.306$, $df = 1$, $P = 0.129$).

Cat and dog trap success, GFC20 and total core area were the most important covariates (summed model weight > 0.5 ; Supplementary Table 3) in explaining fosa occupancy across the landscape (Table 2). Dog trap success had a weak positive relationship with fosa occupancy, whereas cat trap

success, GFC20 and total core area had a negative relationship with fosa occupancy (Table 3).

Cat occupancy was best explained by bird trap success, trail width and VCF (Table 2). Bird trap success and trail width were negatively correlated with cat occupancy, whereas there was a positive association between occupancy and VCF (Table 3).

Dog occupancy was best explained by civet trap success, forest type, number of patches and trail width (Table 2). Civet trap success and trail width were positively correlated with dog occupancy, whereas old-growth, savannah and total patches negatively affected occupancy (Table 3).

Discussion

Overall our results were unclear regarding the relationship between the fosa, landscape degradation and exotic species, with no clear relationship evident between fosas and degradation, but a clear negative relationship between fosas and cats. Our findings regarding dog and cat occupancy concur with previous studies documenting the negative effect of exotic species on Madagascar's endemic carnivores (Gerber et al., 2012a; Farris et al., 2015b, 2016; Murphy et al., 2017). The fosa appears to be more resilient to habitat disturbance within contiguous forests than other euplerids but the loss of Madagascar's forest is likely to inhibit their long-term persistence. The high occupancy of free-ranging cats and dogs in the landscape indicates considerable competition with fosas through the consumption of shared prey (Brockman et al., 2008) and exclusion from habitat. The

TABLE 3 Landscape single-season occupancy models for fosa, cat and dog, including all best performing, uncorrelated covariates. Model data were from camera-trap surveys conducted in Ankarafantsika National Park and Andranomena Special Reserve, Madagascar (Fig. 1) during 2014–2015.

Model	Covariate ¹	Estimate	SE	z	P (> z)
Fosa	(Intercept)	1.023	0.414	2.471	0.014
	Trail width	−0.331	0.281	−1.177	0.239
	Cat trap success	−0.915	0.429	−2.134	0.033
	GFC20	−0.986	0.895	−1.102	0.271
	Total edge	−0.542	0.505	−1.074	0.283
	Total core area	−0.658	0.383	−1.719	0.086
	Village distance	0.252	0.406	0.621	0.534
	Dog trap success	0.891	0.585	1.524	0.127
	Lemur trap success	−0.352	0.303	−1.160	0.246
	Water distance	0.138	0.302	0.456	0.648
	Road distance	−0.071	0.496	−0.143	0.887
	Bird trap success	−0.262	0.353	−0.741	0.459
	Cat	(Intercept)	1.080	0.593	1.823
Trail width		0.012	0.228	0.050	0.960
Bird trap success		−0.615	−0.325	1.892	0.059
Civet trap success		−0.664	−0.374	0.483	0.629
VCF		0.434	0.273	1.588	0.112
Forest distance		0.082	0.482	0.171	0.865
Drainage		0.111	0.355	0.314	0.754
Zebu trap success		0.030	0.340	0.088	0.930
Water distance		0.336	0.274	1.227	0.220
Pig trap success		0.654	0.536	1.219	0.223
Road distance		0.048	0.263	0.181	0.857
Total core area		−0.092	−0.257	0.359	0.720
Dog		(Intercept)	17.252	18.983	0.909
	Trail width	0.459	0.575	0.798	0.425
	Civet trap success	2.682	5.059	0.530	0.596
	Lemur trap success	2.578	6.223	0.414	0.679
	Zebu trap success	1.336	2.638	0.506	0.613
	Forest distance	−0.472	1.152	−0.410	0.682
	Landscape patch index	−0.973	0.875	−1.111	0.266
	Forest: old-growth	−8.321	12.923	−0.644	0.520
	Forest: savannah	−6.867	13.027	−0.527	0.598
	VCF	1.588	1.232	1.289	0.197
	Number of patches	−1.498	1.102	−1.359	0.174
	Trail: game	7.043	152.808	0.046	0.963
	Trail: MNP	−4.115	13.577	−0.303	0.762
Trail: disused logging	3.699	65.202	0.057	0.955	
Trail: local	−4.241	13.580	−0.312	0.755	

