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RESEARCH ARTICLE

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Abstract

Invasive feral cats threaten biodiversity at a global scale. Mitigating feral cat impacts and reducing their populations has therefore become a global conservation priority, especially on islands housing high endemic biodiversity. The New Caledonian archipelago is a biodiversity hotspot showing outstanding terrestrial species richness and endemism. Feral cats prey upon at least 44 of its native vertebrate species, 20 of which are IUCN Red-listed threatened species. To test the feasibility and efficiency of culling, intensive culling was conducted in a peninsula of New Caledonia (25.6 km²) identified as a priority site for feral cat management. Live-trapping over 38 days on a 10.6 km² area extirpated 36 adult cats, an estimated 44% of the population. However, three months after culling, all indicators derived from camera-trapping (e.g.,

abundance, minimum number of individuals and densities) suggest a return to pre-culling levels. Compensatory immigration appears to explain this unexpectedly rapid population recovery in a semi-isolated context. Since culling success does not guarantee a long-term effect, complementary methods like fencing and innovative automated traps need to be used, in accordance with predation thresholds identified through modelling, to preserve island biodiversity. Testing general assumptions on cat management, this article contributes important insights into a challenging conservation issue for islands and biodiversity hotspots worldwide.

Keywords
Camera trap monitoring, invasive predator, invasive species control, live-trapping, SECR analysis

Introduction

Feral cats are among the most harmful invasive predators for insular native fauna (Bonnaud et al. 2011; Medina et al. 2011; Bellard et al. 2016; Doherty et al. 2016). They threaten more than 430 vertebrate species, including mammals, birds and reptiles, and are implicated in the recent extinction of 63 species (40 bird, 21 mammal and 2 reptile species), i.e. 26% of recent terrestrial vertebrate extinctions since AD 1500 (Doherty et al. 2016; Palmas et al. 2017). Mitigating feral cat impacts and reducing their populations has therefore become a global conservation priority (Doherty et al. 2017), especially on islands housing high endemic biodiversity (Nogales et al. 2013). Feral cat eradications have been successfully conducted on islands worldwide, generally resulting in clear conservation benefits for many island mammals, birds and reptiles (e.g. Campbell et al. 2011; Jones et al. 2016). However, although recent management actions succeeded in eradicating cats from small and medium-sized islands (up to 29,000 ha – Marion, Bester et al. 2002 and up to 63,000 ha – Dirk Hartog – Algar et al. 2020) including fenced enclosures, to date feral cat eradications remain largely unfeasible on the largest islands, particularly when inhabited (Nogales et al. 2004; Campbell et al. 2011; Oppel et al. 2011; DIISE 2020), and even harder to achieve in mainland areas.

If eradication is not feasible, population control – i.e. local limitation of predator abundance by culling or other measures – could constitute an alternative management strategy (Doherty et al. 2017). As for any "open" populations though, cats present a high risk of re-invasion since they can move rapidly and over long distances (Schmidt et al. 2007; Moseby and Hill 2011; Leo et al. 2016; McGregor et al. 2017): a typical response to spatially restricted culling is compensatory immigration from surrounding source populations (e.g. Lieury et al. 2015; Millon et al. 2019). Population control may thus entail a continuous removal of individuals (Lazenby et al. 2015). This is generally not a sustainable management strategy given the usually limited resources and time available for such conservation programmes (e.g. Doherty and Ritchie 2017; Venning et al. 2020). Most studies that found feral cat culling to be effective and with a lasting impact on the cat population were examining either intensive and sustained

management efforts (Algar and Burrows 2004) or situations where populations are relatively closed (e.g. peninsulas and fenced areas, Short et al. 1997; Moseby and Read 2006). Our study area, a peninsula, was chosen for its potential to act as a population filter and limit immigration from surrounding populations (like Heirisson Prong in Short et al. 2002, and the Tasman Peninsula in Lazenby et al. 2015).

Camera trapping and a spatially explicit capture-recapture approach (hereafter, SECR) are novel and effective tools that are increasingly used to estimate occupancy rates, abundances and densities for feral cats in natural areas. They provide relevant information for conservation practitioners (such as recolonisation rate, spatial distribution of cats) and allow for testing the efficiency of culling as a management technique (Robley et al. 2010; Bengsen et al. 2012; Lazenby et al. 2015; McGregor et al. 2015). Surprisingly little is known about the speed with which a treated area is recolonised by cats. This is a crucial parameter for managers to estimate how long the positive effect of their control operations is lasting, so as to determine how frequently these have to be repeated in order to maintain invasive predators at a low density (Denny and Dickman 2010; Leo et al. 2018). The rate of re-invasion probably depends on the abundance of cats outside the treated area, the degree of connectivity of the treated area with the untreated peripheral areas and the intensity of removal of individuals during culling. Nor is there adequate data on the magnitude of control (i.e. the number of individuals or percentage of a population to remove) required to successfully reduce the invasive predators' population and impacts (e.g. Reddiex et al. 2006; Kapos et al. 2009; Denny and Dickman 2010; Walsh et al. 2012). Modelling studies can estimate optimal removal rates (e.g. Lohr et al. 2013), but proper modelling requires information on numerous parameters like the biology and distribution of both managed and sympatric species, or population sizes (Leo et al. 2018). This would enable to determine the viability of prey populations in the face of predation under different conditions and management programmes (e.g. King and Powell 2011).

We report herein a short but intensive feral cat culling operation conducted at Pindaï peninsula (New Caledonia), which is a priority conservation area for seabirds (it hosts a large colony of Wedge-tailed shearwaters, *Ardenna pacifica*) (Spaggiari et al. 2007). It is a case study of how efficient and durable the effects of such short intensive operations are, taking advantage of the peninsula's setting and simulating the typical resources currently available to local managers of natural areas (DDEE – Province Nord, New Caledonia).

Our specific aims were to (i) assess feral cat abundance and density, (ii) test a live-trapping protocol and its success in controlling feral cats, (iii) test the durability of the culling effect on feral cat abundance and densities, and (iv) derive guidance for adaptive and effective management.

While a compensatory effect from immigration was expected, we hypothesised that the lower connectivity between treated and untreated areas at this peninsular tip would limit cat re-colonisation as observed in different studies conducted in peninsulas or fenced areas (Short et al. 1997; Read and Bowen 2001).
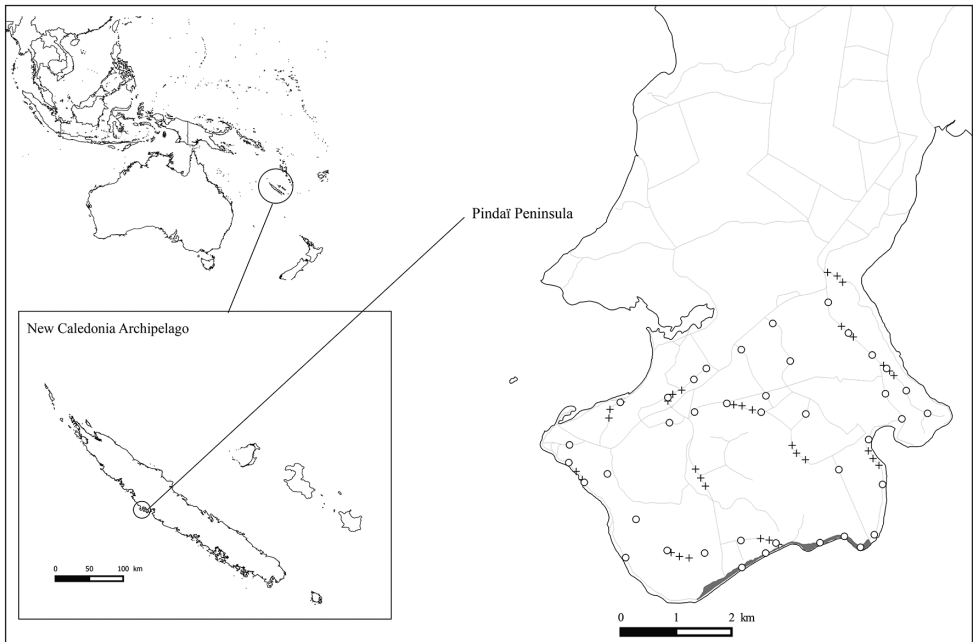
Figure 1. Location of the Pindaï Peninsula and sampling design; camera trap stations (cross, n = 77), live-trap positions (circle, n = 32), seabird colony (grey area), roads and trails (grey lines).

Materials and methods

Study site

The New Caledonia main island ("Grande Terre") is an old continental island located in the Pacific Ocean (Grandcolas et al. 2008). With an area of 16,372 km², it houses three main natural habitats: Dry forest, Humid forest and Maquis mosaic. The New Caledonian biodiversity hotspot shows outstanding terrestrial species richness and endemism rates (Myers et al. 2000; Mittermeier et al. 2011).

Since their introduction around 1860 (Beauvais et al. 2006), cats have invaded the New Caledonian archipelago, from seashore habitats to the highest altitude forest (1,628 m). A recent study showed that feral cats preyed upon at least 44 native vertebrate species, 20 of which are IUCN Red-listed threatened species (Palmas et al. 2017). As a result, the feral cat has been listed among the five priority invasive species for future management in New Caledonia. The Pindaï peninsula (Northern Province) has been identified as a priority site for feral cat management, part of a move to address conservation issues in natural areas through expert management.

The Pindaï Peninsula (21°19.40'S, 164°57.50'E; Fig. 1), with an area of 25.6 km², is between 2.45 km and 3.24 km wide and a maximum 7 km long. It has a low (<15 m) canopy and mean annual rainfall of less than 1,100 mm (Jaffré et al. 1993). It is covered in dry forest composed of a mosaic of sclerophyllous and mesic forests on

Table 1. Control schedule using live-traps and camera trapping according to Wedge-tailed shearwater breeding periods. Dash indicate inter-periods.

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Wedge-tailed shearwater presence (P.) and breeding periods	P.	P. Hatching		P.		P. Juv. Fledging		–			P. Adult arrival	P.	P. Laying
Camera trapping		–		908 trap-days			–				1181 trap-days		–
Feral cat control by live-traps			–				1200 trap-days				–		

sedimentary and metamorphic rocks (Gillespie and Jaffre 2003; Isnard et al. 2016). Secondary successional sclerophyllous forests dominate this peninsula with *Acacia spirorbis* and *Leucana leucocephala* formations, and there is a large remnant of closed sclerophyllous forest to the East and South. To implement our culling campaign, we specifically chose the southern part of the peninsula because (i) it houses the largest Wedge-tailed shearwater colony of Grande Terre, the mainland of New Caledonia, with about 10,000–15,000 breeding pairs present from mid-October (adult arrival) to the end of May (juvenile fledging) (Table 1; Fig. 1) (Spaggiari and Barre 2003; BirdLife International 2016); (ii) the peninsula narrows (2.45 km) in the middle, providing lower connectivity between treated and untreated areas ; and (iii) it affords an area of 10.6 km^2 for intensive treatment, using the available human and material resources (i.e. local managers).