¹Trail width, mean trail width (m); Trap success (cat, dog, lemur, bird, civet, zebu, pig), species encounter rates (total detections/total sampling days × 100); GFC20, % global forest cover at 20% threshold level (30 m resolution); Total edge, sum of all edge segments in camera-trap buffer; Total core area, in each patch (m²); Village/Water/Road/Forest distance, mean distance (m) to nearest village/water source/road/forest edge; VCF, vegetation continuous field (% forest cover at 250 m resolution); Drainage, mean distance (m) to nearest drainage point (lowest point of elevation); Landscape patch index (% of landscape in the largest patch); Forest, forest classification (old-growth, degraded, savannah); Number of patches, number of patches of a class type; Trail: game, game trail; Trail: MNP, Madagascar National Park trail; Trail: disused logging, disused logging trail; Trail: local, trail actively used by local people.

spread of disease, such as toxoplasmosis (Pomerantz et al., 2016; Rasambainarivo et al., 2017), between exotic species, fosas and their prey is of concern, potentially imperilling the health of the fosa population in the long term.

Effect of exotic species on fosa occupancy

Cats had the strongest negative association with fosa occupancy. It is widely acknowledged that cats have a negative

impact on native wildlife through predation, competition, hybridization and disease (Medina et al., 2011). In Madagascar predation on endemic species by cats has been reported (Sauther, 1989; Goodman et al., 1993; Brockman et al., 2008), and in Andranomena Special Reserve cats were photographed with a red-fronted brown lemur *Eulemur rufus* and speckled hognose snake *Leioheterodon geayi* (Plate 1). In our study the number of cats recorded was negatively associated with bird presence, a relationship reported previously in

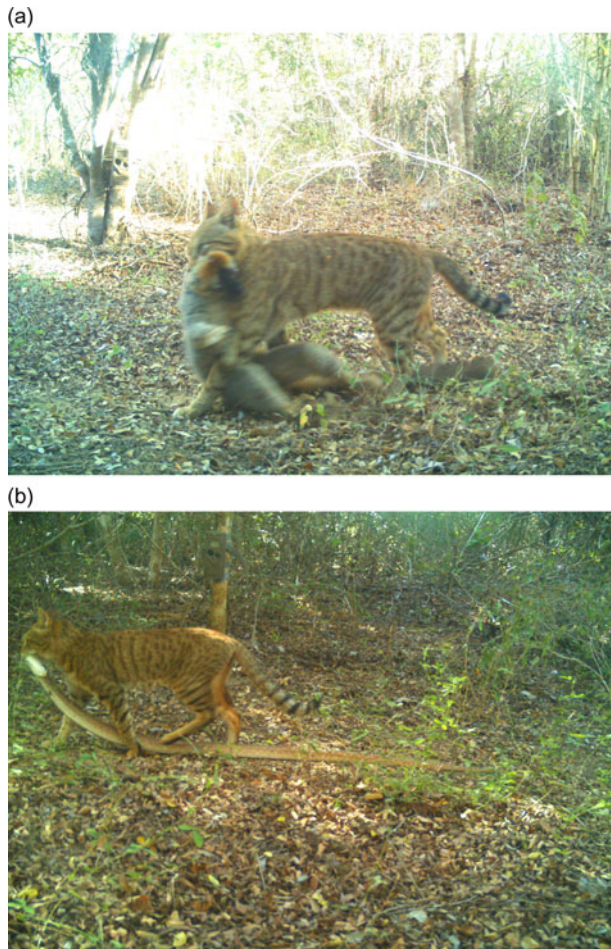


PLATE 1 Wild cats *Felis* sp. preying on (a) a red-fronted brown lemur *Eulemur rufus* and (b) a speckled hognose snake *Leioheterodon geayi* in Andranomena Special Reserve, Madagascar (Fig. 1).

Masoala–Makira (Murphy et al., 2018a); negative associations have also been recorded between cats and the rainforest-dwelling euplerids *Galidia elegans* and *Fossa fossana* (Gerber et al., 2012a; Farris et al., 2015b). Collectively these results suggest that cats are probably having a negative impact on the fosa and other endemic species, at the very least through direct predation and competition for prey.