Camera trapping design

40 camera traps (three were stolen during the study period) were deployed along paths and unsealed roads according to a systematic grid covering the study area (10.6 km^2). This grid was constructed on GIS (QGis 2.2.0), and was overlaid on an aerial photograph of the Peninsula to maximise homogeneity of camera trap distribution. Automated digital cameras with flash (7), infrared flash (2), black light (31) (CuddebackAmbush 1170, Cuddeback Attack IR 1156, Moultrie M1100i, respectively) were used. To ensure homogeneous detection probabilities throughout a camera trapping session, no baits or lures were used. Cameras were set up at a height of between 30 and 100 cm (to cover cat body height), directed towards the track preferentially used by cats (Turner and Bateson 2014; Recio et al. 2015), and were checked to confirm that the camera's shutter was triggered (Wang and Macdonald 2009; Nichols et al. 2017). There was an interval of ten seconds between trigger events, with three images captured in each of them, to maximise cat identification and to reduce the risk of fuzzy pictures.

Camera trapping was conducted for 30 successive days in both sessions (Table 2). A capture event was defined as all photographs of unique individuals within a 30-min time period (Di Bitetti et al. 2006; Farris et al. 2015). A sampling occasion was considered as one day (24 h) (Otis et al. 1978; Wang and MacDonald 2009). Camera traps were inspected at least once every two weeks to check battery system charge and

Table 2. Model selection results for density estimation (SECR) using four habitat masks (ZE; study area, ZE_AV; using MDMM pre-culling, ZE_AP; using MDMM post-culling and ZE_moy; using mean MDMM pre- and post-culling). Models are based on Akaike's information criterion corrected for small sample sizes (AICc). Delta AICc is the difference in AIC values between each model and the model with the lowest AIC. AICcwt is the model weight.

Model N°	Model name	Model	Detection function	No. Par	LogLik	AICc	delta AICc	AICcwt
M1	#secr_dfn15_ZE_Buffer_AP	λ(0)~1 σ~1 z~1	hazard hazard rate	3	-1853.106	3712.798	0	0.5325
M2	#secr_dfn1_ZE_Buffer_AP	g0~1 σ ~1 z~1	hazard rate	3	-1853.236	3713.058	0.26	0.4675
M3	#secr_dfn15_ZE_Buffer_Moy	λ(0)~1 σ ~1 z~1	hazard hazard rate	3	-1864.527	3735.64	22.842	0
M4	#secr_dfn1_ZE_Buffer_Moy	g0~1 σ ~1 z~1	hazard rate	3	-1864.62	3735.826	23.028	0
M5	#secr_dfn15_ZE_Buffer_AV	λ(0)~1 σ ~1 z~1	hazard hazard rate	3	-1874.757	3756.1	43.302	0
M6	#secr_dfn1_ZE_Buffer_AV	g0~1 σ ~1 z~1	hazard rate	3	-1874.792	3756.169	43.371	0
M7	#secr_dfn1_ZE	g0~1 σ ~1 z~1	hazard rate	3	-1884.633	3775.851	63.053	0
M8	#secr_dfn15_ZE	λ(0)~1 σ ~1 z~1	hazard hazard rate	3	-1884.694	3775.973	63.175	0
M9	#secr_dfn2_ZE_Buffer_AP	g0~1 σ ~1	exponential	2	-1887.627	3779.54	66.742	0
M10	#secr_dfn16_ZE_Buffer_AP	λ(0)~1 σ ~1	hazard exponential	2	-1889.41	3783.105	70.307	0
M11	#secr_dfn2_ZE_Buffer_Moy	g0~1 σ ~1	exponential	2	-1897.213	3798.711	85.913	0
M12	#secr_dfn16_ZE_Buffer_Moy	λ(0)~1 σ ~1	hazard exponential	2	-1898.902	3802.091	89.293	0
M13	#secr_dfn2_ZE_Buffer_AV	g0~1 σ ~1	exponential	2	-1906.91	3818.106	105.308	0
M14	#secr_dfn16_ZE_Buffer_AV	λ(0)~1 σ ~1	hazard exponential	2	-1908.556	3821.397	108.599	0
M15	#secr_dfn2_ZE	g0~1 σ ~1	exponential	2	-1920.357	3844.999	132.201	0
M16	#secr_dfn16_ZE	λ(0)~1 σ ~1	hazard exponential	2	-1921.938	3848.162	135.364	0
M17	#secr_dfn0_ZE_Buffer_AP	g0~1 σ ~1	halfnormal	2	-1942.385	3889.055	176.257	0
M18	#secr_dfn14_ZE_Buffer_AP	λ(0)~1 σ ~1	hazard halfnormal	2	-1942.945	3890.175	177.377	0
M19	#secr_dfn0_ZE_Buffer_Moy	g0~1 σ ~1	halfnormal	2	-1946.147	3896.58	183.782	0
M20	#secr_dfn14_ZE_Buffer_Moy	λ(0)~1 σ ~1	hazard halfnormal	2	-1946.684	3897.653	184.855	0
M21	#secr_dfn0_ZE_Buffer_AV	g0~1 σ ~1	halfnormal	2	-1952.44	3909.165	196.367	0
M22	#secr_dfn14_ZE_Buffer_AV	λ(0)~1 σ ~1	hazard halfnormal	2	-1952.966	3910.217	197.419	0
M23	#secr_dfn0_ZE	g0~1 σ ~1	halfnormal	2	-1963.612	3931.509	218.711	0
M24	#secr_dfn14_ZE	λ(0)~1 σ ~1	hazard halfnormal	2	-1964.072	3932.429	219.631	0

to download data from memory cards. At the end of each trapping period, the cameras were retrieved and the images downloaded. The trapping effort was obtained by multiplying the number of traps by the number of active capture days over the considered periods (Table 1). Capture per unit effort (camera trapping sampling occasion) was calculated by dividing the numbers of trapped cats per 100 trap-days.

Feral cat trapping and culling

Cat trapping and culling were carried out for 38 days over 3.5 months (2–3 working days per week) during the dry cold season (between mid-May and July 2015, austral winter) in collaboration with wildlife rangers. In predator trapping, food availability in the targeted site may be decisive for control efficiency (i.e., baited traps may be more attractive when few alternative food resources are available) (Algar et al. 2013; Rocamora and Henriette 2015). Therefore, feral cat trapping and culling were carried out during the dry cold season, when resources are scarcer (i.e., before seabird arrival, a low activity period for squamates and invertebrates and probably the lowest rodent abundance).

Live traps (2 WIRETAINERS models, CatTrap and PossumTrap; 32 traps in total, 17 and 15 respectively of each model) were deployed across the 10.6 km² covered (Fig. 1). The trapping density rate (3 traps per km²) was comparable to that of similar studies (e.g. Algar et al. 2010; Lazenby et al. 2015). Traps were deployed near paths and unsealed roads used by cats (Turner and Bateson 2014; Recio et al. 2015; Palmas et al. 2017). They were hidden in vegetation and out of direct public sight. Feral cats were live-trapped during both day and night, since our study site does not house non-target native species liable to be caught by this type of trap (Desmoulins and Barré 2005). Traps were checked and baited with oiled fish (tinned sardines) twice a day (Peters et al. 2011).

Trapped cats were euthanised by an accredited veterinarian using first a light anaesthetic via intramuscular injection of Tiletamine/Zolazepam (10 mg kg⁻¹ body-weight), followed by an intracardiac injection of Pentobarbital 500 mg/cat. The cats were handled in compliance with the directives of the Department of Conservation's Animal Ethics Committee, and the traps were used in accordance with New Caledonian regulations (Northern Province Environmental Code, New Caledonia).

Data analyses

Camera trapping was used to calculate three complementary indicators of population abundance and density pre- and post-culling: (i) a general index of feral cat activity (GI), (ii) the minimum number of feral cats present in the study area (MKTBA), and (iii) feral cat absolute density (SECR).

The general index (GI) allowed us to estimate feral cat activity over the study area by measuring the mean of virtual camera capture events per station and per sampling occasion. This index follows the equation of Engeman (2005):

$$GI = \frac{1}{d} \sum_{j=1}^{d} \frac{1}{sj} \sum_{i=1}^{sj} x_{ij} \, ,$$

with d = the day, s = the station, and x_{ij} the number of captures at the ith station on occasion jth.

To compare the GI calculated before and after culling, we used bilateral mean comparison: t-test with Welch approximation for unequal variance.

Camera-trapped cats were identified based on distinct natural markings (Karanth and Nichols 1998; Bengsen et al. 2012). First, adult cats were classified by coat colour and patterns on left or right flanks. Then morphological criteria were used: number, shape, dimension and position of stripes, bands and spots on the trunk and limbs; number and shape of rings on the tail; body signs such as scars or other distinctive traits; and sex (observation of the genital area or female with cubs). Pictures from each session were sorted into folders, one for each potential individual (McGregor et al.

2015). All identification folders were checked twice, by two different operators, for any inconsistencies requiring the pictures to be reassigned. The folders were then reviewed by another operator for validation.

Culled cats were identified using the same morphological criteria from the pictures of both flanks to (i) identify cats camera trapped during the pre-culling session and (ii) match right- and left-flank pictures of the same individual from the pre-culling pictures.

The minimum number of feral cats known to be alive (MKTBA, Lazenby et al. 2015) was calculated as the total number of individuals identified from one side (left or right side of all cat pictures). This ensured the identification of a maximum of individual cats. Since uniformly black cats are very difficult to identify individually, we assumed that our number of different black individuals was an underestimation.