In concordance with previous studies in rainforest, dogs did not have a negative association with fosa occupancy (Gerber et al., 2012a; Farris et al., 2015b). This is in contrast with the reported impact of dogs on the euplerid *Galidictis fasciata* (Gerber et al., 2012a) and incongruous with the damaging effects of dogs globally (Hughes & Macdonald, 2013). However, activity pattern analyses have indicated fosas display temporal activity shifts towards greater nocturnality (Farris et al., 2015a; Merson, 2018), and/or absence from sites with higher frequency of dog detections (Gerber et al., 2012a; Farris et al., 2015b). The sociality and size of dog packs (L.J. Dollar, unpubl. data) may be a source of interference competition for fosas, but the predatory

impact of dogs on Madagascar's ecosystem is still being investigated.

Disease transmission from cats and dogs is a significant threat to the long-term health of endemic species. Fatal cases of *Toxoplasma gondii* infection have been recorded in captive fosas (Corpa et al., 2013) and lemurs (Juan-Sallés et al., 2011; Siskos et al., 2015), highlighting their vulnerability to lethal infections. Field studies of exotic carnivores in Ankarafantsika National Park have identified the occurrence of multiple viruses and parasites, including canine parovirus, feline calicivirus and *T. gondii* (Pomerantz et al., 2016), the latter prevalent in > 93% of captured wild fosas. The detrimental impact of disease on Madagascar's wild fosa populations could be significant, reflecting disease-related species population declines elsewhere (Pedersen et al., 2007).

Habitat degradation impact on fosa occupancy

Fosa occupancy was higher in Andranomena Special Reserve, possibly because of greater forest cover, and lower dog and human presence. However, within our models fosa occupancy was not influenced by any habitat degradation parameters, with results similar to those reported for Madagascar's rainforests (Gerber et al., 2012a; Farris et al., 2015b). Despite this, surveys have not recorded fosas in areas > 5 km from the nearest contiguous forest (Kotschwar Logan et al., 2015) or in forest fragments > 2.5 km from the nearest contiguous forest (Gerber et al., 2012a). This suggests that despite their resilience to habitat degradation within contiguous forest, fosas are unable to persist far from intact forest. Considering Madagascar's highly fragmented forests (Vieilledent et al., 2018), it is likely that most forest areas are of insufficient size to support fosa populations in the long term (Hawkins & Racey, 2005).

Cat occupancy was higher in the Reserve, positively associated with higher vegetation cover and weakly associated with narrow trails. This could be attributed to their avoidance of larger carnivores (dogs, fosas) and people. Farris et al. (2015b) found similar positive associations with forest cover, possibly confirming their preference for areas of greater prey abundance.

Dogs had the highest occupancy in the Park. They had a positive association with large trails, and civets, and a negative association with old-growth forest, and savannah, possibly explained by dogs accompanying people during forest-related activities. This was apparent in the Park, where the forest surrounding rural villages encompassed a mixture of savannah and degraded forest, with high presence of people and exotic species (e.g. zebu, civet).

Long-term implications

Looking beyond the snapshot view of single-season occupancy models, recent multi-year studies in north-eastern Madagascar recorded occupancy of endemic and exotic

carnivores, indicating long-term decline and replacement of endemic species by exotic species (Farris et al., 2016). In Ranomafana National Park a multi-year occupancy study reported the long-term decline of fosas, their strong co-occurrence with dogs being a likely source of competition or disease (Farris et al., 2017). This supports our speculation that fosa resilience to habitat degradation inside contiguous forests is probably short-term, with a long-term population decline evident (Hawkins, 2016). This is largely the result of the severe reduction of Madagascar's forests, the killing of fosas for bushmeat and in retaliation for poultry depredation, and the increase in abundance of dogs and cats, increasing competition and disease transmission. Steps to mitigate the impact of exotic species on fosas and the ecosystem as a whole need to be explored. Sterilization programmes for domestic cats and dogs, along with culling of free-ranging cats and dogs should be trialled to evaluate their effectiveness in improving the abundance of native species. If they prove to be both cost-effective and beneficial to the ecosystem, we propose the incorporation of these programmes into an island-wide forest management strategy.

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Ethical standards This research complies with *Oryx's* Code of Conduct for authors.

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