Spatially explicit capture-recapture models were applied to capture-mark-recapture data to provide population density estimations (Efford et al. 2015). This allows not to use the study area calculation as a density reference (a major bias) and gives greater flexibility in study design (Efford et al. 2009). SECR models require that: (i) every animal has a non-zero probability of encountering a camera trap station during the sampling period (Karanth and Nichols 1998), (ii) the location and density of stations ensure that any feral cats (adult) can be photographed from at least two camera trap stations (Foster and Harmsen 2012; McGregor et al. 2015), and (iii) sampling design maximises capture probabilities (Burnham et al 1987). SECR estimations also require encounter histories for density calculations (Efford et al. 2015; McGregor et al. 2015). Here, such histories were built separately for pre- and post-culling sessions by dividing each of them into a series of 25 and 35 days, respectively (one sampling occasion corresponding to 24 h). This involved identifying each cat as observed or not, with the location of the camera trap. Cat density was estimated using the 'secr' library in R (Efford 2020). To avoid bias linked to low confidence in identification of black cats, the latter were excluded from the analyses (McGregor et al. 2015). Excluding black cats from SECR analyses reduced photo capture events by 13.05%, while black cats accounted for 11.1% of total culled cats.

The sampled population was assumed to be demographically closed during each camera trap session, based on the fact that (i) kittens were not considered in the analyses (Otis et al. 1978; McGregor et al. 2015 who used a 3–6 week survey period and SECR analysis for closed populations), (ii) there was a very low probability of mortality over the period considered, as this site houses no cat predators and is infrequently used by humans. The spatial-history capture matrix for camera trapping data was then constructed by linking each capture of each individual with the respective coordinates of the camera station and j-occasion, which covered 24 h. Trap detector type 'count' was chosen for the SECR analysis (allowing for multiple detections of the same individual within the same occasion, and including the two camera trapping sessions within the same analysis).

We evaluated six different spatial detection functions (half-normal, hazard half-normal, hazard rate, hazard hazardrate, hazard exponential, exponential), using two different functions for the distribution of home range centres: (i) a Poisson point

process (Borchers and Efford 2008) and (ii) a binomial point process (Royle et al. 2009). We created four habitat masks using (i) the Mean Maximum Distance Moved (MDMM), the average maximum distance between detections of each individual (Otis et al. 1978), and (ii) the function *SECR* which excludes areas inaccessible to cats (open water) (Oppel et al. 2012). This yielded twenty-four different candidate models using all combinations of detection functions and masks. Root Pooled Spatial Variance (RPSV) was used to measure the dispersion of the sites where individual animals were detected, pooled over individuals (Calhoun and Casby 1958; Slade and Swihart 1983; Efford 2011). Mean home ranges pre- and post-culling were calculated using MDMM estimations (O'Connell et al. 2010).

SECR models were compared using delta-corrected Akaike Information Criterion (AICc) values and selected using the weighted AIC (AICwt) of each model (Burnham and Anderson 2002).

We then compared home range at individual level between the two sessions. Home range was calculated per individual using a Minimum Convex Polygon estimator (MCP 95%) and the "sf" package (Pebesma 2018), and compared using mean comparison analysis after checking that variance is homogeneous. Individuals with more than three dots from three different detectors out of alignment were kept. Generalized Linear Models (GLM) were run to test the effect of period on home range size. A Gaussian distribution and 'weights' option were used.

Residual homoscedasticity and normality were assessed via Q-Q plots and Shapiro-Wilk tests. All statistical analyses were conducted with R 3.0.3 software (R Core Team 2014), using "ade4" (Chessel et al. 2004), "pROC" (Fawcett 2006) "plyr" (Wickham 2011), "varComp" (Qu et al. 2013), "maptools" (Bivand and Lewin-Koh 2013) and "GISTools" (Brunsdon and Chen 2014) packages. For all analyses, significant relationships were inferred at $\alpha = 0.05$.

Results

Camera trapping

There were 908 camera trap-days in the pre-culling session and 1181 camera trap-days in the post-culling session. These yielded 473 feral cat detections from 51 of the 77 stations for pre-culling and 514 feral cat detections from 35 of the 40 stations for post-culling (Fig. 2). The camera trapping rates for the pre- and post-culling sessions were 50 and 43 detections/100 trap-days, respectively. Feral cat camera trapping rates varied spatially between pre- and post-culling sessions (Fig. 2).

Camera trapping yielded 416 feral cat pictures showing identifiable cats (209 left-flanked and 207 right-flanked). Pictures of cats' left flank, matched with the corresponding right flank, were used for the pre- and post-culling camera trap analyses MKTBA and SECR.
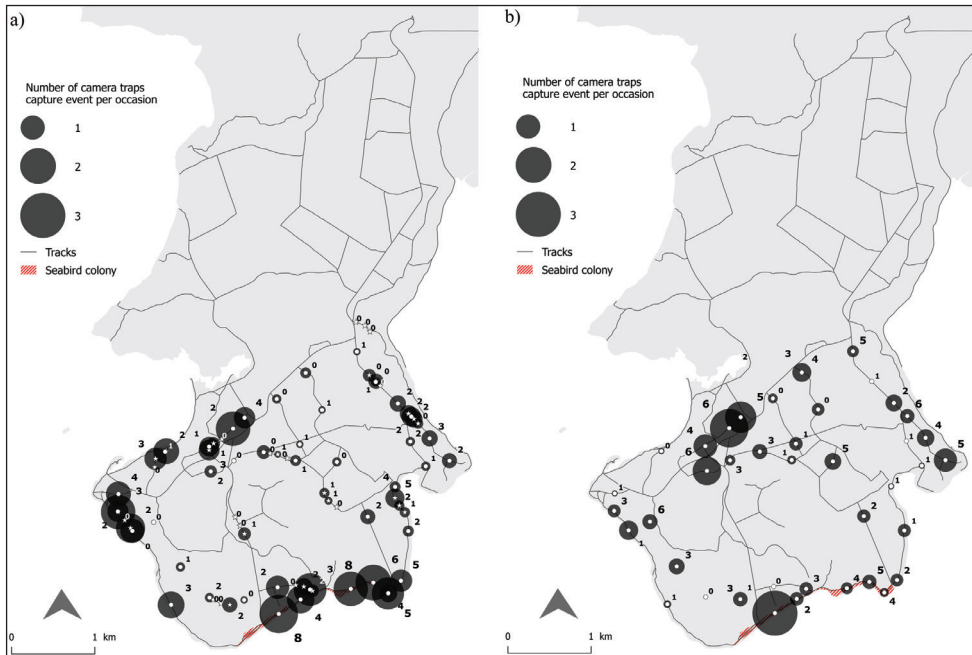
Figure 2. Variation in number of camera trapping events (black circles) and number of cats individually identified at camera trap stations pre- (**a**) and post- (**b**) culling. The sizes of black circles are proportional to the number of camera-trap capture events per sampling occasion. Camera trap stations; temporary locations (white stars), permanent locations (white points).

There was at least one uniformly black individual in the pre-culling session and two in the post-culling session, one of which was distinguished by distinctive damage to its tail. Uniformly coloured (here black) cats' pictures were not included in the SECR.

Live-trapping

A total of 36 cats were trapped and culled during the campaign (26 females, 10 males), with a trapping effort of 1200 trap-days representing a capture per unit effort of 3 trapped cats / 100 trap-days. Females comprised 72.2% of all captured cats. The trapping campaign culled 44% of the feral cats previously identified by the pre-culling camera trap survey.

Culling effect on cat indices and density

The General Index (GI $\pm$ S. E) did not differ significantly between pre- and post-culling sessions (t = 1.28, df = 37, p-value = 0.21), with respectively 0.50 $\pm$ 0.24 and 0.43 $\pm$ 0.15 virtual capture per sampling occasion per station (Suppl. material 3: Fig. S3).

A total of 40 different cats (MKTBA) were identified over the whole study period, with 25 and 23 different individuals from pre- and post-culling camera trap

Table 3. Mean Maximum Distance Moved (MDMM), the average maximum distance between detections of each individual (km²) and feral cat density estimations (number of individuals per km²) pre- and post-culling of feral cat populations. Results are given for the best SECR models; Model 1 (M1) and Model 2 (M2) according to AIC criteria.

Model	Session	MDMM (km²)	Density ± S. E (cat. km⁻²)	Inf. limit 95%	Sup. limit 95%
M1	Pre-culling	11.00	1.601 ± 0.327	1.077	2.380
	Post-culling	16.68	1.379 ± 0.301	0.903	2.105
M2	Pre-culling	11.00	1.600 ± 0.327	1.077	2.379
	Post-culling	16.68	1.378 ± 0.300	0.903	2.104

sessions, respectively. Eight individuals (29%) were identified during both pre- and post-culling periods.

Of the twenty-four models tested (Table 2), model M1 (parameters: "hazard hazard rate" function, a probability function of λ(d) and mask « ZE+Buffer S2 ») and model M2 (parameters: "hazard rate" function, a probability function of g(d) and mask « ZE+Buffer S2 ») gave the best estimation of cat densities. Model M1 showed a ΔAICc = 0 and AICwt = 0.53, and Model M2 showed a ΔAICc = 0.26 and AICwt = 0.47 (Table 2). These two models yielded very similar parameter values (λ(0), g(0), σ, z) and densities (Table 3).

Estimated feral cat densities (D ± S. E.) were 1.60 ± 0.33 adult cats/ km² pre-culling and 1.38 ± 0.30 adult cats/ km² post-culling. The movements and home range of feral cat populations did change following culling. Root Pooled Spatial Variance (RPSV) was higher post-culling, with 752.2 m pre-culling and 878.9 m post-culling. The mean home range estimation using MDMM was more than twice as high post-culling (0.95 km² pre-culling and 2.21 km² post-culling). Mean home range (95% MCP) did not differ significantly between sessions, but appeared slightly higher post-culling (0.784 ± 0.338 km² pre-culling and 0.827 ± 0.351 km² post-culling). Before culling, the highest numbers both of detections and of identifications of individual cats were in the South of the Peninsula, around the seabird colony. After culling, the highest numbers of detections were in the North-West of the study area and the highest number of individually identified cats in the North-West and North-East (Fig. 2).

Discussion and conclusion

The camera trapping method provided adequate cat detection, enabling us to estimate, for the first time, accurate cat densities in New Caledonia. It also provided an effective way to monitor variations in feral cat abundance, as in previous studies (e.g. Comer et al. 2018). Moreover, this trapping design enabled us to live-trap cats with a success rate within, or even slightly above, the range of other studies using wire cage traps (Algar et al. 2010; McGregor et al. 2015; Lazenby et al. 2015). This short but intense culling of resident feral cats proved to be effective in rapidly reducing the target population.

However, three months later, the different cat population indicators calculated post-culling showed little difference from those calculated pre-culling. Our culling campaign simulating the resource effort that might currently be expected from local natural site managers failed to reduce the feral cat population over the mid-term. Despite the favourable peninsula setting, this cat population recovered through recolonisation faster than expected. The natural geography of the site, a semi-isolated peninsula, did not limit connectivity between the treated and untreated feral cat sub-populations.

Camera trap monitoring: advantages and consistency of the three indicators

Camera trapping at our study site resulted in a high level of feral cat detection, similar to or even higher than in studies using either un-baited or baited camera trapping methods. The high level of detection, and the high number of individual cats identified from at least two different stations, met the two requirements for accurate SECR calculations (Efford et al. 2015; McGregor et al. 2015). In addition, camera trap capture probabilities were optimised in this study by positioning camera trap stations close to open roads and tracks. Thus, we were able to almost systematically observe pictures of the stripe patterns on cat legs, which are considered to be suitable for individual identification (Bengsen et al. 2012). However, more pictures of cats' two flanks could be obtained by using paired cameras at each camera station (Karanth and Nichols 1998; McGregor et al. 2015), which would further improve cat identification. Moreover, all undistinguishable black cats were excluded from MKTBA and SECR analysis. Future studies could usefully attempt to incorporate uniformly coloured cats in analysis when they represent a significant proportion of the population, for example by using robust home range data based on a sample of GPS-tracked animals (e.g. Bengsen et al. 2011). Our camera trapping method provided an effective way to monitor variations in feral cat abundance, and the consistency of its estimation calculated with GI, MKTBA and densities via SECR should prove widely useful. The GI could be used to monitor changes in the feral cat population as an alternative to SECR estimations, which require more time and can be used to respond to more specific research questions (Bengsen et al. 2012; Legge et al. 2017). However, conclusions are often based on relative abundance indices, and this kind of index does not consider important parameters such as variable detection (Sollman et al. 2013). Since relative abundance indices do not systematically reflect differences in density (Sollman et al. 2013), a valuable avenue for future research would be to compare these different indices. In particular, we recommend that in areas of interest to managers, the first step should be to calculate all of the different indices (GI, MKTBA, densities). Second, the relationship between GI and the other indices should be determined; if GI is sufficiently reliable and in line with the densities estimated by SECR, only GI should be used. For this reason, we advocate hand-in-hand collaboration between researchers and managers from project set-up to evaluation of management results, especially in such remote areas (Meyer et al. 2018).

Effect of culling on cat abundance/density over time

Three months after the end of the culling campaign that eliminated 36 cats over 10.6 km², no meaningful differences in the relative abundance and density of feral cats were observed in response to culling, whatever the indicator of population size considered. The abundance index (GI) indicated a similar cat presence in the peninsula, the minimum number of individuals (MKTBA) decreased by only 8%, and estimated feral cat densities (SECR) were similar between the two sessions. No lasting effect of culling effort was therefore observed, despite the intensity of trapping and of traps deployed.

The recovery of the feral cat population is probably attributable to the immigration of new individuals rather than to a demographically-dependent process, as cat detections were mainly recorded in the North of the peninsula during the post-culling session. Culling operations could have removed dominant individuals whose extirpation enhanced the permeability of the population to young individuals. In fact, the abundance and distribution of feral cats are partly controlled by territorial behaviour and social interactions (Goltz et al. 2008). Removing dominant individuals could increase numbers, particularly of sub-adults (e.g. Lazenby et al. 2015) presenting lower home-range fidelity than adults and still seeking and delimiting their home ranges (McGregor et al. 2014). The probable attractiveness of the tip of this peninsula, with its large shearwater colony, could explain the rapid recolonisation of the culled area and the changes observed in activity patterns.

Post-culling, estimated home range and RPSV (Root Pooled Spatial Variance) increased by approximately 132% and 16.8% respectively. We also observed a trend towards a higher home-range Minimum Complex Polygon (MCP). Taken together, these findings may indicate that the cats recolonising the peninsula are largely young males travelling long distances in search of a territory (Algar et al. 2013; McGregor et al. 2014). These results could also support the hypothesis that the remaining cats may increase their range post-culling, having to move farther to access mates. Male territories are primarily determined by access to females, whereas female territories are primarily determined by prey availability and distribution of other females (Liberg et al. 2000; Turner and Bateson 2014). For this reason, the cats increasing their range in our study are more likely to be males, since we removed more females. The female-biased sex ratio of culled feral cats probably reflects a trapping bias due to differences between male and female behaviour (females may seek food resources more actively due to reproductive costs, "sex-bias" on trap attractiveness may also be linked to trapping method), rather than a disproportionate number of females (Molsher 2001; Short and Turner 2005; Algar et al. 2014). If future studies show a female-biased sex ratio, however, this would suggest faster population growth than with a non- or male-biased sex ratio (Short and Turner 2005). In any case, trapping more females could significantly contribute to controlling cat population dynamics, which suggests that trap attractiveness to females might be worth investigating.

Culling may provide a greater access to resources for the remaining local cats, thus promoting juvenile survival, although this would probably be more pronounced at a larger temporal scale. Since we only measured density across one season, we are unable to identify possible season-related or breeding-related changes in cat density.

While recovery or even increases in populations due to compensatory demographic response have been documented for numerous species, in contrast to our study, these were observed following low-level culling (Sinclair et al. 2006; Lazenby et al. 2015). Fortunately, most studies report a post-culling reduction in feral cat numbers, although often after an intensive and sustained control effort (Algar and Burrows 2004) or in situations where populations show limited population flows (e.g. peninsulas and fenced areas, Short et al. 1997; Moseby and Read 2006).

Local and general implications for feral cat management

Camera trapping yields data on pre-culling population density, key information for scientists and managers who aim to control invasive predators. We provide here the first feral cat density estimates from New Caledonia. At our study site, feral cat density was estimated to be relatively high compared to many places in Australia (Bengsen et al. 2012; McGregor et al. 2015; Hohnen et al. 2020) and on two Salomon islands (Lavery et al. 2020). However, it is lower than at other locations: one Salomon island (Lavery et al. 2020), Great Britain (Langham and Porter 1991), Europe (Liberg 1980), New Zealand (Macdonald et al. 1987), United States (Warner 1985), and highly modified landscapes in Australia (Legge et al. 2017). According to the model by Legge et al. (2017), the feral cat density at Pindaï Peninsula (1.6 cats/ km²) is higher than expected (0.5–1 cat/ km²). This unexpected density illustrates the importance of specifically evaluating animal densities at each site before management actions start, especially given that New Caledonia tends to use base data from Australia. The higher density found here and the rapid return to initial densities argue for increasing the intensity and/or duration of trapping, which we calculated based on mean densities found in the literature.

As we co-conducted an intense but short culling effort, our trapping success is similar to that reported in comparable studies using wire cage traps (Algar et al. 2010; Lazenby et al. 2015; McGregor et al. 2015). The culling of 44% of camera-trapped feral cats is within or slightly below the range of other studies (e.g. 65% for Kangaroo Island in Bengsen et al. (2012), 44% and 56% for the Mount Field and Tasman Peninsula sites in Lazenby et al. (2015)). This culling effort can therefore be concluded to have been effective, but should be implemented longer (i.e. continuously) if possible, using more cage traps and at peninsula scale. Our findings support the view that lethal control in unfenced areas needs to be intense and continuous to reduce populations of resident animals, and immigration from the perimeter of core conservation areas needs to be limited (Veitch 1985; Norbury et al. 1998; Short et al. 1997; Edwards et al. 2001; Campbell et al. 2011; McCarthy et al. 2013). This applies even when recolonisation seems low due to the natural geography of the site, like a peninsula. Intense lethal control could be implemented during the presence of Wedge-tailed shearwaters in the

Pindaï peninsula colony, but their long breeding cycle (from October to May) makes this type of annual control costly and labour-intensive. Moreover, it is likely to result in large numbers of trap-shy feral cats (Parkes et al. 2014). We also recommend acting on a larger spatial scale, i.e. on the scale of the whole peninsula, which is rather wide and short compared to other peninsulas (e.g. Heirisson Prong in Short et al. 2002 and Tasman Peninsula in Lazenby et al. 2015).

For several years, innovative technical solutions have been sought to optimise the management of feral cats. These include both baiting and trapping strategies, as well as the development of efficient baits (e.g. Eradicat and Curiosity baits) and of automated traps that specifically recognise and poison feral cats (Algar et al. 2011; Johnston et al. 2011; Fisher et al. 2015; Fancourt et al. 2019; Read et al. 2019; Moseby et al. 2020). Other highly innovative genetic, cellular or behavioural methods are also being developed and offer promise for controlling feral cats in the future (Kinnear 2018; Moro et al. 2018). An interesting physiological and behavioural method called "Toxic Trojan prey", based on making the prey of feral cats specifically toxic to them, could be considered for feral cat control on our study site (Read et al. 2016).

Guard dogs could also be trained to protect wildlife and to prevent predation by feral cats on the Wedge-tailed shearwaters' breeding colony, as reported in two cases in South-West Victoria involving little penguins *Eudyptula minor* and gannets *Morus serrator* (van Bommel et al. 2010; Doherty et al. 2016). Exclusion fencing, widely used in Australia and New Zealand to protect biodiversity (Long and Robley 2004; Woinarski et al. 2014), might be another effective way to limit the recolonisation process that is particularly profitable and efficient in the peninsular context (Young et al. 2018; Tanentzap and Lloyd 2017). Last but not least, modelling approaches can provide numerical estimates of parameter values (e.g. predation rate) beyond which the prey population will decrease and/or cannot be sustained (Keitt et al. 2002; Peck et al. 2008; Bonnaud et al. 2009). Knowing such threshold values would support and greatly improve future management decisions.

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Supplementary material 1

Figure S1
Authors: Pauline Palmas, Raphaël Gouyet, Malik Oedin, Alexandre Millon, Jean-Jérôme Cassan, Jenny Kowi, Elsa Bonnaud, Eric Vidal
Data type: figure
Explanation note: Box plot home range MCP pre post.
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Supplementary material 2

Figure S2
Authors: Pauline Palmas, Raphaël Gouyet, Malik Oedin, Alexandre Millon, Jean-Jérôme Cassan, Jenny Kowi, Elsa Bonnaud, Eric Vidal
Data type: figure
Explanation note: Accu curve preculling.
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Supplementary material 3

Figure S3
Authors: Pauline Palmas, Raphaël Gouyet, Malik Oedin, Alexandre Millon, Jean-Jérôme Cassan, Jenny Kowi, Elsa Bonnaud, Eric Vidal
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